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## ANALYSIS

# Modelling conflicting objectives in the management of a mobile ecological resource: Red deer in the Scottish Highlands

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## ABSTRACT

Free-ranging ecological resources are frequently managed with an age- and gender-structured complexity beyond that handled routinely in optimising bioeconomic analysis. Here we use a Hamiltonian-based solution method to develop optimal management prescriptions for a bioeconomic system comprising 14 state variables and 6 control variables: red deer management in the Scottish Highlands. We consider management on estates where deer are husbanded as a sporting resource, and on sites where deer density is reduced to promote the regeneration of native woodland. We focus in particular on the consequences of deer emigration/immigration, between neighbouring sites pursuing conflicting management objectives. Our results suggest that a strong stock effect on culling cost and a wide disparity in value between culled males and females underlie the high population densities and female-biased herd structures which prevail across the Highlands. Neither of these effects have been included in earlier ecological models of red deer management. Results also suggest that managing deer density to secure the regeneration of native woodland will incur considerable costs. We also show that emigration/immigration of immature male deer between a neighbouring sporting estate and woodland regeneration site carries adverse cost implications for both parties. Whilst deer management on sporting estates may respond to financial incentives, the strong inverse relationship between deer density and culling cost will prevent such mechanisms from delivering substantial reductions in deer density under current property rights.

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## 1. Introduction

Conflict frequently surrounds the management of mobile ecological resources, and is particularly likely to occur where resource users pursue disparate management objectives, where property rights are ill-defined and when structural complexities exist in the temporal or spatial dynamics of the resource itself or within the management strategies of resource users (Conover, 2002; Milner-Gulland, 2001). Bioeconomic models are much used to study the consequences of

disparate management objectives and ill-defined property rights, but existing implementations of such models can rapidly become intractable as structural complexity increases. In this paper we introduce a novel solution methodology to utilise an optimising bioeconomic model of considerable age- and gender-structured complexity to analyse the management of wild red deer (*Cervus elaphus* L.) in the Highlands of Scotland — a mobile ecological resource whose management is complicated by all of the problematic features highlighted above.

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Red deer are widespread throughout the Scottish Highlands (Deer Commission for Scotland, 2003). When alive they belong to no one, but land ownership confers the property right to shoot resident deer (Parkes and Thornley, 2000), and considerable revenue can be generated by leasing shooting (stalking) rights for mature males (stags) with antler trophy heads. Sporting estates, large tracts of upland devoted to deer stalking, cover considerable areas of the Highlands and make significant direct and indirect contributions to the rural economy (Callander and MacKenzie, 1991). Biological and economic characteristics (e.g. survivorship, fecundity, carcass weight and trophy value) differ between sex and age classes of deer, and these differences are reflected in the age structure and intensity of culls extracted by sporting estates (Mitchell et al., 1977; Trenkel et al., 1998). A further complication arises because the capital value of a sporting estate is derived partly from its annual stag cull, with a capital value increment of £20,000–£30,000 typically associated with each trophy stag culled (Trenkel et al., 1998). Estate owners are thus inclined to maintain stag culls fixed at 'traditional' levels (Buckland et al., 1996; Staines, 1978; Staines et al., 1995) to safeguard their capital investment and also to access privileged stalking opportunities for themselves, their families, friends and business acquaintances (MacMillan, 2004; MacGregor and Stockdale, 1994).

Grazing and browsing pressure by red deer present at high density throughout most the Scottish Highlands is currently preventing natural regeneration of native trees such as Scots pine (*Pinus sylvestris*) and birch (*Betula* spp.) (Miller et al., 1998; Scottish Natural Heritage, 1994). Grazing and trampling damage to fragile moorland and montane ecosystems, carrying the prospect of long term habitat change, is also causing considerable concern (Staines et al., 1995). Conservation organisations now own substantial areas of land in the Scottish Highlands, with the aim of restoring native habitats and increase biodiversity value — primarily through the regeneration of native woodland (Scottish Natural Heritage, 1994). Such organisations have called for widespread and substantial reductions in red deer density (Hunt, 2003; Scottish Natural Heritage, 1994), but these calls have not been well received by the owners and managers of sporting estates, or by their stalking workforce (Bullock, 1999). A wariness between organisations and individuals representing sporting and conservation interests is acknowledged on both sides of the debate (McKelvie, 1991; Ramsay, 1997; Scottish Natural Heritage, 1994; Wigan, 1993).

Deer management in pursuit of conflicting objectives would have no impact upon neighbouring businesses if adjacent properties carried isolated herds of red deer. Tagging and collaring studies (Clutton-Brock et al., 2002, 1997; Milner-Gulland, 2001; Red Deer Commission, 1983–1985; Sibbald, 2001) have, however, shown that red deer cross ownership boundaries in the Highlands on a temporary and/or permanent basis, transmitting the external consequences of management action between adjacent properties. In this paper we focus on the external consequences which arise from permanent movement, i.e. emigration/immigration, between neighbouring sites.

Prior research has addressed red deer management primarily from an ecological perspective, employing complex

ecological simulations (Buckland et al., 1996; Clutton-Brock and Lonergan, 1994; Trenkel, 2001), but largely ignoring economic elements of the management problem. Stock depletion effects were considered by Milner-Gulland et al. (2000) in their investigation into the management implications of intra-herd spatial structure, but this study did not address trophy stag culling, the main focus of management on sporting estates. Similarly, lack of computing power in the 1970s prevented Beddington's initial bioeconomic analyses of red deer management (Beddington, 1973; Beddington et al., 1975) from addressing fundamental differences in management strategy for stags and hinds (females).

Our bioeconomic model, including relevant ecological and economic complexities, is outlined in Section 2 together with its solution algorithm. In Section 3 the management of a deer herd on a sporting estate and a woodland restoration site is examined under sole ownership as benchmarks. Management outcomes on a neighbouring sporting estate and woodland restoration site are then considered, with management impacts mediated between the sites by density-dependent emigration. Finally, the potential which incentive mechanisms offer for conflict reduction is examined.

## 2. The bioeconomic model

### 2.1. Culling

The culling process for red deer on the open hill in Scotland can be described by a three-input Cobb–Douglas production function (Beddington, 1973):

$$K = q E^\alpha N^\beta L^\gamma \quad (1)$$

$K$  is the size of the cull,  $q$  is a scaling constant,  $E$  is the stalking effort applied (number of stalkers per year),  $N$  is the total population size and  $L$  is the land area over which the herd is dispersed (in units of 100 acres, for compatibility with Beddington's earlier work). Exponent  $\alpha$  is the effort elasticity,  $\beta$  is the herd size elasticity and  $\gamma$  is the land area elasticity. Estimated values for these exponents are shown in Table 1.

Red deer on the open hill aggregate into herds of stags and herds of hinds, calves and juveniles which remain separate for most of the year (Clutton-Brock et al., 1982). A herd of the requisite composition is first located and a target animal for culling is selected from within that herd. Using an approach analogous to that adopted by Bjørndal and Lindroos (2004) when apportioning the North Sea herring stock between fishery jurisdictions, the deer culling function can be partitioned as:

$$K = q E^\alpha \cdot (M^I + M^M)^\beta \cdot L^\gamma \quad \text{for stags and} \quad (2)$$

$$K = q E^\alpha \cdot (C + H^I + H^Y + H^M)^\beta \cdot L^\gamma \quad \text{for hinds and calves} \quad (3)$$

where  $M$  denotes stags (males),  $C$  calves and  $H$  hinds (females), with the superscripts denoting management classes within those categories as indicated in Table 1.

