Evolution of Cooperative Behaviour in the Management of Mobile Ecological Resources

Julia Touza, Martin Drechsler, James C.R. Smart and Mette Termansen

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Email: julia.touza@uvigo.es

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Abstract

We study management of deer populations in a landscape where reciprocal externalities between landholders affect net benefits from management using evolutionary game theory. The net benefits arising from deer populations at particular densities typically differ among landowners. Higher densities are preferred by landowners primarily interested in shooting revenues, whereas lower densities are generally required for biodiversity imperatives. An individual-based model is used to represent spatially defined interactions among landholders’ decisions in a landscape. Emergence of cooperative strategies is explored among each type of ownership and related to the interaction between the local density of the managed deer population and the costs and benefits which arise from management action. Results show that while cooperation strategies survive in the sporting scenario by forming compact clusters, in the biodiversity scenario cooperative behaviour is rare. Furthermore, our analysis of the co-evolution of resource management strategies and resource population dynamics shows a more complex relationship between cooperative behaviour and individuals’ actions than that which would have been expected from non-spatial classical games.

Key words: deer management, evolutionary game theory, cooperation, spatially explicit model.

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About the Authors

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 ecological-economic systems therefore result from spatially defined interactions between human management activities and the evolving natural resource. In such a complex natural-social context, an increased understanding of the factors that affect the levels of cooperation among actors may help to design effective institutions for managing environmental public goods. The problem of cooperation or lack of cooperation is captured in the idea of social dilemmas, in which cooperation is prone to exploitation by “selfish” individuals and society ends up in a situation dominated by defectors, at a loss to all, famously characterised by “the tragedy of the commons” (Hardin, 1968). In this context, a cooperating individual helps others at a cost to himself, i.e. someone who pays a cost through which another individual receives a benefit. A defector, on the other hand, incurs no costs and reaps the benefits. There is much current interest in studying how individuals overcome the strong temptation not to cooperate in social dilemmas, and instead cooperate to get joint benefits (e.g. Axelrod, 2005, Janssen and Ostrom, 2005a, more references). In the literature on evolutionary game-theory such behaviour has been modelled to explain the emergence of cooperation in biological and economic systems. E.g. in biology, Nowak (2006) proposes that five mechanisms exist that promote cooperative interactions: kin selection, direct reciprocity, indirect reciprocity, network reciprocity, and group selection. In human society altruism, punishment and fairness, and indirect reciprocity, have been suggested to play a key role in the evolution of cooperation (e.g. Fehr and Gintins 2007, Jansen and Ostrom 2005b).

The effect of spatial interdependence on the level of cooperation has also been studied in evolutionary game-theoretic work using standard games like the prisoners dilemma or the snowdrift game (e.g., Doebeli and Hauert 2005, Ohtsuki et al. 2006, Nowak 2006, Noailly et al. 2007, and references therein). The payoffs arising from various behavioural strategies of agents, the persistence of strategies and
cooperation among agents are analysed in terms of the setting of the game, and particularly in terms of the ratio of costs and benefits incurred by a player in the game. These spatial game simulations typically assume four discrete payoffs depending on the actions of a focal individual and the action of the neighbours. The four discrete payoffs arise from the binary choice of “cooperation” or “defection” strategies by the individual and a selected neighbour. The game theoretic analyses do not acknowledge that the costs and benefits which arise from management decisions may be dependent on an underlying dynamic such as that of a managed ecological resource; nor do they acknowledge that this ecological dynamic is, in turn, affected by the players’ actions and evolves according to its own rules (e.g. growth rate and movement). Continuous (i.e. non discrete) actions have been implemented within the evolutionary cooperation literature, (e.g. Killingback et al. 1999, Wahl and Nowak 1999, Doebeli et al. 2004), but these also assume a fixed payoff structure indicative of a uniform resource base unaffected by agents’ management decisions.

