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Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors

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Summary

1. Deer numbers have increased dramatically throughout Europe and North America over the last century, but empirical analyses of variation in harvesting and the influence of biological and cultural factors are lacking.

2. We examined trends in size and composition of red deer *Cervus elaphus* harvests over the last three to four decades in 11 European countries with contrasting deer productivity, management strategies and hunting traditions.

3. The harvest increased exponentially in all countries except Austria and Germany, where it was stable, and Poland, where it has declined in recent years. Harvest growth rates ranged from 0·009 in Austria to 0·075 in Sweden and depended on the management system and harvest composition, being negatively related to the proportion of females in the adult harvest.

4. Within four focal countries (France, Hungary, Norway and Scotland), there was considerable spatial variation in harvest growth rates. These tended to be higher in recently colonized areas than in traditional hunting areas and were often higher than the maximum possible population growth rate. Range expansion was an important component of the increase in total harvest in France and Scotland, but not in Hungary or Norway.

5. Harvest composition was available for seven countries, all of which showed a strong increase in the proportion of calves in the harvest. The sex ratio of the adult harvest was relatively stable, being strongly male-biased in Norway and marginally female-biased elsewhere. The proportion of males in the harvest was unrelated to trophy hunting objectives.

6. *Synthesis and applications*. Our study emphasizes that cultural aspects of management need to be accounted for, as well as biological factors, when interpreting the patterns of harvest growth and composition across Europe. Widespread sustained harvest growth has occurred, suggesting continued growth of deer populations with consequent social and economic impacts. Population control is therefore a major challenge for the future, currently hampered by inadequate population data and a decreasing number of hunters in some countries. Increasing the motivation of hunters to harvest female deer is one possible solution, although this may conflict with hunting traditions and economic considerations in some areas.

Key-words: deer management, exploitation, large herbivores, population dynamics, selective hunting, sustainable management, ungulates, wildlife cropping

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Introduction

The numbers of many deer species have increased dramatically throughout Europe and North America over the last century (Gill 1990; Clutton-Brock & Albon 1992; McShea, Underwood & Rappole 1997; Côté *et al.* 2004; Gordon, Hester & Festa-Bianchet 2004), as a result of both increases in density and range expansion. There are a number of causes, both direct and indirect, with no single explanation applicable to all countries or species (Fuller & Gill 2001). Factors unrelated to cervid management include increased availability of forage resulting from changes in land use (Ahlén 1975), agricultural and silvicultural practises (Mysterud *et al.* 2002) and the climate (Mysterud *et al.* 2003). However, the direct management of cervids has also played a part. For example, protection from overhunting and poaching, the use of selective harvesting regimes (Langvatn & Loison 1999; Solberg *et al.* 1999), supplementary feeding in winter (Peek *et al.* 2002) and reintroduction programmes (McShea, Underwood & Rappole 1997; Mattioli *et al.* 2001; Leduc & Klein 2004) have all contributed to rising numbers. As a result, in many areas management objectives are beginning to change from species protection to population control (Buckland *et al.* 1996; Brown *et al.* 2000; Côté *et al.* 2004; Gordon, Hester & Festa-Bianchet 2004).

Red deer *Cervus elaphus* L. are widely distributed across Europe (Fig. 1; Koubek & Zima 1999) and have increased in both abundance and geographical range in recent decades (Gill 1990; Csányi 1992; Mattioli *et al.* 2001; Clutton-Brock, Coulson & Milner 2004), although reliable quantitative data on population sizes are generally lacking. Red deer are primarily found in forest or woodland-edge habitats, often associated with land of low productivity, including open moorland in Scotland. The widespread distribution and large body size of red deer makes it an important game species (Koubek & Zima 1999). Hunting rights in Europe are generally held by the landowner (Gill 1990), in contrast to North America where hunting is accessible to a wide sector of the general public (O'Gara 2002). Consequently hunting in Europe tends to be limited to landowners (state or private) and/or their associates and paying leaseholders or trophy-hunting clients. The size of red deer harvests has increased considerably in many European countries over recent decades (Gill 1990).

