

Interactions between Interactions

Predator–Prey, Parasite–Host, and Mutualistic Interactions

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Ecological interactions such as those between predators and prey, parasites and hosts, and pollinators and plants are usually studied on their own while neglecting that one category of interactions can have dramatic effects on another. Such interactions between interactions will have both ecological and evolutionary effects because the actions of one party will influence interactions among other parties, thereby eventually causing feedback on the first party. Examples of such interactions include the effects of predators and parasites on the evolution of host sexual selection, the effects of parasites and predators on the evolution of virulence, and the effects of parasites and predators on the evolution of pollinator mutualisms. Such interactions among interactions will generally prevent simple cases of coevolution, because any single case of interaction between two parties may be affected by an entire range of additional interacting factors. These phenomena will have implications not only for how ecologists and evolutionary biologists empirically study interactions but also on how such interactions are modeled.

Key words: multispecies interactions; mutualism; sexual selection; virulence

Introduction

Ecological interactions between individuals belonging to different species have traditionally been classified depending on the costs and benefits attributed to the interacting parties (Begon *et al.* 1972; Krebs 1972; Ricklefs 1975). Such interactions, including those between competitors, predators and prey, parasites and hosts, and pollinators and plants, are usually studied on their own, while neglecting that one category of interaction can have dramatic effects on

another. In ecological studies of predation and pollination, there is currently an increasing interest in the effects of multiple interactions (e.g., special feature on intraguild predation in *Ecology* 88: 2679–2728, 2007). However, the lack of studies of multiple interactions is surprising given the current interest in integrating different fields of research.

Such interactions between interactions will have both ecological and evolutionary effects. The actions of one party will influence interactions among other parties, thereby eventually causing feedback on the first party, and such feedback can act on both ecological and evolutionary time scales. Cases of strict coevolution between two players are relatively uncommon (Thompson 1994, 2005), and this finding may partly be attributed to interactions between

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any two parties being influenced by many additional interactions that each may perturb the focal coevolutionary interaction.

This report's objective is to emphasize the importance of simultaneously studying multiple interactions because without such an integrative approach there is little possibility of understanding the focal interaction of interest. To this end, I first present three examples of multiple interactions that all illustrate the importance of considering not only the interaction of interest but also additional interactions that may impinge on the focus of a specific study. Finally, I discuss some generalities that arise from such studies of multiple interactions and provide an overview of the potential empirical and theoretical consequences of such multiple interactions.

Examples

Sexual Selection and Biological Interactions

The role of predators and parasites in the evolution of host sexual selection constitutes a prime example of multiple interactions. Cott (1947) and Baker and Parker (1979) suggested that secondary sexual characters may signal the degree of lack of profitability of prey because individuals with the most exaggerated secondary sexual characters also have the greatest ability to escape predation. Baker and Parker (1979) and Baker and Bibby (1987) showed in comparative analyses that bird species had differentially exaggerated sexual visual signals in parts of the body that were most likely to be exposed to predators during a predator attack. Subsequently, several different interspecific studies suggested that secondary sexual characters increase the risk of predation (Huhta *et al.* 2003; Møller & Nielsen 2006), whereas males with the most exaggerated traits generally suffered lower risk of predation than the average male in the population (Petrie 1992; Götmark 1993; Møller & Nielsen 1997). These findings are consistent with the unprofitable prey hypothesis. Thus,

there are clear patterns describing intraspecific and interspecific variation in expression of secondary sexual characters in relation to risk of predation, potentially causing predation to be the force of natural selection imposing reliability on sexual signals.

Using a different kind of interspecific interaction as the basis for extreme mate preferences in females, Hamilton and Zuk (1982) suggested that males, through the expression of their secondary sexual characters, might signal their health status and that choosy females might benefit from mate choice through acquisition of resistance alleles for their offspring. Although several different mechanisms may account for such parasite-mediated sexual selection, including avoidance of contagion and direct material benefits arising from an absence of parasites, Møller *et al.* (1999) showed in an extensive meta-analysis of the literature that by and large there was a negative relationship between expression of male secondary sexual characters and parasitism estimated as Pearson's product-moment correlation of -0.12 (weighted by sample size), whereas the measure of effect size was -0.42 for experimental studies. Although many parasites might be relatively benign, and hence be of little interest for choosy females, measures of immunity may be more relevant for females because the strength of immunity must have evolved to optimize costs in terms of development and maintenance relative to benefits in terms of resistance (Møller *et al.* 1999). In fact, mean effect size for immunity was -0.43 , whereas it was only -0.06 for parasitism (Møller *et al.* 1999). Thus, there is extensive evidence consistent with a role of parasitism in accounting for directional mate preferences.