**Table 1 – Parameter nomenclature, parameter values, and biological and management classifications in the bioeconomic model**

T=planning horizon=50 years for the sporting estate, 5 years for the woodland restoration site  
 P<sub>V</sub>=price of venison=£1.00 per carcass kg

Biological class <i>b</i>	Symbol	Carcass weight <i>W<sup>b</sup></i> (kg)	Trophy value <i>P<sub>A</sub></i> (£)
Hind calves	<i>H<sup>C</sup></i>	24.2	0
Yearling yield hinds	<i>H<sup>Y1</sup></i>	35.9	0
2-year old yield hinds	<i>H<sup>Y2</sup></i>	46.8	0
3-year old yield hinds	<i>H<sup>Y3</sup></i>	51.0	0
Mature yield hinds	<i>H<sup>YM</sup></i>	53.0	0
2-year old milk hinds	<i>H<sup>M2</sup></i>	40.0	0
3-year old milk hinds	<i>H<sup>M3</sup></i>	43.6	0
Mature milk hinds	<i>H<sup>MM</sup></i>	46.8	0
Stag calves	<i>M<sup>C</sup></i>	25.6	0
Yearling stags	<i>M<sup>1</sup></i>	37.9	0
2-year old stags	<i>M<sup>2</sup></i>	49.7	50
3-year old stags	<i>M<sup>3</sup></i>	66.2	100
4-year old stags	<i>M<sup>4</sup></i>	75.1	175
Mature stags	<i>M<sup>M</sup></i>	83.9	250

<i>c</i> =annual cost of employing a unit of stalking labour=£12,000
<i>q</i> =0.578
<i>α</i> =0.512
<i>β</i> =1.093
<i>γ</i> =−0.453
<i>N<sub>t</sub></i> =initial population size=3750; (initial population density=15 deer per km <sup>2</sup> )
<i>L</i> =land area modelled=250 km <sup>2</sup> ; (equivalent to 618×100 ac)
<i>δ</i> =0.05
Parameters in the population model obtained from the literature. See Appendix 2.
Population model calibrated to a carrying capacity of 25 deer per km <sup>2</sup> .

Management class <i>m</i>	Symbol	Comprises
Hind calves	<i>C</i>	<i>H<sup>C</sup></i> + <i>M<sup>C</sup></i>
Immature hinds	<i>H<sup>I</sup></i>	<i>H<sup>Y1</sup></i> + <i>H<sup>Y2</sup></i>
Yield hinds	<i>H<sup>Y</sup></i>	<i>H<sup>Y3</sup></i> + <i>H<sup>YM</sup></i>
Milk hinds	<i>H<sup>M</sup></i>	<i>H<sup>M2</sup></i> + <i>H<sup>M3</sup></i> + <i>H<sup>MM</sup></i>
Immature stags	<i>M<sup>I</sup></i>	<i>M<sup>1</sup></i> + <i>M<sup>2</sup></i> + <i>M<sup>3</sup></i> + <i>M<sup>4</sup></i>
Mature stags	<i>M<sup>M</sup></i>	<i>M<sup>M</sup></i>

2.2. Population dynamics

Survivorship and fecundity show strong differences between the two sexes and/or between age classes in red deer in Scotland (Clutton-Brock et al., 1982). Those differences which appear most influential over population dynamics are: (a) between stags and hinds in the density-dependent winter survivorship of calves and yearlings — survivorship being lower in stags than in hinds, and (b) in density-dependent fecundity between hinds which have, and have not, suckled a calf through the summer preceding the autumn mating season, (milk hinds *H<sup>M</sup>* and yield hinds *H<sup>Y</sup>*, respectively) — average fecundity in yields being higher than that in milk hinds. These differences must be represented if the dynamics of structured red deer populations are to portray features of central importance to management, e.g. the proportions of stags and hinds in the managed herd, and a population model of considerable structural complexity is therefore required (Buckland et al., 1996; Clutton-Brock and Loneragan, 1994; Trenkel et al., 2000). Here we depict the

population dynamics of red deer by a discrete-time, deterministic, difference equation model, based on published ecological research (Buckland et al., 1998; Trenkel et al., 2000). The model features 14 biological classes (Table 1) with significant differences in survivorship, fecundity, body weight and/or trophy value. The population model is described in more detail in Appendix B.

2.3. Management objectives

Two different portrayals of the objectives of deer management on sporting estates are implemented using the model. As an initial benchmark, management on the sporting estate is considered to maximise the net present value of net revenues from stalking, accounting for the venison and trophy values of culled animals and the cost of employing stalking labour:

$$\max \sum_{t=0}^{(T-1)} \frac{1}{(1+\delta)^t} \cdot \left[ \sum_{b=H^C}^{b=M^M} (P_V \cdot W^b + P_A^b) K_t^b - c \sum_{m=C}^{m=M^M} E_t^m \right] + \frac{1}{(1+\delta)^T} \cdot \sum_{b=H^C}^{b=M^M} (P_V \cdot W^b + P_A^b) N_T^b \tag{4}$$

Profit maximisation is subject to the discrete-time, density-dependent population dynamics of Appendix B and the effort requirements inherent in the culling production function (Eqs. (2) and (3)).

To avoid the animal welfare implications of orphaning calves, it is usual to cull dependent calves and their mothers as pairs. This is represented by adding a culling restriction to Eq. (4);

$$K_t^C \geq K_t^{HM} \quad \text{for } t = 0, 1, \dots, (T-1). \tag{5}$$

Once the profit maximising benchmark has been established a second portrayal of deer management on the sporting estate examines the consequences of adhering to a ‘traditional’ stag cull by introducing direct constraints on the number of mature stags culled;

$$K_t^{M^M} \geq K_{\min}^{M^M} \quad \text{or} \tag{6}$$

$$K_t^{M^M} \leq K_{\max}^{M^M} \quad ; \quad \text{both for } t = 0, 1, \dots, (T-1).$$

These constraints allow adherence to traditional culling levels to override the profit maximisation motive, a behaviour which is common amongst estate owners (MacMillan, 2004; Wightman et al., 2002). Enforcing a stag culling requirement in excess of the profit maximising stag cull effectively turns the problem into a constrained cost minimisation.

In the foregoing equations, *t* denotes the timestep, *T* the planning horizon, *δ* the discount rate and *c* the annual cost of employing a unit of stalking labour. The prices attached to culled animals of each biological class in each timestep (*K<sub>t</sub><sup>b</sup>*) comprise the venison revenue realised by their carcass weight (*P<sub>V</sub> · W<sup>b</sup>*) together with any trophy value which they attract (*P<sub>A</sub><sup>b</sup>*). The superscript *b* here denotes generic biological class (Table 1), hence carcass weight varies with age and only stags command a trophy value, which itself only becomes appreciable once the animals approach maturity.

Management cannot be implemented at full biological resolution because even experienced stalkers can only achieve a coarse categorisation of each sex by age out on the hill. The

**Table 2 – Profit maximisation on the sporting estate with sole ownership ( $\delta=5\%$ )**

Steady state results : with and without trophy values, and with maximum and minimum constraints imposed on the mature stag cul

	Zero trophy value	Trophy values of Table 1	$K_{\max}^{MM} = (K^{MM} + 15\%)$ and trophy values of Table 1	$K_{\min}^{MM} = (K^{MM} - 15\%)$ and trophy values of Table 1
Annual profit (£ per km <sup>2</sup> )	65	240	234	239
Stalking effort (stalkers per 100 km <sup>2</sup> )	0.33	1.06	0.78	1.27
Population density (deer per km <sup>2</sup> )	21	20	20	20
Cull (% of autumn population)	8	11	10	11
Mature stag cull (% of autumn population)	7	22	16	26
Percentage of annual profit from stag cull	36	79	79	80
Herd structure: stags/hinds/calves (%)	43/42/15	36/47/17	37/46/17	36/47/17
Hind to stag ratio	1.04:1	1.30:1	1.25:1	1.30:1

 $K^{MM*}$  is the steady-state profit-maximising cull of mature stags with the trophy values of Table 1.