In this paper, we aim to analyse further the emergence of cooperative behaviour in dynamic resource management. We focus particularly on the influence of payoff structures and the ecological dynamics on the evolution and persistence of cooperation. We develop a continuous game-theoretic analysis of the evolution of management strategies and cooperation among resource managers, further developing the approach of Killingback et al. (1999) to take into account that (i) cooperation level can vary smoothly between full cooperation and complete defection, (ii) the payoffs obtained from management are dependent on the underlying stock level of the managed resource, and (iii) the ecological dynamics of the resource (temporal and spatial) are influenced by management actions of agents. This implementation is consistent with a wildlife management context in which cooperation reflects the continuously varying level of culling effort, and the level of culling applied affects the temporal and spatial dynamics of the managed resource. In contrast to the spatial game-theoretic models mentioned earlier, we do not know a priori, and make no assumption about, what level of management (culling) corresponds to “cooperation” and what level does not. Instead we simulate the coupled ecological-economic dynamics and then classify the cooperation level of the emerging actions of the players. Cooperation is quantified by an intuitive index.
developed from Wahl and Nowak (1999). This cooperation index provides a measure of the level of cooperation in the system.

1.2 The management problem

The analysis is implemented using the example of deer management in the UK. 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 *Cervus elaphus* and *Capreolus capreolus* with antler trophy heads. In some areas, notably the Highlands of Scotland, landowners can realise profits from these sport shooting revenues. 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. Deer management issues that have arisen against this background include: (a) calls for substantial reductions in deer densities in areas where grazing and browsing pressure is damaging biodiversity interests; and (b) attempts to coordinate the management actions of private landowners to deliver meaningful reductions in deer density across wider areas and improve the net benefits of deer management by restoring or enhancing the biodiversity of native woodland. Effective coordination among landowners has, however, proved elusive (Nolan, et al. 2001) and substantial reductions in deer density have proved very difficult to achieve on a landscape scale. The present research contributes to understanding the barriers to landscape scale cooperative management of mobile ecological resources and, in particular, how interdependence between landowners’ management decisions interacts with the ecological dynamics of the resource.

To cope with the complexity and the nonlinearity of the system, we adopt a grid-configured agent-based model in this paper for simulating management behaviour in a spatial setting. This approach has been intensively used to study the governance of natural-social systems, and the conditions that may foster cooperative behaviour (Janssen and Ostrom 2005). In the building of the model we follow the principles
outlined by Grimm and Railsback (2005) and we use two types of agents; sporting landowners and biodiversity landowners, to portray two polar characteristics of deer management in the UK. We explore the evolution of management strategies and cooperation in the sporting and biodiversity contexts separately, i.e. within landscapes which contain only one type of owner; sporting or biodiversity. Both types of agents implement management through culling, but they pursue different deer management objectives and perceive different culling benefits and biodiversity damage costs. Sporting owners are portrayed to derive higher revenues per deer culled, in recognition of sporting and trophy income, and are assumed to place little emphasis on biodiversity damage costs. Biodiversity owners are portrayed to regard biodiversity damage as a considerable cost, and to realise no sporting or trophy revenues from culling.¹ Both types of owner incur culling costs on the same basis where a strong stock effect increases marginal culling cost as deer density falls. Spatial externalities arise from management through density-dependent movement of deer between neighbouring landownerships. If an agent culls deer heavily, fewer deer will tend to move to the neighbours landholdings. Heavy culling by the focal agent could thus impose a positive or negative externality on neighbouring agents, depending on their current deer levels and whether their particular management objective requires an increase or decrease in density on their own land.

The paper proceeds as follow. Firstly, we cast our model in the empirical context of deer management in the UK. Secondly, the model is specified, a cooperation index, and the functional forms used to depict benefits, costs and deer movement are described. Thirdly, we present the results generated for two different specifications of the model representing landscapes dominated by sporting and biodiversity conservation respectively. Finally we draw conclusions on the evolution of cooperation and identify policy implications.

2 The Model

The model is individual-based and spatially explicit. It models the evolution of management strategies and cooperation among landowners based on deer

¹ Deer management for biodiversity protection is akin to pest control and it is uncommon for sporting and trophy revenues to be realised from biodiversity protection culls in the UK.
management in a UK setting as described above, but simplifies the problem by considering only worlds which contain landowners with the same interests (i.e. either a world containing only sporting owners or a world containing only biodiversity owners).

