Modelling the harvest of an insect pathogen

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ABSTRACT

Ensuring a sustainable yield is essential for continued survival of a natural resource, however over-exploitation can easily occur. Therefore, understanding how increasing the harvesting rate affects the yield is vital. Harvesting of infected hosts in a host–pathogen system, for example the fungal pathogen *Cordyceps sinensis* which is harvested for medicinal use, has not been explored mathematically in the literature. We present a generalized host–pathogen model in which the infected host is harvested. Two strategies are explored; proportional harvesting at a constant rate and in an open-closed setting (a repeating cycle of a period of harvest followed by a period where the resource is left to recover). We present yield-effort curves for both strategies and find that open-closed harvesting affects the traditional yield-effort curve, with the system able to support a greater range of harvesting rates. Furthermore, host–pathogen systems may exhibit more complex population dynamics than single equation/species models, depending on the eigenvalues of the linearised system. In the open-closed setting we find that if there are complex eigenvalues in the absence of harvesting although small changes in the length of open season have little impact on the maximum sustainable yield, it can dramatically change the harvesting rate needed to achieve this. For proportional harvesting in a constant setting our model shows that if there are real eigenvalues in the absence of harvesting, then resilience–harvest relationship agrees with accepted theory, where as yield initially increases so too does the return time (a measure of the long-term resilience). However, when there are complex eigenvalues we see, counter to intuition, that the return time initially decreases whilst still providing increased yield. We also study the transient (short-term) reactivity, which shows that in both cases harvesting can initially decrease the reactivity. These results show that harvesting can in some instances enhance the ability of host–pathogen systems to respond to perturbations in both the short- and long-term.

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1. Introduction

Harvesting of a biological resource is modelled for many purposes including management of fisheries (Conover and Munch, 2002; Yakubu et al., 2011) or forest, (Gustafson, 1996) and conservation of populations (Beissinger and Bucher, 1992). The vast majority of models applied to systems of interest model the species using a single equation to which a term is added, which represents a harvesting strategy. A classic example of this is Beddington and May (1977), which demonstrated the existence of an economic threshold at which the yield is maximised for some intermediate harvesting rate (termed maximum sustainable yield (MSY)). Beddington and May (1977) also showed that overexploitation results in a smaller population than that at the MSY and high harvesting effort produces a low average yield with higher variance, and hence higher system recovery times. The implications for harvesting management are clear, and sustainable harvesting strategies must be employed to ensure cost-effectiveness as well as to prevent extinction of the harvested species.

However, most species experience interspecific interactions, and sustainable strategies will be influenced by the type and strength of the interactions. For example, harvesting of prey species can significantly affect predator abundance and may even cause system collapse if the harvesting rate is sufficiently high (Legović et al., 2010; Kar and Ghorai, 2011). Whilst harvesting interactions and their effects were analysed other measures such as return time and reactivity, which are important

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indicators of ecosystem health (Beddington and May, 1977; Neubert and Caswell, 1997), were not studied. Harvesting within other types of interspecific interactions have been considered, such as competition, (Geček and Legović, 2012), mutualism (Legović and Geček, 2012) and predator–prey–parasite systems (Bairagi et al., 2009). In contrast, there are no examples in the literature of harvesting in host–pathogen systems, and we aim to address this gap here. Furthermore, simple single species models, such as the Beddington and May (1977) model, exhibit very stable dynamics, where return to the equilibrium after perturbations is monotonic. However, for higher order models (e.g. interacting predator–prey or host–pathogen models) the dynamics may be more complex, which is the focus of this article.

Whilst harvesting in host–pathogen systems may not occur in reality as frequently as in other types of species interactions, there are a number of economically important examples, such as baculovirus collection for biocontrol (Grzywacz et al., 2008; Mushobozi et al., 2005). A particularly important example is harvesting of *Cordyceps sinensis*, which is the motivation for this study. This entomopathogenic fungus infects caterpillars of the ghost moth genus *Thitaordes* (*Hepialiade*) (Cannon et al., 2009; Maczey et al., 2010) by penetrating the host exoskeleton (Cannon et al., 2009) or by host ingestion of the fungal spores (Boesi, 2003). After killing the caterpillar, the fungus produces a fruiting body (stromata) which appears above ground to release spores which infect other susceptible hosts (Cannon et al., 2009; Winkler, 2008). The fruiting bodies are harvested for medicinal purposes in their native range in the Tibetan Plateau (Negi et al., 2006; Winkler, 2008), and this is important to local economies (Weckerle et al., 2010). It is thought that increases in harvesting have decreased yield by as much as 30–50% in some areas (Negi et al., 2006).