The steady state results quoted for each scenario are taken from the 25th year of the planning horizon in each instance.

bioeconomic model therefore features six management classes, denoted generically by the superscript  $m$ , with a single management class encompassing between one and four biological classes (Table 1). The effort expended to extract the cull is indexed by management class ( $E_t^m$ ), and the total cost of culling in each timestep is calculated accordingly. The gross value of the herd at the end of the planning horizon is included in the net revenue calculation as a bequest value (the second term in Eq. (4)).

#### 2.4. Profit maximisation with a population target

Deer management on a woodland restoration site can be considered to comprise two sequential phases; (a) a population reduction phase when the resident deer population is reduced to a desired target density to initiate the regeneration of native woodland, and (b) a population maintenance phase during which deer density is held at its desired level for sufficient time to allow the regenerating woodland to establish.

Management costs during population reduction are minimised in accordance with Eq. (4), but now the bequest value is modified to include a penalty function which assigns a large negative value to terminal shadow prices if deer density exceeds the target level at the end of the allotted timespan. The influence which bequest value exerts over the optimal management prescription via the co-state equations will ensure that the desired population density is achieved.

The total cost of population maintenance can be calculated by summing the cost of removing the annual population increment throughout the maintenance period (in accordance with Eqs. (2) and (3) and the density-dependent population dynamics), discounted back to the start of the population reduction phase.

#### 2.5. Spatial movement

Dispersal in red deer is most common amongst juveniles between the ages of 2 and 4 (Clutton-Brock and Albon, 1989; Mitchell et al., 1977), and dispersal outwith natal areas on the scale of typical land ownerships in the Highlands is much more frequent in stags than in hinds (Clutton-Brock et al., 1982; Red Deer Commission, 1983–1985). Emigration of imma-

ture stags has been shown to be a function of hind density at the natal site, and density-dependent emigration in published data (Clutton-Brock et al., 2002) is well described by a generalised linear model with a logistic link function ( $\chi^2=6.71$ ,  $df=1$ ,  $p=0.01$ ). Immature stag emigration between neighbouring sites is modelled here by the inclusion of this logistic density-dependent relationship into the population dynamics of the relevant biological classes.

Management on an adjacent sporting estate and conservation site is analysed by assuming a representative density and structure for the deer population resident at the ‘other’ site, linking the sites by the emigration/immigration of immature stags, and then optimising management for each site in turn as described in Sections 2.3 and 2.4 above. Given their different management objectives, hind density will be lower on the woodland restoration site than on the sporting estate and net emigration of immature stags from the estate to the restoration site will occur as a consequence. Population sizes on the two properties therefore include emigration/immigration effects and this influences the marginal cost of culling and shadow prices, with consequent impacts on the optimal management prescriptions.

#### 2.6. Benchmark parameters

Benchmark analyses for the profit-maximising sporting estate were undertaken with the parameter values and notation shown in Table 1. Venison price and estimated trophy values were obtained from experienced current practitioners (Charles Critchley (Forestry Commission) and Hugh Rose (British Deer Society), personal communication, 2003). Carcass weights are the mean values recorded from an extensive long-term study in the central Highlands (Mitchell et al., 1986). The cost of employing a stalker for a year comprises the national minimum wage for an agricultural worker (Department of Trade and Industry, 2003) plus employer’s national insurance contribution (Inland Revenue, 2003).

Production function parameters (Eqs. (2) and (3)) were obtained by log–log regression ( $R^2=0.983$ ,  $F_{3,6}=134.2$ , sig.  $F<0.0001$ ) on data reported by Beddington (1973), and Milner et al. (2002) in combination. An area of 250 km<sup>2</sup> is representative of a medium to large estate. The initial population

density of 15 deer per km<sup>2</sup> used in the sporting estate analysis here is lower than that reported over much of the Highlands (Deer Commission for Scotland, 2003), but is useful for illustration.

Initial parameter settings for density-dependent fecundity and survivorship in the discrete-time population model were obtained from the literature (Albon et al., 1983; Trenkel, 2001; Trenkel et al., 2000). The population model was validated by comparing model predictions with long term population data from studies on the Isle of Rum and at Glenfeshie in the Cairngorms (Buckland et al., 1996; Clutton-Brock et al., 1985; Mitchell et al., 1986).

When modelling management on the woodland restoration site, target deer densities were taken to be between 4 and 8 deer per km<sup>2</sup> (Palmer and Truscott, 2003), and the population reduction and maintenance phases were assumed to last 5 years and 20 years, respectively (Ramsay, 1997). Trophy values were neglected on the assumption that culling would be undertaken by contractors rather than fee-paying clients. An initial population density of 20 deer per km<sup>2</sup> was assumed, as would be appropriate if the site had been purchased from a sporting estate. Other parameters were as shown in Table 1.

2.7. Optimisation method

Matlab routines were written to utilise an iterative engineering technique (Noton, 1972) as a novel method for solving a current-value Hamiltonian setting of the net revenue maximisation problem with 14 state variables and 6 control variables. State variables (the population sizes of each biological class) and control variables (the culls extracted from each management class), overlap to differing extents. The solution equations and iteration method are described in Appendix A. Analyses under different management regimes, pricing structures and culling constraints are described in the following sections.

3. Management in different settings

3.1. The sporting estate

We consider profit maximisation under Eq. (4) initially with the sporting estate as the sole owner of the resource stock. Four circumstances are considered. Firstly, for illustrative purposes only, stag trophy values are set to zero. Secondly, trophy values are restored to the representative levels of Table 1. In the third and fourth instances mature stag culls are constrained to differ from their profit maximising level by ±15% to examine the consequences of adhering to ‘traditional’ culling levels for stags.

Results for the sporting estate under sole ownership are summarised in Table 2. Fig. 1 illustrates culls and population sizes across the 50 year planning horizon for the management prescription which maximises profit under sole ownership with the representative trophy values of Table 1. The impact of the initial conditions and the inclusion of the gross value of the herd within bequest value are evident. The optimum total deer density in the steady state remains

virtually constant at c. 20 deer per km<sup>2</sup>, irrespective of changing trophy value and the imposition of constraints on the cull of mature trophy stags (Table 2). This arises from the conflicting influences of deer density on culling cost and population dynamics. Culling cost increases rapidly as the herd size decreases, since herd size elasticity is high (Table 1); but density exerts only a modest influence over the survivorship and fecundity of most biological classes until population size approaches 80% of carrying capacity, whereupon its impact becomes severe (Appendix B). Under sole ownership, the profit maximising estate therefore has little to lose, and everything to gain, by holding deer density near this threshold of c. 20 deer per km<sup>2</sup>. The same is true of the