The model depicts a set of landowners (agents) in a landscape grid. Each landholding is represented as a grid cell, and all landholdings are of the same size. The landscape grid is a torus (no edge effects), and comprises 80*80 landholdings. We simulate management over a timeframe of 500 years, however the choice of time horizon is not impact on the results. Each agent ‘owns’ and manages one cell in the grid and can decide what proportion of the deer population in that cell should be culled in every timestep (year) of the simulation. Agents choose the intensity of their culling with the aim of obtaining higher payoffs based on their own cost and benefit functions. Landholdings are characterised by deer dynamics variables (e.g. growth, emigration); and landowners’ management is characterised by culling intensity, the revenues accruing from culling activities, the costs incurred in culling and the biodiversity damage costs caused by deer on their landholding. These elements are combined appropriately for each type of landowner to determine the total payoff each landowner obtains from deer management. The payoffs of sporting and biodiversity owners differ for the reasons described below. Revenue, culling cost and damage cost functions use forms and parameterisations from Smart et al. (2008), as reported in Table 1.
Table 1: Model parameters and default values

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Default values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Landowners</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$w$</td>
<td>Unitary costs per culling effort: wages</td>
<td>Sporting 10</td>
</tr>
<tr>
<td>$r$</td>
<td>Unitary benefits from culling</td>
<td>Biodiversity 10</td>
</tr>
<tr>
<td>$v$</td>
<td>Unitary damage costs</td>
<td></td>
</tr>
<tr>
<td>$\alpha$</td>
<td>Output elasticity of culling effort</td>
<td>0.5</td>
</tr>
<tr>
<td>$\beta$</td>
<td>Output elasticity of deer density</td>
<td>1.1</td>
</tr>
<tr>
<td>$d$</td>
<td>Maximum density difference for payoff comparison among neighbours</td>
<td>0.15</td>
</tr>
<tr>
<td>$p_m$</td>
<td>Mutation rate</td>
<td>0.01</td>
</tr>
</tbody>
</table>

| Landsholdings | |                |
|---------------|----------------|
| $e$           | Movement parameter                     | 0.2            |
| $N$           | Number of neighbours                    | 4              |

Agents’ management actions can be interpreted in the phraseology of the evolutionary game theory literature as follows: agents invest in management action by choosing to cull a proportion ($k$) of the deer population in their grid cell. Culling proportion $k$ can vary smoothly from 0 to 1. Culling incurs costs in accordance with cull size, population density and the wage cost of culling effort following the Cobb-Douglas-form relationship shown in the Appendix, and delivers benefits to the focal agent as quantified by the payoff function. Payoffs for sporting and biodiversity agents differ, but the general form is: \( \text{payoff} = \text{culling revenue} - \text{culling cost} - \text{biodiversity damage cost} \). Sporting agents realise higher marginal revenues from culling, in recognition of sporting and trophy income, but the damage costs on biodiversity is perceived as negligible. Biodiversity agents obtain lower marginal revenues from culling, lacking the sporting and trophy revenues, as they tend just to sell the meat. However, they do consider biodiversity impacts to be considerable.

2.1 Deer population dynamics

In our model local populations of the resource (deer) evolve on the individual grid cells and animals can disperse among the grid cells. Dispersal is driven by resource density at the source cell and this dispersal produces a spatial coupling between
landholdings (grid cells) which transmits the consequences of agents’ management decisions through to the payoffs of their neighbours. In each landholding deer population dynamics is determined by natural growth, spatial movement and culling activities. After culling at the beginning of the season, the change in deer density $dX$ during time interval $dt$ is determined by growth following a logistic distribution, minus movement away from the focal landholding and plus movement from nearby landholdings onto the focal plot of land:

$$\frac{dX_k}{dt} = X_k (1 - X_k) - eX_k + e \sum_{l \in L(k)} X_l$$  \hspace{1cm} (1)

Here $L(k)$ is the set of neighbouring cells around focal cell $k$ and the neighbourhood can be of either von Neumann (4 neighbours) or Moore (8 neighbours) type. In each year season, deer can move to the neighbouring cells. The proportion of deer density leaving a cell is assumed to be constant and given by parameter $e$, which assumed to be equal for all landholdings. We set $e=0.2$, which approximates the flat initial tail of the logistic density dependence in movement which Smart et al. (2008) applied based on the findings of Clutton-Brock et al. (2004) across a wide range of deer densities for a representative UK deer species.