Harvesting represents a major source of mortality in many North American elk *Cervus elaphus* L. populations where predators are absent (Ballard *et al.* 2000; Biederbeck, Boulay & Jackson 2001; McCorquodale, Wiseman & Marcum 2003). While few empirical studies have documented this in Europe, it is also likely to be true for many red deer populations (Langvatn & Loison 1999), although predation may play a more significant role in some protected areas (Jedrzejewski *et al.* 2002). Consequently, selective harvesting is likely to influence strongly population composition, dynamics (Langvatn & Loison 1999; for moose Alces alces see Solberg *et al.* 1999) and genetics (Coltman *et al.* 2003). At the European scale, the basis for red deer management varies depending on cultural traditions and the environmental constraints of habitat and latitude (Bonenfant *et al.* 2004; Loe *et al.* 2005). We might therefore expect harvest rates, selectivity and composition to differ between countries, with consequences for population dynamics. However, it is currently not possible to address empirically how regional variation in selective harvesting regimes has affected population dynamics, as the required data simply do not exist for most red deer populations. In the absence of such data, we aimed to describe the main patterns in the size of the red deer harvest over the last three to four decades in 11 European countries with contrasting hunting objectives, management strategies and environmental conditions. In addition, we investigated trends in the composition of the harvest in seven of the countries and made a more in-depth analysis of spatial variation in four focal countries, France, Hungary, Norway and Scotland.

Harvest development is likely to follow general trends in population development (Forchhammer *et al.* 1998 and references therein), although often with a 1–2-year time-lag (Fryxell *et al.* 1991; Solberg *et al.* 1999). Harvest size is also influenced by policy and cultural factors, including harvesting strategies (Giles & Findlay 2004) and quotas, which explain some of the time lags (Solberg *et al.* 1999). We therefore also investigated the following predictions. (i) P1: harvest growth rates will be highest where deer populations are growing fastest. Consequently, we expect harvest growth rates to be lower in traditional deer hunting areas than in areas of recent colonization where lower densities and thus higher recruitment rates are likely (unless habitat differs markedly). (ii) P2: harvest growth rates will be lower with a higher proportion of adult females in the harvest because of the sensitivity of population growth to adult female survival (Gaillard, Festa-Bianchet & Yoccoz 1998), assuming a close link between population growth and harvest growth. (iii) P3: there will be positive covariation between harvest size, hunter numbers and size of red deer range. (iv) P4: a higher proportion of adult males relative to females will occur in the harvest in trophy-hunting cultures (Ginsberg & Milner-Gulland 1994).

Materials and methods

Annual statistics for the size of the total red deer harvest were obtained for Austria, Denmark, France, Germany, Hungary, Norway, Poland, Scotland, Slovenia, Sweden and Switzerland from national bodies in the respective countries (Table 1). The year of harvest was taken from the start of the hunting season. Harvest composition, in terms of the number of calves, adult (including yearling) males and females shot, were available for seven countries (Table 1). Data describing population size and structure were unfortunately unavailable for most of the countries studied. However, as our investigation was of variation at a continental scale, we assumed