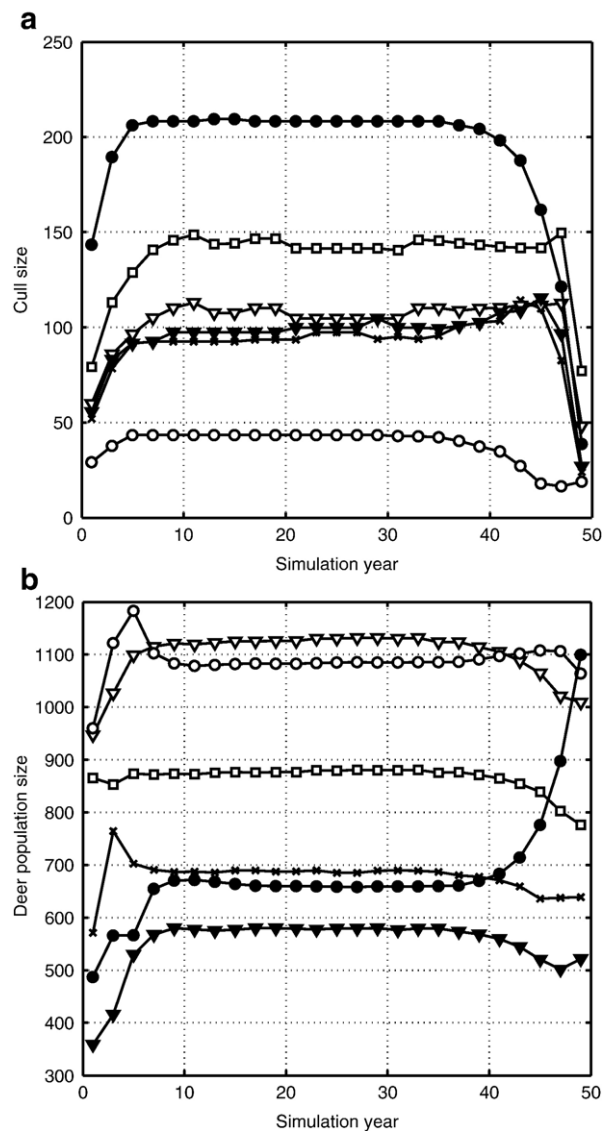
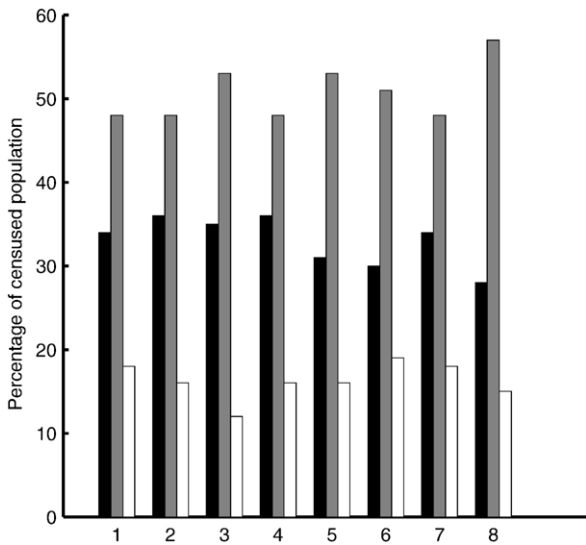


Fig. 1—(a) Culling prescriptions and (b) population sizes for profit maximisation on the sporting estate under sole ownership, using the trophy values of Table 1. Management classes depicted as follows; calves — open squares, immature hinds — crosses, milk hinds — open triangles, yield hinds — filled triangles, immature stags — open circles, mature stags — closed circles.



**Fig. 2**—(1) Optimal herd structure (stags — black; hinds — grey; calves — white) predicted on the sporting estate under sole ownership with representative trophy pricing of Table 1, in comparison with herd structures reported at sites across the Highlands; (2) Cairngorms 2000/2001, (3) East Grampians 1994/1995, (4) Monadhliaths 1998/1999, (5) South Ross 1995/1996, (6) West Ross 1998/1999, (7) Glenfishie Estate 1967/1968, (8) Letterewe Estate 1997/1998.

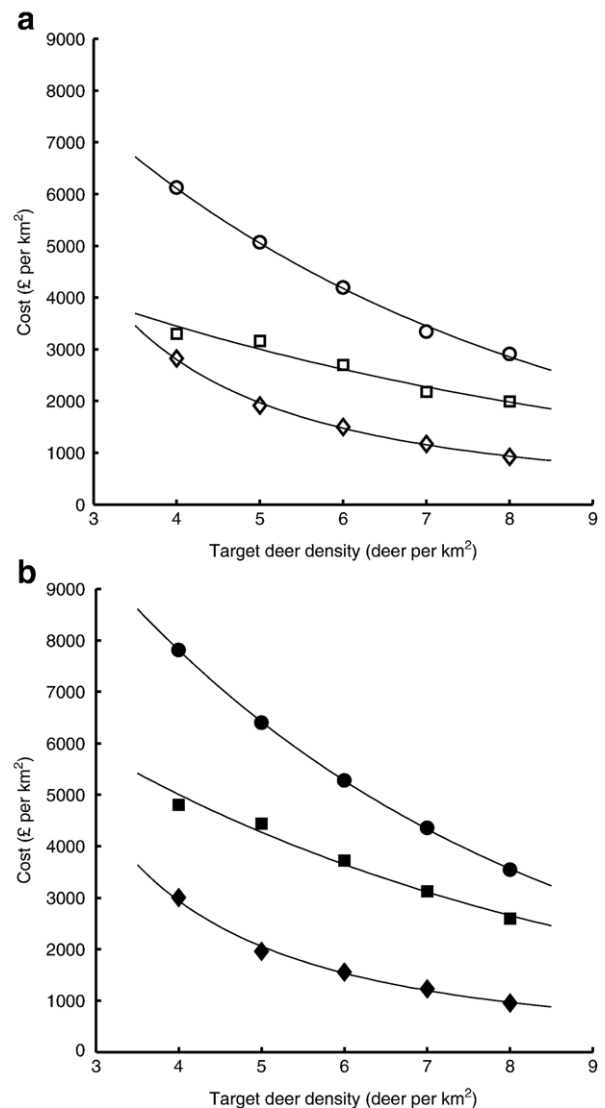
estate where management is constrained to achieve a stag cull in excess of the profit maximising level. The small reduction in optimum density from 21 to 20 deer per km<sup>2</sup> when representative trophy values are introduced arises because survivorship in stags, which under these conditions generate the majority of profits, falls more rapidly than that in hinds as population density increases. Densities of c. 20 deer per km<sup>2</sup> are common throughout the Highlands (Deer Commission for Scotland, 2003).

The optimal herd structure predicted under sole ownership with representative trophy values, with or without constraints on the stag cull, (35% stags, 47% hinds 18% calves; hind:stag ratio 1.34:1) is very similar to that observed across the Highlands (typical hind:stag ratio 1.33:1) (Fig. 2) (Deer Commission for Scotland, 2001, 2002, 2003; Milner et al., 2002; Mitchell et al., 1986). The comparison suggests that the management prescription of the model provides a reasonable approximation to observed practice. Management prescriptions within the ecological literature advocate hind:stag ratios of between 0.6:1 and 1.09:1 in the managed herd, but these disregard the impact of stock depletion on culling cost.

The gross value of a culled mature stag is elevated to more than six times that of a culled mature hind by trophy revenues. The consequent disparity in gross value between stags and hinds exerts a strong influence over the structure of the optimally managed herd (Table 2). The comparisons of Fig. 2 indicate that this disparity in value between stags and hinds is of central importance in practical deer management since it underlies hind:stag ratios which match observed practice. Disparity in value could arise directly from trophy values, or as a consequence of owners placing a substantially

higher subjective value on trophy stags because trophy stalking for family, friends and business acquaintances is a prime motivation for their ownership of the estate.