2.2 Benefits and costs from deer management

We use a Cobb-Douglas production function to represent the deer culling process.

$$K = AE^\alpha X^\beta$$

$$\Rightarrow E = \frac{1}{A} \frac{1}{\alpha} \frac{1}{X} \frac{\partial K}{\partial A}$$

$$\Rightarrow C = wE = wA^{-\frac{1}{\alpha}} K^\frac{1}{\alpha} X^{-\frac{\beta}{\alpha}}$$

$$\Rightarrow C = c(K, X)$$

$$\Rightarrow \frac{\partial C}{\partial K} = \frac{1}{\alpha} \frac{C}{K} \quad \text{and} \quad \frac{\partial C}{\partial X} = -\frac{\beta}{\alpha} \frac{C}{X}$$  \hspace{1cm} (2)

where $K$ is cull size, $E$ is culling effort (hours of culling contractor time), $X$ is density of population before culling begins, $A$ is a constant, $w$ represents wage rate (per hour of
culling contractor’s time), and the relationship between $\alpha$ and $\beta$ define the intensity of the returns to scale. This implies that culling cost changes depending on the size of the pre-cull population and the size of the total cull extracted. Thus, culling costs increase rapidly in low deer density patches, and this makes the net culling benefit (culling benefits minus culling costs) density-dependent. Benefits from culling are simply assumed to be a fixed amount per deer culled, i.e. $B = rK$. Unit profits, $r$, are assumed greater for the sporting owners as explained earlier. Biodiversity-motivated landowners also incur biodiversity damage. Damage costs increase with deer density, and we assumed this relationship to be a quadratic $D = \nu X^2$, where $\nu$ is the unitary damages.

2.3 Degree of cooperation

The degree of cooperation which the management action (culling decision) of the agent in the focal cell displays towards an agent in a neighbouring cell is defined by drawing on the cooperation index proposed by Wahl and Nowak (1999). Wahl and Nowak denote the benefit arising to individual $j$ through the action of individual $i$ as $b_j = a_i b$ where $a_i = 0$ denotes ‘defection’ by individual $i$ (minimising the benefit to individual $j$) and $a_i = 1$ represents ‘cooperation’ by individual $i$ (maximising the benefit to individual $j$). The cost to individual $i$ is modelled as $c_j = a_i c$ so that cooperation ($a_i = 1$) maximises the costs of individual $i$ and defection ($a_i = 0$) minimises it. In our case we cannot use this approach directly, because (a) our cost and benefit functions are non-linear (which could be considered though, as Wahl and Nowak 1999 argue), and, crucially, (b) the costs and benefits in our case are not fixed but depend on the evolving deer population density and spatial distribution of the deer. Nevertheless we do take from Wahl and Nowak (1999) that ceteris paribus ‘cooperation’ maximises the other player’s payoff while ‘defection’ minimises it. On this observation we define cooperation as follows. Let the maximum level of cooperation of land user $i$, $a_i^*$ be defined as: $a_i^* = \arg \max a_i \Pi_j(a_i)$, where $\Pi_j(a_i)$ is the net benefits accruing to land user $j$ which depends on the culling level $a_i$ of land user $i$. The minimum level of
cooperation is defined as: \( a_i^* = \arg \min_{a_i} \Pi_j(a_i) \). The actual level of cooperation which land user \( i \) affords to his neighbour \( j \) at any other culling level \( a_i \) is then defined as:

\[
Coop_i(a_i) = \frac{a_i - a_i^*}{a_i^* - a_i}
\]

This cooperation index ranges from 0 (full defection) to 1 (full cooperation). To evaluate the level of cooperation of a land user \( i \) in the simulations, a neighbour \( j \) is chosen randomly and the value of cooperation between that pair of agents is evaluated. Cooperation can thus be evaluated across the whole landscape grid and depicted graphically as a filled contour map.

