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Emergence of cooperative behaviours in the management of mobile ecological resources☆

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ABSTRACT

Cooperation at neighbourhood and landscape scale is frequently advocated as a means of improving the management of ecological resources. Such management often involves multiple agents and takes place in spatially structured landscapes where interactions between management actions are mediated via spatio-temporal dynamics of the managed resource. Evolutionary game theory has sought mechanisms to explain the emergence of cooperation among selfish individuals in these complex socio-ecological contexts, and spatial implementations of standard games have shown that the development and persistence of cooperation is affected by spatial structure. However, existing game theoretic models do not incorporate the dynamics of the managed resource or cross-linkages between resource dynamics and management actions and payoffs. We use a spatial agent-based modelling approach to investigate how ecological dynamics, payoff structures, and their interdependencies, influence the emergence and persistence of cooperative behaviours in the management of red deer (*Cervus elaphus*) in Scotland. Simulation results for landscapes comprised of agents with (i) only sporting, and (ii) only biodiversity management objectives show significant differences in the spatial patterns of management action and cooperative behaviour which emerge as limit cycle attractors. Compact clusters of cooperative agents arise in the sporting scenario, culling at low intensity to maintain advantageously high deer densities. Cooperative behaviour in the biodiversity scenario emerges as a context-dependent function of deer density in filament-like structures along the boundaries between linear regions of high or low culling intensity. These findings suggest that mechanisms driving the emergence of cooperative behaviours can be complex and that the opportunities for, and benefits derived from, cooperation are likely to depend critically on both the management objectives and dynamics of the resource.

1. Introduction

1.1. General background and research questions

The use of natural resources often involves multiple actors and takes place in spatially structured landscapes where interactions among users, and the dynamics of the resource, are distance-dependent. The dynamics of such coupled socio-ecological systems therefore result from spatially defined interactions between human management activities and the evolving natural resource. Social dilemmas arise because cooperation is prone to exploitation by "selfish" individuals which typically leads to a situation dominated by defectors, at a loss to all, as famously characterised by "the tragedy of the commons" (Hardin, 1968). There is much current interest in studying how individuals facing such social dilemmas overcome the strong temptation to defect and instead cooperate to deliver benefits (e.g. Ostrom, 1990; Fehr and Gächter, 2000; Janssen and Ostrom, 2006; Fehr and Gintis, 2007). The literature on evolutionary game theory has modelled such behaviours to explain the emergence of cooperation in biological and economic systems through mechanisms such as kin selection, punishment, reward, policing or direct/indirect/network reciprocity (Axelrod, 2006; Nowak, 2006; Noailly et al., 2007, 2009; Suzuki and Iwasa, 2009). The importance of spatial linkages and

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structure in the development, extent and persistence of cooperation have been studied in evolutionary game theoretic work using spatial implementations of standard games like the prisoners dilemma or the snowdrift game (also referred to as the chicken game) in which four discrete payoffs are assumed to arise from an *a priori* binary choice of "cooperation" or "defection" strategies by a selected individual and their neighbours (e.g. Doebeli and Hauert, 2005; Ohtsuki et al., 2006; Nowak, 2006; Noailly et al., 2007; and references therein). Under the prisoners dilemma game agents benefit most if all were to cooperate but their individual interests leads them to defect. While under the snowdrift game, agents also prefer not to cooperate, but the worst possible outcome is one in which no other agent cooperates, so an agent will cooperate if he/she thinks that the others will not.

Previous game theoretic settings of cooperation do not, however, fully apply to the analysis of socio-ecological systems as they do not model the dynamics of the managed ecological resource. There is, in particular, no acknowledgement that the costs and benefits arising from management decisions may be dependent on the stock of the ecological resource; nor is it acknowledged that the ecological dynamic is, in turn, affected by the players' actions and evolves according to its own rules (e.g. regarding growth rate and movement). Furthermore, the usual consideration of only two actions, cooperation and defection, defined rigidly *a priori* is insufficient when management adapts in response to a resource which changes continuously in time.

In this paper, we address the emergence of behaviours in dynamic resource management which can be classified, *a posteriori,* as being cooperative. Our particular focus is on the influence which payoff structures and ecological dynamics exert over the evolution and persistence of such cooperative behaviours, and on the conditions under which these behaviours can emerge among "selfish" individuals. We adapt the spatially-specific, agent-based approach of Killingback et al. (1999) to make it more relevant to the practical management of ecological resources by (i) making the payoffs obtained from management dependent on the stock level of the managed resource, (ii) allowing management actions of agents to influence the ecological dynamics of the resource (temporal and spatial), (iii) using density-dependent movement of the resource between agent's landholdings as a means of transmitting the effects of management actions across the landscape, and (iv) reporting the level of *a posteriori* cooperation achieved within the local neighbourhood using an index which varies continuously between full cooperation and complete defection.