Once trophy values are in place, profitability is insensitive to modest self-imposed constraints on the annual cull of mature stags, provided that stalking effort is adjusted accordingly (Table 2). This may explain why professional stalkers typically express strong reservations to proposed reductions in the stag cull (Bullock, 1999). Even the maximised stalking profits of Table 2 are, however, insufficient to cover the opportunity cost of land ownership (at  $\delta=5\%$ ) (Wightman and Butterfield, 2000), which accords with many estate owners' view of deer stalking as 'an expensive hobby' (Milner et al., 2002). This suggests that many estate owners may derive



**Fig. 3**—Management costs (total cost — circles; maintenance cost — squares; reduction cost — diamonds) on the woodland restoration site, under (a) sole ownership in the absence of immigration, and (b) when a neighbouring sporting estate maintains its herd at 20 deer per km<sup>2</sup> and density-dependent emigration of immature stags can occur between the properties. ( $\delta=5\%$  in both cases)

**Table 3 – Optimal management outcomes in the steady state on the sporting estate with net emigration of immature stags to a neighbouring woodland restoration site where deer are maintained at a population density of  $D_{WR}$**

	Benchmark under sole ownership with no emigration	$D_{WR}=15$ deer per km <sup>2</sup>	$D_{WR}=10$ deer per km <sup>2</sup>	$D_{WR}=5$ deer per km <sup>2</sup>
Annual profit (£ per km <sup>2</sup> )	241	229	215	205
Stalking effort (stalkers per 100 km <sup>2</sup> )	1.08	1.04	0.98	0.92
Population density (deer per km <sup>2</sup> )	20	20	20	20
Mature stag cull (mature stags per km <sup>2</sup> )	0.82	0.78	0.73	0.69
Net emigration (immature stags per km <sup>2</sup> )	0	0.10	0.20	0.28
Herd structure: stags/hinds/calves (%)	36/47/17	35/48/17	33/49/18	33/49/18
Hind to stag ratio	1.30:1	1.37:1	1.50:1	1.51:1

utility in excess of the financial rewards from stalking trophy stags on their estate. The model’s ability to depict management which is driven by a requirement to maintain stag culls at ‘traditional’ levels is helpful in this situation as the utility maximising behaviour of many owners in these circumstances is enacted by selecting the size of the trophy stag cull on their estate.

**3.2. The woodland restoration site**

Sole ownership is also assumed as a benchmark for the woodland restoration site. The resultant costs as target deer density varies between 4 and 8 deer per km<sup>2</sup> are shown in Fig. 3(a).

The deer management costs incurred at the woodland restoration site are considerable. For comparison, the annual cost of maintaining a red deer density of 5 deer per km<sup>2</sup> at the restoration site is £308 per km<sup>2</sup>, some £68 per km<sup>2</sup> higher than the steady-state annual profit generated from stalking on the sporting estate, both results under sole ownership. These costs are, however, small in comparison with the very substantial net public benefit which has been shown to accrue from the restoration of native woodlands in the Scottish Highlands, £21,600–£38,200 per km<sup>2</sup> annually (MacMillan and Duff, 1998). Maintenance cost exceeds the cost of population reduction in all cases, although the minimised cost of population reduction rises rapidly as target deer density is reduced. These results suggest that considerable savings could be made if locations could be identified where site-specific conditions might permit native woodland to regenerate in the presence of modest densities of red deer.

**3.3. An adjacent estate and woodland restoration site with emigration between the properties**

When the sporting estate neighbours a woodland restoration site which maintains its resident deer density below 20 deer per km<sup>2</sup>, the productivity of the estate herd in respect of mature stags falls because a proportion of immature stags now emigrate to the restoration site each year. This reduces the optimal mature stag cull (Table 3), even though the structure of the herd is adjusted (hind to stag ratio rises from 1.3: 1 to in excess of 1.5: 1) in an attempt to compensate. When deer density on the restoration site is reduced to 5 deer per km<sup>2</sup>, annual profit, stalking effort and the cull of mature stags on the adjacent estate fall by 15%, 15% and 17%, respectively, compared with the baseline case under sole ownership without emigration (Table 3).

At the woodland restoration site, net immigration from the estate has only a modest impact on management cost during the population reduction phase, but the annual cost of maintaining resident deer density at 5 deer per km<sup>2</sup> increases by 44% from £302 per km<sup>2</sup> to £435 per km<sup>2</sup> (Fig. 3(b) and Table 4). Both parties thus suffer as a consequence of deer movement between the neighbouring sites. The underlying cause is the disparity in deer density which results from the incompatible management objectives at the two sites, since this difference in deer density drives emigration/immigration between the adjacent properties.

Conflict will inevitably arise in this situation, because the net public benefit which accrues from the regenerating native woodland is reduced by increased maintenance costs, and profits on the privately-owned sporting estate are reduced as a consequence of that public provision.

**3.4. An incentive to modify management**

Ecological imperatives dictate that deer density on the restoration site cannot be changed if woodland restoration is to be successful. Deer density on the estate however arises as the steady-state solution to the optimisation problem of Eq. (4), and so could potentially change if an appropriate incentive was introduced. Under current property rights, culls on the estate can only be increased, and the disparity in deer density between the two properties thus reduced, at the behest of the estate owner. Since the increase in maintenance cost (£ per km<sup>2</sup>) on the restoration site exceeds the reduction in profit (£ per km<sup>2</sup>) on the estate in the two-site model (Table 3), it is pertinent to consider whether an incentive in the form of a bonus payable to the estate if resident deer density is held below a given threshold might prove effective in reducing the disparity in deer density between the two properties.

The bioeconomic model is modified to examine how three separate indicative levels of bonus influence deer management on the sporting estate. Eq. (4) again describes the basic optimisation problem, but now low, medium and high levels of bonus payment are offered on a sliding scale to augment estate profits in return for reducing deer density (Fig. 4). The estate is assumed adjacent to a woodland restoration site where resident deer density is maintained at 5 deer per km<sup>2</sup>, and immature stags are again free to move between the two properties. In accordance with current property rights, the

**Table 4 – Outcomes on the sporting estate and neighbouring woodland restoration site when the bonus levels of Fig. 4 are offered for reductions in resident deer density on the estate**

	Benchmark under sole ownership with no emigration	Benchmark with emigration but without bonus payment	Emigration with low level of bonus on offer <sup>a</sup>	Emigration with medium level of bonus on offer <sup>a</sup>	Emigration with high level of bonus on offer <sup>a</sup>
<i>On the estate</i>					
Annual profit [including any bonus payment] (£ per km <sup>2</sup> )	241	205	241	247	319
Stalking effort (stalkers per 100 km <sup>2</sup> )	1.08	0.92	1.06	1.14	1.52
Population density (deer per km <sup>2</sup> )	20	20	18	17	16
Net emigration (immature stags per km <sup>2</sup> )	0	0.28	0.252	0.232	0.196
Hind to stag ratio	1.30:1	1.51:1	1.23:1	1.22:1	1.14:1
Incentive payment received (£ per km <sup>2</sup> )	0	0	41	57	153
<i>On the woodland restoration site</i>					
Stalking effort for maintenance (stalkers per 100 km <sup>2</sup> )	3.08	4.35	4.14	4.09	3.91
Annual maintenance cost (£ per km <sup>2</sup> )	302	435	413	407	388
<i>Across both sites combined</i>					
Joint stalking effort (stalkers per 100 km <sup>2</sup> )	4.16	5.27	5.20	5.23	5.43

<sup>a</sup> These results are quoted for year 15 of a 25 year planning horizon for which the stated bonus is on offer.

estate is free to accept the bonus only insofar as acceptance will increase total profits over the planning horizon. The bonus is offered over a 25 year timespan to match a 5 year population reduction phase followed by a 20 year population maintenance phase on the neighbouring restoration site. Initial deer density on the estate is assumed to be 20 deer per km<sup>2</sup>, the benchmark steady-state level under sole ownership. Outcomes with the various levels of bonus on offer are shown in Table 4.