2.4 Process overview, scheduling and culling updating

We test both the case of a homogeneous deer density, i.e. each landholding has a deer density of 0.5 initially, and a random deer-populated landscape where the initial deer abundance per holding is randomly chosen between [0,1]. Landowners adopt a random culling intensity chosen between [0,1]. The model proceeds sequentially through seasonal stages within an annual management cycle. At the start of each year landowners implement culling activities at a level influenced by the payoff they achieved in the preceding year. The deer population is updated synchronously across all cells in the landscape grid to allow for the cull removed from each landholding. The remaining deer population then grows according to a logistic growth function, and the deer density present on a landholding after this growth stage then determines the number of animals from the resident population which will move. Deer disperse equally among either 4 (von Neumann neighbourhood) or 8 (Moore neighbourhood) neighbours. Deer populations are updated once more to allow for movement before the level of damage which this post-cull, post-movement deer population imposes on biodiversity in each landholding is calculated. Knowing culling revenues, culling costs and damage costs for the whole year, owners can now calculate their annual payoff from deer management.\(^2\) These payoffs obtained from

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\(^2\) The relative sequencing of events in the annual management cycle enacted here is broadly representative of deer management in the UK where autumn and winter culling precedes the birth of
local interactions with neighbouring individuals are then used to update the state of the system. From the viewpoint of evolutionary game theory, this updating may be interpreted in terms of imitation and learning (Nowak and Sigmund 2004). In our model, at the end of the year, owners compare the payoffs they achieved with those of neighbours whose land holds deer at ‘similar’ densities (parameter “$d$”, Table 1) to decide whether or not to change their culling intensity. If no ‘similar’ neighbour achieved a higher payoff then landowners will implement their culling intensity from the preceding year again in the year following. If, however, a ‘similar’ neighbour achieved a higher payoff then a landowner will attempt to imitate that neighbour’s culling intensity. In order to explore the continuous culling intensity space, we assume small errors in the selection of culling intensity, i.e. we allow mutations to occur. Following Doebeli et al. (2004) and Hauebert and Doebeli (2005), the model assumes that whenever an owner chooses his intensity for the following year there is probability of 0.01 (i.e. one mutation in the culling rate of 100 owners, parameter “$p_m$”, Table 1) that landowners adopt a culling intensity different to the most successful culling intensity in their neighbourhood. The adopted culling density is calculated as their desired culling intensity with some random error, which is normally distributed with mean equal to the desired culling level and a standard deviation of 0.1 of the mean.

In our analysis we focus on the attractor of the modelled complex system, i.e. the set of states to which the system converges after some transient time (e.g., Auyang (1998)). If we were considering a linear deterministic system this would mean we are analyzing the stable fixed (or, equilibrium) points of the system. Much about economic and other systems has been learned by studying their fixed points. In complex systems like the present one the concept of equilibrium is usually not appropriate. The attractor takes more complicated forms, such as limit cycles (periodic trajectories rather than simple points in phase space) up to so-called strange attractors with fractal dimension in the case of chaotic dynamics. But like the analysis of equilibrium points in simple systems, the shape of and dynamics in the attractor delivers essential insights into the behaviour of the system.

calves, which precedes density-driven emigration of immature individuals (especially males). Grazing damage to biodiversity can occur at different times in the year depending on the ecological setting. Damage inflicted by the post-cull, post-growth, post-emigration population implemented here is more representative of wooded lowland ecosystems than upland ones.
3 Results

We present the results in two parts. The first part focuses on the resource economic dimensions of the deer management problem. This includes the evolution of the deer density and the culling intensity in the landscape, and the relation between the two. In the second part we add the game theoretic dimension of the problem and present the dynamics of cooperation and how cooperation relates to culling intensity. The results presented here are based on the model parameter values shown in Table 1. They also hold, with minor quantitative differences, for a Moore neighbourhood (N=8 neighbours) and any other choice of the maximum density difference for payoff comparison among neighbours (0<d<1) (results not shown in figures).

3.1 Dynamics of deer and culling intensity

The mean deer density in the landscape and the mean culling intensity develop over time in cycles in both types of landscapes; sporting (Fig. 1a) and biodiversity (Fig. 1b). Starting from a relatively high mean deer density and low mean culling intensity, culling intensity gradually increases which is associated with a gradual decrease in deer density. This continues until a relatively high culling intensity and low density is reached. At this stage, the landowners reduce the culling intensity which is followed by an increase in deer density. As a consequence of this dynamic we observe a negative correlation between deer density and culling intensity in both scenarios.
Figures 1: Mean culling intensity vs. mean deer density for the sporting (panel a) and the biodiversity (panel b) scenarios. Each dot represents one time step (100 time steps in panels a and 50 time steps in panel b). The system evolves in the direction of the arrows.