Interestingly, the unprofitable prey hypothesis and the parasite-resistance hypothesis can be reconciled because both may be right at the same time. Predators tend to disproportionately affect prey that are heavily parasitized (Temple 1986; Møller & Erritzøe 2000). Furthermore, predators can cause severe stress in prey by increasing levels of corticosterone (Saino *et al.* 2005), and predators can suppress immunity,

thereby increasing levels of parasitism (Navarro *et al.* 2004). Interestingly, this effect of immunosuppression and associated increase in prevalence and intensity of parasitism depends on the expression of secondary sexual characters (Navarro *et al.* 2004). These findings raise the possibility that predators, through their daily routines, may suppress immunity and increase levels of parasitism in prey populations and that such predator-induced immunosuppression and associated parasitism may be particularly important in species with exaggerated secondary sexual characters, the species that suffer disproportionately from predation (Huhta *et al.* 2003; Møller & Nielsen 2005).

This example of interactions among interactions can be taken one step further. Carotenoid-based sexual signals are widespread among invertebrates and vertebrates, although the function of such signals remains controversial. Carotenoids must be ingested by animals that use them for signals because carotenoids can be synthesized only by plants, fungi, and bacteria. Carotenoids have physiological functions as immunostimulants and antioxidants, and therefore carotenoid-based signals may act as reliable indicators of immune status or antioxidant status, or they may simply act as indicators of foraging propensity (reviewed in Møller *et al.* 2000). The evidence consistent with an antioxidant function is weak at best (Costantini & Møller 2008). Seeds, fruits, and animals have high levels of carotenoids. However, seeds and fruits are also means by which plants disperse by relying on animal seed dispersers. Recent experiments have shown that avian frugivores are particularly susceptible to ultraviolet coloration of certain berries that directly reflect the levels of such carotenoids. Schaefer *et al.* (2007) showed that avian frugivores can distinguish the ultraviolet coloration of fruits reflecting the presence of anthocyanins that act as antioxidants. A subsequent laboratory experiment using blackcaps (*Sylvia atricapilla*) demonstrated that birds in a choice experiment preferred food that contained anthocyanins to similar food without that component. These ex-

periments show that birds can see carotenoids directly based on the color of the food and that they show a strong preference for such food rich in carotenoids. This study provides indirect evidence for coevolution among parasites, sexual selection in avian hosts, and plants that rely on animals for efficient seed dispersal.

Questions arising from these studies include the following: (1) Are sexually dichromatic, brightly colored animals less abundant when predators are common? (2) Is sexual selection less intense with fewer brightly colored species when predators are common because predators reduce the importance of parasite-mediated sexual selection in mate choice? (3) Are animal-dispersed fruits with orange, red, or blue colors more common when there are more sexually dichromatic species of birds in the local community?

Evolution of Virulence

The effects of parasites and predators on the evolution of virulence have only recently attracted attention. The evolution of virulence, broadly defined as reduction in fitness of the host because of the presence and the activity of the parasite, depends on the interactions between mode and rate of transmission by the parasite, rate of replication by the parasite, and parasite dynamics within and among hosts (Frank 1996, 2002; Day 2001). Explicit models that take both within- and among-host dynamics of parasite infections into account suggest that more virulent parasites have higher transmission rates and that such parasites are cleared less rapidly by the immune system (André & Gandon 2006). Empirical studies suggest that immunity indeed selects for higher degrees of virulence in parasites (Fenner & Fantini 1999; Mackinnon & Read 2004). However, both modeling and empirical approaches to the evolution of virulence have generally neglected that predation often disproportionately affects the most heavily parasitized hosts (Temple 1986; Møller & Erritzøe 2000), thereby potentially playing a role in the evolution of

virulence. Therefore, abundant predators may keep prey populations healthy and alert (Packer *et al.* 2003). In an exceptional study, Williams and Day (2001) showed that if the interactions between mortality sources such as those caused by parasitism and predation are sufficiently strong, this actually decreases the evolutionarily stable level of virulence. However, their models did not incorporate that predation is likely to disproportionately affect prey individuals with high levels of infection, making susceptibility to predation a direct function of replication rate. Such replication-dependent mortality rate of hosts caused by predation would select for even further decreases in level of virulence. Therefore, individuals that are caught by predators will have the highest levels of infection, directly selecting against high levels of virulence. Current models of the evolution of virulence suggest that an optimal level is reached as a consequence of the effects of parasites on host fitness and transmission (Frank 1996, 2002; Day 2001). Higher levels of replication and hence higher levels of virulence can be achieved through stronger immune responses of the host against the parasite (Fenner & Fantini 1999; Mackinnon & Read 2004) or through human intervention such as vaccination (André & Gandon 2006). Predation should result in reduced rates of replication by parasites because predators more often eat hosts with high rates of parasite replication before the parasite is transmitted, causing parasites to be less virulent in the presence of predators.

Questions arising from these studies include the following: (1) Are virulent parasites less prevalent when predators are common? (2) Does the virulence of specific strains decrease with level of predation? (3) Are communities of hosts more or less healthy when predators are common?