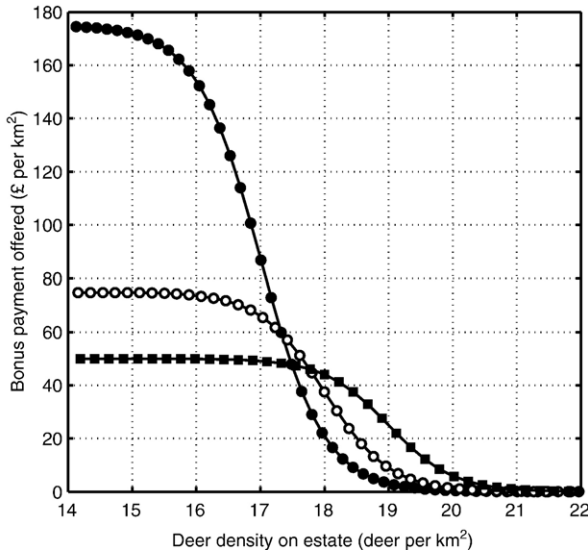
The bonus payment has the desired effect: deer densities on the estate are lowered and net emigration to the woodland restoration site reduces. Density reductions on the estate are only modest however and maintenance costs at the restoration site do not reduce sufficiently to cover the necessary incentive payments (Table 4).

Incentive payments with any of the proposed bonuses in place are, however, sufficient to restore estate profits to the benchmark level under sole ownership in the absence of emigration. With a bonus in place, the estate owner would no longer incur a private cost whilst the neighbouring woodland restoration site generated a public benefit. A third party might therefore consider funding the bonus payments to reduce conflict and to encourage a modest reduction in deer density with an accompanying adjustment of herd structure towards parity between stags and hinds (which would ease subsequent population management for a harem-breeder like red deer). Employment levels across both sites only increase when the highest level of bonus is offered (Table 4), however, making an intervention of this type by an agency of government unlikely.

These results suggest that although management on sporting estates could potentially be modified by introducing bonus payments for reductions in deer density, only modest reductions in density would actually be achieved by such schemes if estate profits were to remain at their benchmark level. The deer densities (c. 16 deer per km<sup>2</sup>) produced with incentives of the relevant level in place would still be too high to allow native tree species to regenerate, or to mitigate the impacts of grazing or trampling damage on the majority of sites (Staines et al., 1995).

Also, economic incentives which act on profit will exert little or no influence over the management behaviour of those estate owners who impose an overriding requirement to maintain the stag cull at traditional levels. Where the traditional stag cull is reasonably close to the profit maximising stag cull, the modelling approach used here is unable to distinguish between outcomes which arise from profit maximising behaviour and those which result from a binding constraint to maintain the stag cull at traditional levels.

This analysis suggests that the apparent rapid increase in marginal culling cost with falling population size will act alongside a binding preference, on the part of at least some estate owners, for the traditional stag cull to prevent incentive-based schemes from affecting substantial reductions in red deer density in the Highlands under existing property rights. An adjustment of property rights to enable innovative approaches such as the introduction of tradeable culling obligations which was proposed recently by MacMillan (2004) may prove a more effective way forward. However,



**Fig. 4**– Three forms of bonus payment offered in return for reductions in resident deer density on the sporting estate. These are termed low (filled squares), medium (open circles) and high (filled circles) levels of incentive in the text and Table 4.

since such an adjustment would itself be controversial, red deer management in the Scottish Highlands appears likely to remain a contentious issue for some time to come.

**4. Conclusion**

We have used a novel implementation technique to apply a highly structured bioeconomic model to analyse red deer management in Scotland. The model produced results which accord closely with the population densities and herd structures typically observed on sporting estates across the Highlands. For profit maximisation under sole ownership, or for cost minimisation whilst adhering to a traditional stag cull, the optimal balance between the marginal cost of culling and population performance is achieved at high deer densities (c. 20 deer per km<sup>2</sup>), and, with representative trophy values in place, or where there is a strong subjective valuation in favour of trophy stags, the optimal herd structure is biased strongly towards hinds. We also considered management on a woodland restoration site and found that the costs incurred in maintaining deer density at a reduced level (c. 5 deer per km<sup>2</sup>) for a sufficient period to allow regenerating native woodland to establish are substantial.

Emigration/immigration of immature stags between an adjacent estate and woodland restoration site in response to the disparity in hind densities on the two properties has been shown to have unwelcome cost implications for both parties. An incentive in the form of a bonus paid to sporting estates in return for making a reduction in resident deer density has been shown to modify estate management in the desired fashion, but only modest changes in deer density would be produced by such a mechanism. Those changes would be insufficient to deliver widespread regeneration of

native woodland. Furthermore, the total number of stalkers employed on the estate and restoration site in combination would not increase unless bonus payments were instituted which would increase estate profits well beyond their benchmark level under sole ownership in the absence of emigration. This result is again due, fundamentally, to the rapid increase in the marginal cost of culling as the deer population size reduces.

The role which the balance between culling cost and population performance plays in determining the optimum population density is central to the outcome of these analyses. Population performance is well established in the ecological literature. Culling cost is little researched by comparison. Further empirical investigation of deer culling as a production process would therefore appear very worthwhile.

Similar outcomes result when an overriding objective to maintain the stag cull at traditional levels acts alongside a subjective valuation which is biased strongly towards trophy stags. Further research into the attitudes and motivations which underlie such preferences would inform the development of innovative, inclusive and effective policies for managing red deer in the Highlands.

The implementation method presented here for solving highly structured bioeconomic optimisation problems which feature differing degrees of overlap between state and control variables is novel in the literature. This approach could prove helpful for examining other problems in which spatial or temporal resource dynamics, financial outcomes or management stratification require highly structured representation within a bioeconomic model.

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**Appendix A. Optimisation method**

Eq. (4) is solved in a current value Hamiltonian setting. The solution equations in generic form are as follows.

The maximum principle equations for each management class  $m = C \dots M^M$  yield;

$$\frac{\partial \pi(\cdot)}{\partial K_t^m} = - \left( \rho \lambda_{t+1}^{HC} \frac{\partial H_{t+1}^C}{\partial K_t^m} + \rho \lambda_{t+1}^{H^Y1} \frac{\partial H_{t+1}^{Y1}}{\partial K_t^m} + \dots + \rho \lambda_{t+1}^{M^M} \frac{\partial M_{t+1}^M}{\partial K_t^m} \right) = - \rho \cdot \sum_{b=HC}^{b=M^M} \lambda_{t+1}^b \cdot \frac{\partial b_{t+1}}{\partial K_t^m} \forall t = 0 \dots (T - 1) \tag{7}$$

where  $b$  denotes generic biological class,  $\pi$  denotes profit ( $\sum_{b=HC}^{b=M^M} (P_V \cdot W^b + P_A^b) K_t^b - c \sum_{m=C}^{m=M^M} E_t^m$ ) as indicated in Eq. (4),  $\lambda$  denotes shadow price (indexed by biological class  $b$ ), and other symbols are as defined in Table 1.

The co-state equations for each biological class  $b=H^C \dots M^M$  are;

$$\begin{aligned} \lambda_t^B &= \frac{\partial \mathcal{H}}{\partial B_t} + \rho \cdot \lambda_{t+1}^B \\ &= \frac{\partial \pi(\cdot)}{\partial B_t} + \rho \cdot \lambda_{t+1}^{H^C} \cdot \frac{\partial H_{t+1}^C}{\partial B_t} + \rho \cdot \lambda_{t+1}^{H^Y} \cdot \frac{\partial H_{t+1}^Y}{\partial B_t} + \dots + \rho \cdot \lambda_{t+1}^{M^M} \cdot \frac{\partial M_{t+1}^M}{\partial B_t} \\ &= \frac{\partial \pi(\cdot)}{\partial B_t} + \rho \cdot \sum_{b=H^C}^{b=M^M} \lambda_{t+1}^b \cdot \frac{\partial b_{t+1}}{\partial B_t} \quad \forall t = 0 \dots (T - 1) \end{aligned} \tag{8}$$

where  $B$  denotes the specific biological class to which the calculated shadow price refers and  $\mathcal{H}$  denotes the current value Hamiltonian (whereas  $H$  refers to a class of hinds within the biological or management classifications).