Our implementation is consistent with a wildlife management context in which cooperative behaviours (or their opposite) arise from varying levels of management effort affecting the temporal and spatial dynamics of the natural resource, which then in turn affect the payoffs from subsequent management actions. Agents are assumed to be motivated by their own net benefit (payoff), and cooperation is defined to be a behaviour that delivers benefits to neighbouring agents, irrespective of the level of self benefit achieved (West et al., 2007). Within this context, a continuous definition of cooperation at the neighbourhood scale (i.e. cooperation as benefit conferred to immediate neighbours) is used, similar to that of Killingback et al. (1999), Wahl and Nowak (1999) and Doebeli et al. (2004). The level of cooperation at the neighbourhood scale that is associated with a particular management action is quantified *a posteriori* using an intuitive index developed by Wahl and Nowak (1999).[2]

[2] It is important to appreciate that this local neighbourhood *a posteriori* quantification of cooperation does not relate directly to the maximum level of social welfare attainable across the entire landscape.

The socio-ecological dynamics of natural resource management are simulated using spatially-specific agent-based modelling, which is widely used to study complex system dynamics in ecology (e.g. Grimm et al., 2005; Monticino et al., 2007; Zhang et al., 2011) as well as the governance of socio-ecological systems, including the conditions that may foster cooperative behaviour (e.g. Janssen and Ostrom, 2006; Zhao, 2009; Souchère et al., 2010).

1.2. The management problem

The analysis is implemented using the example of deer management in the UK, loosely based on a bioeconomic parameterisation of the management of red deer (*Cervus elaphus*) in the Scottish Highlands (Smart et al., 2008). Under law in England, Wales and Scotland, landownership confers the right to shoot resident deer (Parkes and Thornley, 2000) and considerable revenue can be generated by leasing shooting rights for mature males of deer species such as *C. elaphus* and *Capreolus capreolus* with antler trophy heads. In some areas, notably the Highlands of Scotland, landowners can realise profits from these sport shooting activities. However, severe grazing and browsing pressure by high density deer populations is altering the ecological characteristics of woodland and moorland in many areas of the UK, with potentially severe adverse consequences for native biodiversity (Fuller and Gill, 2001; Scottish Natural Heritage, 1994). Woodland management objectives are also changing to focus increasingly on recreation and biodiversity rather than timber production (Forestry Commission, 2008). Deer management issues that have arisen against this background include: (a) calls for coordinated culling action to maximise delivery of sporting objectives in areas where deer are regarded primarily as a sporting resource (Association of Deer Management Groups, 2009), (b) calls for substantial reductions in deer densities in areas where grazing and browsing pressure is damaging biodiversity interests (Scottish Natural Heritage, 1994) and (c) attempts to coordinate the culling actions of private landowners to deliver meaningful reductions in deer density across wider areas and improve the net benefits of deer management (Scottish Government, 2008).

Substantive and lasting cooperation in deer management at the landscape scale has proved elusive in situations where deer are regarded as a resource which ranges across landownership boundaries, a pest which ranges across landownership boundaries, or as both a pest and a resource simultaneously by landowners with different management objectives operating in the same landscape (Nolan et al., 2001; Ramsay, 1997; Scottish Natural Heritage, 1994). In this respect, the management of deer has similarities with that of other mammal species such as foxes in Australia (Jones et al., 2006), elephants in southern Africa (Walpole, 2008) and seals in northern Europe (Bruckmeier, 2005). The present research aims to improve understanding of factors which act to increase or decrease cooperation at the neighbourhood scale, and to examine the implications which such increases or decreases in neighbourhood cooperation carry for coordinated resource management at the landscape scale. We therefore choose a modelling setting which recognises that interactions between landowners' management decisions and the ecological dynamics of the resource may influence the development of cooperative behaviour.

The paper proceeds as follows. Firstly, the model is specified, cooperation at the neighbourhood scale, and an appropriate index to measure this cooperation, are defined, and the functional forms used to depict benefits, costs, deer population dynamics and deer movement are described. Secondly, we present the results generated for two different specifications of the model representing landscapes dominated by sporting estates and biodiversity conservation respectively. Finally we draw conclusions on factors