To combat over-exploitation, a number of different harvesting strategies have been investigated in harvesting models. Beddington and May (1977) compared two harvesting strategies: proportional harvesting and constant harvesting. In the former, a constant proportion of the population is harvested at each time, making yield dependent on the harvesting effort and the availability of the resource. In contrast, the constant strategy simply removes a constant number of individuals from the population, which is independent of the population size. Interestingly, these two strategies predict identical MSYs in single species model. However, whilst the proportional harvesting strategy has only one steady state (other than the trivial steady state) under the constant harvesting strategy there are two steady states; one stable and one unstable. After small perturbations the system will return to the stable steady state. However, larger perturbations have different effects; a large perturbation above the stable steady state will cause the system to take a long time to recover, whilst those below the steady state will cause population extinction (Beddington and May, 1977). For these reasons, proportional harvesting strategies are advised rather than constant harvesting (Bairagi et al., 2009; Beddington and May, 1977; Cooke and Witten, 1986; Yakubu et al., 2011).

Despite the relative benefits of a proportional harvesting strategy, over-harvesting may still lead to population extinction and therefore adaptations to this strategy have been developed. One such is open-closed harvesting, by which harvesting occurs during the open period and stops during the closed period, allowing the resource to recover partially or completely. In fisheries management, these closures, varying in time length from weeks to years (Cinner and Aswani, 2007), can have an impact on both the size and biomass of fish (Bartlett et al., 2009; McClanahan et al., 2009). The timing of the open period of harvesting can have a great effect on the MSY (Kokko and Lindström, 1998), and if harvesting does not start at the beginning of the prescribed open period the overall yield can be decreased (Xu et al., 2005). It has also been shown that if a population has strong Allee effects then harvesting mid-season can make the population more prone to over-exploitation (Cid et al., 2013).

Modelling different harvesting strategies allows us to answer questions regarding yield of the resource, recovery time, resilience and reactivity. In interacting multi-species systems, an understanding of how harvesting affects all species is vital to their continued survival. In predator–prey systems, harvesting either trophic level has implications for the MSY, and so it is necessary to consider the interaction between the two (Beddington and May, 1980; Kar and Ghosh, 2013). However, it is unclear how guidance about harvesting from existing modelling studies translates to host–pathogen species interactions.

To this end, we explore the impact of harvesting on a compartmentalized host–pathogen model in which we harvest the infected stages. We apply proportional harvesting over a constant rate and in an open-closed setting to determine the MSY and determine how the different strategies affect the yield that can be attained. We also consider three system measures that are affected by harvesting: recovery time, resilience and reactivity. Using these measures, we find that the results do not always coincide with single species harvesting theory and that harvesting in host–pathogen systems may have beneficial effects, depending on the system interaction strengths and the level of harvesting. Using an open-closed harvesting strategy we find that small changes in the length of open period can have a dramatic impact on the harvesting effort that produces the maximum yield. Finally, we discover that in an open-closed setting it is better to harvest for a long open period at a lower effort than to harvest for a shorter time at a higher effort if we wish to maximize the yield.

2. Materials and methods

We base host–pathogen dynamics on 'Model G' by Anderson and May (1981). This classic compartmentalised differential equation model has three compartments; susceptible hosts, $X(t)$, infected hosts, $Y(t)$ and free-living infective stages of the pathogen, $W(t)$, at time t. The free-living stages of the pathogen are explicit in the model, as infection occurs through this means. In addition to this model, we make additional realistic assumptions to include a rate at which susceptible and infected hosts take up the pathogen (Boots, 1999), and density-dependence acting upon the susceptible hosts (Bowers et al., 1993; Caraco and Wang, 2008; Dwyer, 1994).

We assume that all hosts grow according to the logistic equation in the absence of the fungal pathogen, where r is the intrinsic growth rate of the hosts and k is the carrying capacity of the susceptible hosts. It is important to note that $r = a - b$ where a is the birth rate of hosts and b the natural morality rate. The rate of transmission is modelled by the law of mass action. Infected hosts have an induced mortality rate α, and each dead host produces an average λ spores. Free-living pathogen spores decay in the environment at a constant rate μ.

In many multi-species and predator–prey model systems harvesting occurs at the bottom trophic level, however there are examples of models where harvesting occurs at more than one trophic level (Beddington and May, 1980; Legović and Geček, 2012; Kar and Ghosh, 2013). Here we investigate the scenario where harvesting occurs at an upper trophic level. Specifically, using *C. sinensis* as our motivation, we assume harvesting occurs in the infected compartment, since it is the fruiting bodies of the fungal pathogen (along with their dead infected host) that are collected for medicinal use. We therefore wish to maximise the yield without eradicating the pathogen, so that (a) local communities are able to benefit economically from selling the fruiting bodies and (b) the fungus can continue to infect the caterpillar so that the fruiting body can be used for medicinal purposes. We denote $H(Y)$ as the rate at which infected hosts are harvested.