An iterative engineering technique (Noton, 1972) is modified as follows to produce a structured management prescription which optimises the discounted stream of profits of Eq. (4) under the requisite constraints. From a known starting point, the structured population is projected across the planning horizon using the density-dependent population model and an initial (guessed) structured culling prescription. The marginal costs and benefits of culling are then evaluated in each year of the planning timeframe. This requires that the marginal value of a live animal of each biological class (its shadow price) is established in each year. These shadow prices are calculated using the co-state equations (Eq. (8)) once terminal shadow prices had been anchored, nominally, at the gross value of a live animal of the requisite class. Knowing the population size, the proposed culls and the shadow prices, the marginal costs and benefits of culling can then be determined in each timestep using the maximum principle (Eq. (7)). Culling levels for each timestep across the planning horizon can then be adjusted appropriately to move the solution closer to ‘marginal culling balance’ (which satisfies the Maximum Principle conditions of Eq. (7)) in each timestep. With these adjusted culls in place, population size is then again projected across the management timeframe, and culling balance checked once more. This sequence is repeated iteratively until the system converges on the optimal solution in which the marginal costs and benefits of culling are balanced in each and every timestep, to the requisite precision. The solution thus fulfils the Maximum Principle conditions and the co-state equations simultaneously within the constraints imposed by population dynamics and any relevant restrictions on culling action or terminal population density.

In the sporting estate model, initial population size and structure typically influence the first 5–7 years of the optimal management prescription, and terminal shadow prices the final 10–12 years, over a 50 year planning horizon (Fig. 1). Between these boundaries, the management prescription provides the steady state profit-maximising solution.

### Appendix B. Population dynamics

The deterministic, discrete-time, density-dependent population model used here is a simplified version of a detailed model of red deer population dynamics within the ecological literature (Partridge et al., 1998; Trenkel, 2001; Trenkel et al., 2000).

The model uses 14 biological classes which differ significantly in one or more of the following characteristics; density-dependent survivorship, density-dependent fecundity, carcass weight and trophy value.

For stags (denoted  $M$  (for males)) from yearlings ( $M^1$ ) to 4-year olds ( $M^4$ ), population size in year  $t+1$  is given by;

$$M_{t+1}^a = (M_t^{a-1} - K_t^{M^a}) \cdot S_t^{M^a} \tag{9}$$

where  $a$  denotes age in years (1, 2, 3 or 4),  $K$  denotes cull size and  $S$  denotes density-dependent survivorship, (both indexed by biological class).

For mature stags (superscript  $M$ ) aged 5 or more;

$$M_{t+1}^M = \left( [M_t^4 + M_t^M] - K_t^{M^M} \right) \cdot S_t^{M^M} \tag{10}$$

The population difference equations for hinds (denoted  $H$ ) are complicated by the significant difference in fecundity ( $F$ ) between milk (superscript  $M$ ) and yield (superscript  $Y$ ) animals, together with variation in fecundity by age class in both groups.

Generally, milk hind population sizes in year  $t+1$  are given by;

$$H_{t+1}^{Ma} = \left( [H_t^{Ya-1} \cdot F_t^{H^{Ya-1}} + H_t^{Ma-1} \cdot F_t^{H^{Ma-1}}] - K_t^{H^{Ma}} \right) \cdot S_t^{H^{Ma}} \tag{11}$$

thus, next year’s milk hinds of age  $a$  are this year’s hinds of censused age  $(a-1)$  (both milk and yield) which gave birth to a calf and then escaped the cull and survived the winter. Similarly, yield hind population sizes in year  $t+1$  are given by;

$$H_{t+1}^{Ya} = \left( [H_t^{Ya-1} \cdot (1 - F_t^{H^{Ya-1}}) + H_t^{Ma-1} \cdot (1 - F_t^{H^{Ma-1}})] - K_t^{H^{Ya}} \right) \cdot S_t^{H^{Ya}} \tag{12}$$

Next year’s yields of age  $a$  being this year’s hinds (both milk and yield) of age  $(a-1)$  which did not produce a calf, escaped the cull and survived the winter. The uppermost ‘mature’ age class in both yields and milks is accommodated by the mechanism shown in Eq. (10).

The hind and stag calf populations ( $H^C$  and  $M^C$  respectively) are determined by;

$$H_{t+1}^C = \left( \left[ \sum_{a=1}^{a_{\max}} H_t^{Ya} \cdot F_t^{H^{Ya}} + \sum_{a=2}^{a_{\max}} H_t^{Ma} \cdot F_t^{H^{Ma}} \right] \cdot B_H - K_t^{H^C} \right) \cdot S_t^{H^C} \tag{13}$$

$$M_{t+1}^C = \left( \left[ \sum_{a=1}^{a_{\max}} H_t^{Ya} \cdot F_t^{H^{Ya}} + \sum_{a=2}^{a_{\max}} H_t^{Ma} \cdot F_t^{H^{Ma}} \right] \cdot (1 - B_H) - K_t^{M^C} \right) \cdot S_t^{M^C} \tag{14}$$

where  $B_H$  denotes the proportion of calves born female (taken to be 0.5 throughout our analyses). When a management class comprises more than a single biological class (Table 1), management class culls ( $K_t^M$ ) are split between constituent biological classes in direct proportion to population size. This produces culls at full biological resolution ( $K_t^b$ ) for insertion in Eqs. (9)–(14).

Fecundity ( $F$ ) is modelled as a logistic function of body weight (which varies with age and breeding status (Mitchell and Brown,

1974)), with the weight at median fecundity varying linearly with population density (Albon et al., 1983; Trenkel, 2001; Trenkel et al., 2000). Survivorship ( $S$ ) is modelled as a logistic function of age and population density (Trenkel, 2001; Trenkel et al., 2000). Initial settings for the parameters which define density dependence in survivorship and fecundity were obtained from the referenced publications.

Survivorship typically shows minimal response to increasing population size in all biological classes except stag calves, hind calves and yearling stags until approximately 75–80% of carrying capacity is reached, whereupon it decreases dramatically. Fecundity in yield hinds aged three and above appears virtually insensitive to population density, whereas fecundity in all age classes of milk hind typically displays strong density dependence once population density exceeds 55–65% of carrying capacity (Trenkel, 2001; Trenkel et al., 2000).