Figure 2 shows phase diagrams of local deer density and local culling intensity for a randomly selected owner. Similar to the mean values (Fig. 1) we observe cycles (including a negative correlation between deer density and culling intensity) whose shapes however differ considerably from those in Fig. 1. The first difference is that the observed local culling intensity and deer density both span almost their entire feasible range \([0,1]\). Second, in both scenarios the cycles exhibit a pronounced triangular shape. Starting from relatively high deer density and low culling intensity, an increase in culling intensity is followed rapidly by a decrease in deer density (similar to Fig. 1). The landowner responds to the decline in the deer density by reducing his culling intensity. However, the reduction in the culling intensity does not induce an immediate recovery in the deer population. It is only after low culling has been applied for some time that the deer population increases again. After it has recovered to a relatively high density the cycle starts again and the landowner decides to increase his culling intensity.
**Figure 2:** Local culling intensity vs. local deer density for a randomly sampled land owner for the sporting (panel a) and the biodiversity (panel b) scenarios. Each dot represents one time step (100 time steps in panels a and 50 time steps in panel b). The system evolves in the direction of the arrows.

Although both sporting and biodiversity scenarios share this feature, they do differ markedly in that in the sporting scenario culling intensity may assume practically all values from the feasible interval, while in the biodiversity scenario it takes only large or small values. Furthermore, in the biodiversity scenario the culling intensity jumps between high and low levels within only very few (often a single) time steps, while in the sporting scenario it generally changes more gradually. Altogether, in the biodiversity scenario the dynamics of local culling intensity are more constrained in terms of assumed culling intensities and run much faster than in the sporting scenario.

These differences between the two scenarios can also be seen in the spatial structure of the landscape. Figure 3 shows the spatial distribution of culling densities for a particular point in time. In both scenarios the landscape is structured by patches consisting of cells with similar culling densities. However in the sporting scenario almost all culling densities can be observed while in the biodiversity scenario there are only patches either with low culling intensity or with high culling intensity. This is further emphasized in the frequency distributions of culling intensities (Fig. 4) which
also shows that in the sporting scenario the deer density tends to be higher than in the biodiversity scenario. The second marked difference between the two scenarios is in spatial correlation of the culling intensities. In the sporting scenario the spatial correlation length which measures the distance at which cells with similar culling density can be observed is much longer than in the biodiversity scenario (Fig. 5). So in the biodiversity scenario the culling intensity in a particular cell changes not only on a shorter time scale than in the sporting scenario, but it also varies among cells on a much shorter spatial scale.

**Figure 3:** Snapshots of equilibrium culling intensities on a 25*25 square lattice (t=500). Panel a: sporting scenario. Panel b: biodiversity scenario.
**Figure 4:** Frequency of culling intensity and deer density sampled over all cells at time \( t=500 \). Panel a: culling intensity, sporting scenario. Panel b: culling intensity, biodiversity scenario. Panel c: deer density, sporting scenario. Panel d: deer density, biodiversity scenario.
Figure 5: Correlation length of culling intensities at equilibrium. A measure of spatial correlation with respect to distance under the assumption that a cell is a hectare. Panel a: sporting scenario. Panel b: biodiversity scenario.

3.2 Analysis of cooperation

Figure 6 shows snapshot configurations of the cooperation index at a moment of time during the stationary situation for both scenarios: biodiversity and sporting. Compact clusters of cooperative behaviour are found in the sporting scenario (Fig. 6a). The frequency of cooperative behaviour in the sporting scenario is characterised by a unimodal distribution with most individuals displaying medium levels of cooperative behaviour as quantified by their cooperation index (Fig. 7a). Figure 8a shows that the cooperation index in the sporting scenario is strongly negatively correlated with culling intensity; i.e. cooperative individuals are those that undertake low culling, while defecting individuals are those that apply high culling intensities. This leads to the conclusion that in the sporting world clusters of cooperative behaviour are formed by individuals culling at low intensity, which allows the resource to recover. Defecting individuals will be those that free-ride on the cooperative individuals by culling higher proportions of the deer population.
Figure 6: Snapshots of equilibrium cooperation index on a 25*25 square lattice (t=500). Panel a: sporting scenario. Panel b: biodiversity scenario. (Culling intensities are those shown in Figure 3).