Evolution of Mutualisms

Animals are common pollinators of many species of plants, providing important services for plants, which in turn compensate by pro-

viding pollinator rewards. However, many pollinators are also exploited by parasites that use pollinators as vehicles for efficient spore transmission among plant individuals (Wanky 1997). Furthermore, some pollinators such as moths of the genus *Hadena* also lay eggs in the flowers that they pollinate, and the larvae hatched from these eggs then act as seed predators on the seeds that were produced as a consequence of the pollination event (Collin *et al.* 2002). However, *Hadena* moths can also be vectors of *Microbotryum violaceum* (Collin *et al.* 2002), a parasitic fungus that sterilizes the host plant. Interestingly, the frequency of host plant sterilization is extremely low because the larvae of *Hadena*, through their consumption of seeds, eat the developing spores that would otherwise have infected the plant (Collin *et al.* 2002). This example shows not only that pollinators and their services may be exploited by other taxa with parasitic inclinations but also that the pollinator may have the ability to retaliate against such exploitation by elimination of parasitism.

Fig wasps provide a classical example of mutualism where fig wasps pollinate figs that provide the wasps with nutrients (Machado *et al.* 2005). Because of relatedness among fig wasps, sex ratios are skewed as originally predicted by sex ratio theory (Hamilton 1967). However, figs are also inhabited by parasitic nematodes that arrive with fig wasps, and such nematode parasites act virulently against their fig wasp hosts depending on the level of multiple infection (Herre 1993). Therefore, fig wasps may on average provide pollinator services for the fig. Although fig wasps on average are beneficial to figs, they may be exploited by other interacting parties that attempt to maximize their own evolutionary interests. These average effects conceal interesting variation that can help clarify not only the sex ratios of fig wasps (West & Herre 1998; Hansen & Orzack 2005) but potentially also several other aspects of the interaction between figs and fig wasps. Unfortunately, there has been little experimentation on this system, preventing information to be gleaned from the outcome of perturbations of

the benefits acquired by any of the interacting parties.

Predation affects not only prey but also all parasites and mutualists inhabiting a prey individual. Therefore, predation events will have implications not only for the dynamics of prey populations, as already well established, but also for the dynamics of parasite populations and populations of mutualists. Mutualistic gut inhabitants such as many bacteria help digest food ingested by the host. Any such mutualistic strain that inefficiently digested food would render the host more susceptible to predation, perhaps through a reduced ability of the host to escape from potential predators. A common feature of interactions among microorganisms inhabiting the gut is that mutualists efficiently outcompete virulent strains that can have disastrous effects on the fitness of the host (Fuller 1989; Hutcheson *et al.* 1991). A commonly accepted reason for such differences in competitive ability between benign and virulent bacterial strains is that virulence implies a cost not only for the host but also for the virulent strain of bacteria. Another explanation for such differences is that more mutualistic bacteria have a vested interest in keeping the host well and fully capable of escaping a predator, whereas that might not be the case for more virulent strains that could benefit from infecting not only prey but also their predators.

Questions arising from these studies include the following: (1) How does pollinator specialization evolve when parasites start to exploit the interaction between pollinator and plant? (2) Is the effect of seed predators more likely to be tolerated when the seed predator simultaneously controls parasites? (3) Are gut symbionts better at excluding virulent bacterial strains when predators are more abundant?

General Discussion

The general thesis proposed here is that any interspecific relationship generally will be

affected by many additional interspecific interactions, producing a complex network of interactions. Interactions among interactions as described here may eliminate any simple cases of coevolution because interactions between two parties will be affected by an entire range of additional interacting parties.

The phenomena described here have general implications for how ecologists and evolutionary biologists empirically study interactions. Any two-way interaction between, say, a predator species and a prey species will depend not only on interactions between the two parties but also on the interactions between parasites and the prey species, parasites and the predator species, and how the prey species behaves as a result of carotenoids and other essential biochemicals obtained from the environment. As I have described, the outcome of any interaction can affect others, suggesting that questions about optimal responses by interacting parties will differ between studies that focus on, for example, the interaction between a predator and its main prey or studies that consider the additional interactions that may affect this given focal interaction.

The phenomena described here also potentially have implications for how interactions are modeled. Traditionally, models of the evolution of sexual preferences or virulence have been simplified to include the basic details representing the underlying assumptions. If the evolutionary scenario depends not only on the interaction between females and males or between hosts and parasites but also on additional interactions, these interactions may have to be included to allow identification of the coevolutionary stable strategies for the interacting parties. Some models have included changes in virulence owing to extrinsic causes of mortality such as predation by changing specific static parameters in the models (Williams & Day 2001). However, that approach does not address the evolutionary question about how the dynamic evolutionary responses of the different interacting parties are resolved. It is the evolutionarily stable strategies of these different interacting

parties and the response of each of these to the perturbation of the strength of the interaction by one of the parties that is the critical theoretical issue. I believe that these questions can be resolved by addressing interactions between interactions as described here.

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Conflicts of Interest

The author declares no conflicts of interest.

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