## REFERENCES

- Albon, S.D., Mitchell, B., Staines, B.W., 1983. Fertility and body-weight in female red deer—a density-dependent relationship. *Journal of Animal Ecology* 52 (3), 969–980.
- Beddington, J.R., 1973. The exploitation of Red deer (*Cervus elaphus* L.) in Scotland, PhD. Thesis, University of Edinburgh, Edinburgh UK.
- Beddington, J.R., Watts, C.M.K., Wright, W.D.C., 1975. Optimal cropping of self-reproducible natural resources. *Econometrica* 43 (4), 789–802.
- Bjørndal, T., Lindroos, M., 2004. International management of north-sea herring. *Environmental and Resource Economics* 29, 83–96.
- Buckland, S.T., Ahmadi, S., Staines, B.W., Gordon, I.J., Youngson, R.W., 1996. Estimating the minimum population size that allows a given annual number of mature red deer stags to be culled sustainably. *Journal of Applied Ecology* 33 (1), 118–130.
- Buckland, S.T., Trenkel, V.M., Elston, D.A., Partridge, L.W., Gordon, I.J., 1998. A decision support system for red deer managers in Scotland. In: Goldspink, C.R., King, S., Putman, R.J. (Eds.), *Population Ecology, Management and Welfare of Deer*. Manchester Metropolitan University and Universities Federation for Animal Welfare.
- Bullock, C.H., 1999. Environmental and strategic uncertainty in common property management: the case of Scottish red deer. *Journal of Environmental Planning and Management* 42 (2), 235–252.
- Callander, R.F., MacKenzie, N.A., 1991. *The Management of Wild Red Deer in Scotland*. Rural Forum (Scotland), Perth, UK.
- Clutton-Brock, T.H., Albon, S.D., 1989. *Red Deer in the Highlands*. Blackwell Scientific, Oxford, UK.
- Clutton-Brock, T.H., Loneragan, M.E., 1994. Culling regimes and sex-ratio biases in highland red deer. *Journal of Applied Ecology* 31 (3), 521–527.
- Clutton-Brock, T.H., Guinness, F.E., Albon, S.D., 1982. *Red Deer — Behavior and Ecology of the Two Sexes*. Edinburgh University Press, Edinburgh, UK.
- Clutton-Brock, T.H., Major, M., Guinness, F.E., 1985. Population regulation in male and female red deer. *Journal of Animal Ecology* 54 (3), 831–846.
- Clutton-Brock, T.H., Rose, K.E., Guinness, F.E., 1997. Density-related changes in sexual selection in red deer. *Proceedings of the Royal Society of London. Series B- Biological Sciences* 264, 1509–1516.
- Clutton-Brock, T.H., Coulson, T.N., Milner-Gulland, E.J., Thomson, D., Armstrong, H.M., 2002. Sex differences in emigration and mortality affect optimal management of deer populations. *Nature* 415 (6872), 633–637.
- Conover, M., 2002. *Resolving Human-wildlife Conflicts: The Science of Wildlife Damage Management*. CRC Press, Boca Raton.
- Deer Commission for Scotland, 2001. *Annual Report 1999–2000*. Deer Commission for Scotland, Inverness, UK.
- Deer Commission for Scotland, 2002. *Annual Report 2000–2001*. Deer Commission for Scotland, Inverness, UK.
- Deer Commission for Scotland, 2003. *Annual Report 2001–2002*. Deer Commission for Scotland, Inverness, UK.
- Department of Trade and Industry, 2003. *National Minimum Wage*. HMSO, London.
- Hunt, J.F., 2003. *Impacts of Wild Deer in Scotland — How Fares The Public Interest?* WWF Scotland and RSPB Scotland, Aberfeldy, Scotland, UK.
- Inland Revenue, 2003. *E12(2003) PAYE and NICs Rates and Limits for 2003–2004*. HMSO, London.
- MacGregor, B.D., Stockdale, A., 1994. Land use change on Scottish highland estates. *Journal of Rural Studies* 10, 301–309.
- MacMillan, D.C., 2004. Tradeable hunting obligations — a new approach to regulating red deer numbers in the Scottish Highlands? *Journal of Environmental Management* 71, 261–270.
- MacMillan, D.C., Duff, E.I., 1998. Estimating the non-market costs and benefits of native woodland restoration using the contingent valuation method. *Forestry* 71 (3), 247–259.
- McKelvie, C., 1991. The battle for Scotland. *Shooting Times* 9–15 (May 1991).
- Miller, G.R., Cummins, R.P., Hester, A.J., 1998. Red deer and woodland regeneration in the Cairngorms. *Scottish Forestry* 52 (1), 14–20.
- Milner, J.M., Alexander, J.S., Griffin, A.M., 2002. *A Highland Deer Herd and its Habitat*. Red Lion House, Letterewe Estate, Achnasheen, Ross-shire, UK.
- Milner-Gulland, E.J., 2001. The exploitation of spatially structured populations. In: Reynolds, J.D., Mace, G.M., Robinson, J.G. (Eds.), *Conservation of Exploited Species*. Cambridge University Press, Cambridge, UK.
- Milner-Gulland, E.J., Coulson, T.N., Clutton-Brock, T.H., 2000. On harvesting a structured ungulate population. *Oikos* 88 (3), 592–602.
- Mitchell, B., Brown, D., 1974. The effects of age and body size on fertility in female red deer (*Cervus elaphus* L.). *Proceedings of the International Congress of Game Biologists* 11, 89–98.
- Mitchell, B., Staines, B.W., Welch, D., 1977. *Ecology of Red Deer — A Research Review Relevant to their Management in Scotland*. Natural Environment Research Council, Banchory, UK.
- Mitchell, B., McCowan, D., Parish, T., 1986. Performance and population—dynamics in relation to management of Red Deer *Cervus-elaphus* at Glenfeshie, Inverness-Shire, Scotland. *Biological Conservation* 37 (3), 237–267.
- Noton, M., 1972. *Modern Control Engineering*. Pergamon Press Inc., New York.
- Palmer, S.C.F., Truscott, A.-M., 2003. Browsing by deer on naturally regenerating Scots pine (*Pinus sylvestris* L.) and its effects on sapling growth. *Forest Ecology and Management* 182, 31–47.
- Parkes, C., Thornley, J., 2000. *Deer: Law and Liabilities*. Swan Hill Press, Shrewsbury, UK.
- Partridge, L.W., Trenkel, V.M., Gordon, I.J., Buckland, S.T., Elston, D.A., Milne, J.A., Birch, C.P.D., Forster, J., Mann, A.D., McLeod, J., 1998. *HillDeer: The Red Deer Decision Support System*. Macaulay Land Use Research Institute/Biomathematics and Statistics Scotland, Aberdeen, UK.
- Ramsay, P., 1997. *Revival of the Land*. Scottish Natural Heritage, Perth, UK.
- Red Deer Commission, 1983–1985. *Annual Report*. Red Deer Commission, Inverness, UK.
- Scottish Natural Heritage, 1994. *Red Deer and the Natural Heritage*. Scottish Natural Heritage, Perth, UK.
- Sibbald, A., 2001. Using GPS to track wild red deer stags. *Deer* 11 (10), 524–529.

- Staines, B.W., 1978. The dynamics and performance of a declining population of Red deer (*Cervus elaphus*). *Journal of Zoology* (London) 184, 403–419.
- Staines, B.W., Balharry, R., Welch, D., 1995. The impact of red deer and their management on the natural heritage in the uplands. In: Thompson, D.B.A., Hester, A.J., Usher, M.B. (Eds.), *Heaths and Moorlands: Cultural Landscapes*. Scottish Natural Heritage, HMSO, Edinburgh, UK.
- Trenkel, V.M., 2001. Exploring red deer culling strategies using a population-specific calibrated management model. *Journal of Environmental Management* 62, 37–53.
- Trenkel, V.M., Partridge, L.W., Gordon, I.J., Buckland, S.T., Elston, D.A., 1998. The management of red deer on Scottish open hills: results of a survey conducted in 1995. *Scottish Geographical Magazine* 114 (1), 57–62.
- Trenkel, V.M., Elston, D.A., Buckland, S.T., 2000. Fitting population dynamics models to count and cull data using sequential importance sampling. *Journal of the American Statistical Association* 95 (450), 363–374.
- Wigan, M., 1993. *Stag at Bay: The Scottish Red Deer Crisis*. Swan Hill Press, Shrewsbury, UK.
- Wightman, A., Butterfield, I., 2000. What price mountains? *The Scottish Mountaineer* 5.
- Wightman, A., Higgins, P., Jarvie, G., Nicol, R., 2002. The cultural politics of hunting: sporting estates and recreational land use in the Highlands and Islands of Scotland. *Sport in Society* 5 (1), 53–70.