Figure 7: Frequency distribution of landowners's cooperative behavior at equilibrium. Panel a: sporting scenario. Panel b: biodiversity scenario.
Figure 8: Correlation between landowners’ culling intensity and cooperative behavior at equilibrium. Panel a: sporting scenario. Panel b: biodiversity scenario.

In the biodiversity scenario, where the damage which deer impose on tree growth has a significant impact on landowners’ payoffs, the cooperation index is high only at the boundaries between the high-culling (white in Fig. 3b) and low-culling (black in Fig. 3b) clusters while inside the high-culling and low-culling clusters cooperation is low (Fig. 6b). Compact clusters of cooperating landowners therefore fail to form, with cooperators instead being located in filament-like structures; this explains why the number of cooperators is much smaller than the number of defectors (Fig. 7b). Fig. 7b also shows that the cooperation index has polarised values in the biodiversity world. This agrees with our findings for culling intensity (Fig. 4b); however, the relationship between cooperation index and culling intensity is non-unique. Fig. 8b shows that there are two “modes of cooperation” in biodiversity world: Mode 1 is characterised by a positive relationship, where high culling intensity implies high cooperation and Mode 2 is characterised by a negative relationship, where low culling intensity implies high cooperation. These different modes of behaviour are related to the culling intensity of the neighbour. Mode 1 mainly occurs when the focal individual’s neighbour has a low culling intensity while Mode 2 occurs mainly when the focal individual’s neighbour applies high culling (Fig. 9). According to this, the cooperation index of any owner in the landscape increases with increasing culling when the neighbour applies low culling (Mode 1), and it decreases with increasing
culling when the neighbour is undertaking high culling (Mode 2). This analysis also shows that cooperative behaviour is characterised by doing the opposite to your neighbour (A and B, Fig. 8b); whereas defecting implies applying similar strategies, i.e. either both culling high or culling low (C and D, Fig. 8b). At Point A, the focal individual culls little while the neighbour culls heavily, and this is cooperative behaviour because behaving otherwise would further reduce deer density on the neighbour’s land and therefore increase the neighbour’s culling costs. At Point B, the focal individual culls heavily, while the neighbour is culling little. The focal individual behaves in a cooperative manner in this instance because by culling heavily deer movement to the neighbour’s land is reduced with the positive consequences for damage reduction. Therefore in the cooperation snapshot (Fig. 6b) the defectors are in the high and low culling clusters (Fig. 3b), where neighbouring landowners are pursuing similar culling strategies, but in the filament-like structures at the edges of these culling clusters, where landowners are doing the opposite to their neighbours, their cooperation index is high.

**Figure 9:** Frequency distribution of neighbour’s culling intensity for the two modes of cooperation (biodiversity scenario).

The meaning of cooperative behaviour in both scenarios is consistent with the analysis of only two landholdings. Figure 10 shows the payoffs of two landowners as
a function of their culling intensities. In the sporting scenario, where cooperation is consistently equivalent to low culling, Fig. 10a shows that the lower the culling of owner B, the higher are the payoffs to owner A. It is also evident that once owner A culls at low intensity (below 0.2) then his payoff is virtually unaffected by the culling intensity of owner B. In the biodiversity scenario (Fig. 10b), when the culling intensity of A is low, his payoff will increase as the culling intensity of owner B increases (Mode 1). On the other hand, when the culling intensity of A is high, his payoff will increase as the culling intensity of owner B reduces (Mode 2).

Figure 10: Payoff of player A as a function of player A’s and B’s culling intensities (deer density = 0.4). Panel a: sporting scenario. Panel b: biodiversity scenario. Ligher shades mean higher payoffs.

4 Summary and Conclusions

This paper investigates the emergence of cooperation in natural resource management at a landscape scale. In particular, it studies the spatio-temporal evolution of cooperative behavior in two types of deer management systems: a landscape dominated by sporting estates and a landscape predominantly used for biodiversity conservation. We followed an evolutionary game theory approach, where
individual owners occupy sites on a spatial lattice. The landowners’ payoffs from deer management are a function of the changing level of deer on their landholdings. The deer population depends on biological characteristics (population growth and movement across the lattice), and on the mutually interacting management actions of the landowners. The landowners’ culling decisions depend on their expected payoffs, involving a mechanism of imitation and learning from nearest neighbours. The modelled game is continuous because actors’ action (culling intensity) is defined as a continuous variable - in contrast to the classical “all” or “nothing” strategies that predominate classical games. There are no \textit{a priori} assumptions on the dependence of a landowner’s action on the level of cooperation with or by his/her neighbours. Instead cooperation is defined \textit{a posteriori}, following the evolutionary game theory literature, as a function of the culling intensity. Consequently, there are no \textit{a priori} assumptions about the type of game (prisoners’ dilemma, snowdrift, etc.) played.

The results show a significant difference in the spatial patterns of management action and cooperative behaviour between the two scenarios. In the sporting scenario cooperation emerges, through the formation of compact clusters of cooperative landowners. Cooperative owners prevail surrounded by defecting individuals by culling at low intensities which maintains the deer density at high levels (Figs. 1 and 2), maximizing neighbours’ culling benefits, by minimizing their culling costs and thus maximizing their net benefits (Fig. 10). In the biodiversity world in contrast, cooperators are unable to form compact clusters but occur in filament-like structures along the boundaries of zones of high or low culling intensity. Cooperative behaviour is context dependent, because it is a function of the neighbours’ actions across the full range of culling intensities: cooperation turns out to mean taking the opposite action to your neighbour. This can be explained in terms of the payoff structure that characterizes this type of management. High (low) deer densities reduce (increase) culling costs but increase (reduce) damages. When neighbours cull low, cooperative behavior arises from high culling intensity by the focal owner, because this decreases movement of deer onto the neighbours’ landholdings and reduces neighbours’ damage costs. In this situation the neighbours are free riding on the culling efforts of the focal ‘cooperator’. When neighbours have a high culling intensity, cooperative behavior means low culling intensity by the focal individual because this increases deer movement onto neighbouring landholdings which reduces neighbours’ culling
costs.\(^3\) Cooperative individuals are therefore located along the edges of clusters of high culling and low culling landowners. This analysis shows that the mechanism driving cooperative behavior can be much more complex than just assuming a unique relationship between cooperation and individuals’ action.

In both worlds, cooperative strategies evolve with time and cooperators are not fixed in location, i.e. individuals alternate cyclically between cooperation and defection. This is associated with two effects: (i) once cooperation reaches a certain level it becomes more vulnerable to invasion by defectors, as has been shown in continuous games (Wahl and Nowak 1999); (ii) the benefits derived from cooperation change as the deer population changes. Therefore, in a world where natural resources change with time in response to human actions, this second effect becomes relevant and should be included in evolutionary game theory models of natural resource management. In the biodiversity world, landowners are more distinctively polarised into those carrying out very high and very low levels of culling. While in the sporting world the span of culling intensities applied is lower. As a consequence of this, local deer densities are significantly lower in the biodiversity scenario, as expected.

Different types of games have been demonstrated to produce different spatial structures of cooperators and defectors within a landscape (see Doebeli and Hauert 2005 for a comprehensive review). Our results seem to support the notion that pest control of economically viable species would favour a stationary situation where cooperators are relatively rare and found only in filament-like structures which are formed along the boundaries between high culling clusters and low culling clusters. This hints at the fact that cooperative behaviour may be governed in this context by the snowdrift game, which would imply that cooperating in the neighbourhood of defectors or defecting in the neighbourhood of cooperators maximises landowners’ own benefits. Future research will examine this issue, exploring further which type of game the landowners are actually playing in the context of spatially-explicit evolutionary game theory.

\(^3\) Paradoxically in this situation, if we consider the control cost incurred by the focal individual, it is likely that he is free-riding on the culling efforts of his high-culling neighbour. However, when we consider the effect which low culling by the focal individual carries for the culling cost of his neighbour, we see that this free-riding behaviour is actually cooperative towards costs incurred in the high culling intensity adopted by his neighbour.
We find that this analysis has important implications for the role of policy intervention to promote specific forms of management. The analysis would suggest that landscapes with a high level of conservation effort are likely to require active intervention even though private benefits from cooperation exist. In contrast, if the outcomes generated from sporting estate landscapes are in line with broader objectives for provision of ecosystem goods and services from the landscape, our analysis suggests that such systems are more likely to persist without intervention.

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References