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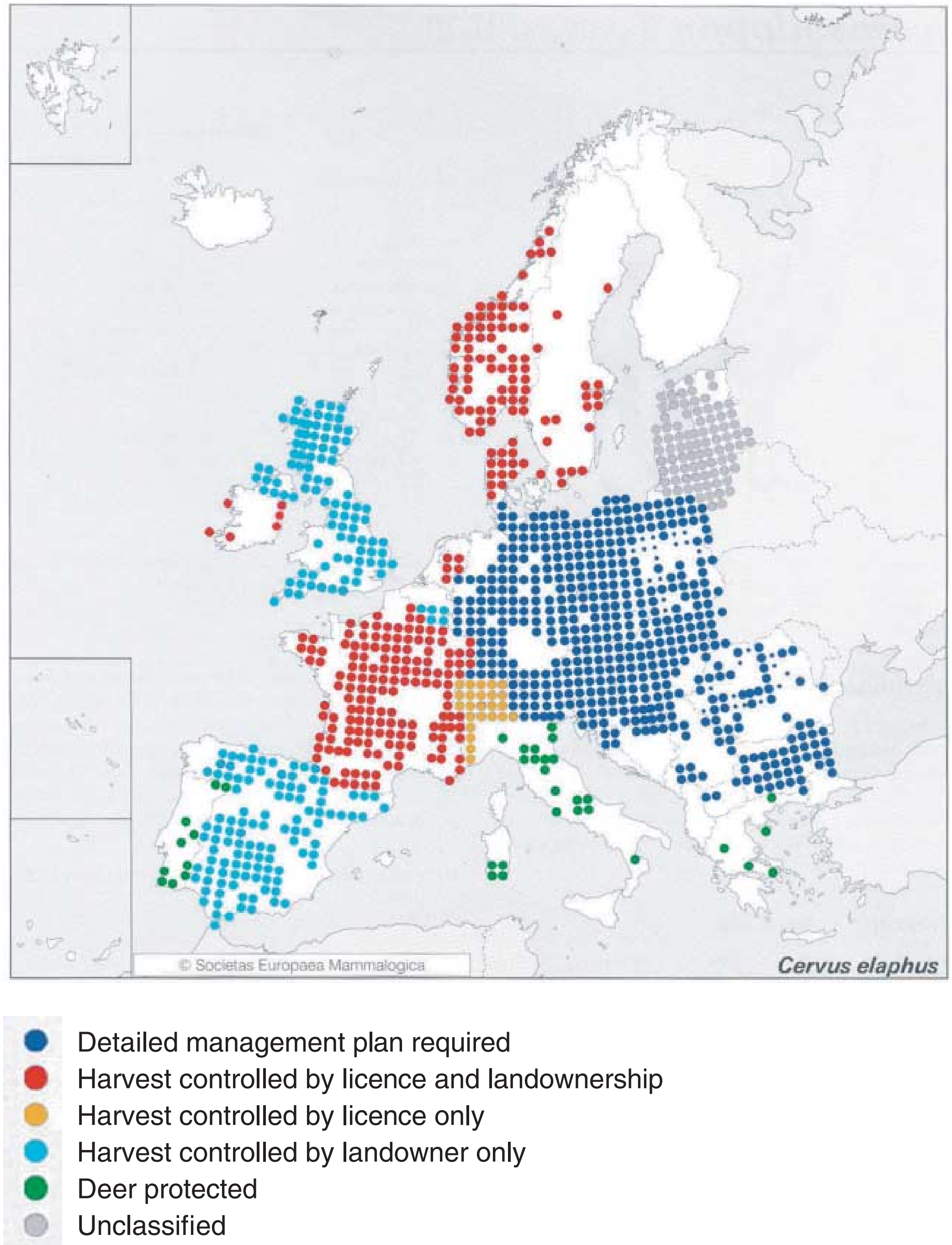

Fig. 1. Map of the current distribution of red deer across Europe by 50-km squares (Societas Europaea Mammalogica; Koubek & Zima 1999) showing management systems in each country, based on Gill (1990). The few small symbols represent presumed distribution from data collected before 1970.

the spatiotemporal variations in age and sex structure at smaller spatial scales would be dampened.

The number of hunters per capita in 2004 (FACE 2004) was used as an indicator of the strength of the hunting culture in each country, while the deer management system was classified according to the groupings identified by Gill (1990; Table 1). Overall hunting objectives representative of a given country were based on personal communications with experts. In recent years, objectives have been shifting towards population control in several countries (e.g. SNH 1994).

FOCAL COUNTRIES

A more detailed analysis of the spatial variation in harvest growth and composition was carried out at a regional level in France, Hungary, Norway and Scotland, which are representative of the main deer management systems in Europe. In France and Norway, hunting is regulated by a quota of licences issued by wildlife authorities to landowners or hunting-right holders (management system 2; Fig. 1). In Hungary, hunting-right holders (hunting clubs, state farms and forests) are

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Table 1. Description of hunting systems, harvest data and harvest growth rates from each study country

Country	Range†	Management system‡	Hunting objective	No. hunters (% of population)§	Hunting season (M: males; F: females)	Harvest data period (harvest composition)	Harvest growth rate, H_r (SD)	Probability $H_r > 0$	Proportion males in adult harvest (2002)	Proportion calves in harvest (2002)	Data source
Austria	34	1	Trophy, minimise forest damage	1·4	M: 01/08–31/12 F: 01/07–31/01¶	1965–2002 (1965–2002)	0·009 (0·066)	0·210	0·42	0·34	Zentralstelle Oesterreichischer Jagdverbaende
Denmark	15	2	Recreation, meat	3·2	M: 01/09–31/01 F: 01/10–31/01	1965–2002	0·042 (0·131)	0·030			Asferg & Olesen (2004)
France	155	2	Trophy, meat	2·3	15/11–31/01	1973–2002 (1983–2002)	0·056 (0·077)	< 0·001*	0·48	0·30	Office National de la Chasse et de la Faune Sauvage
Germany	113	1	Trophy, minimise forest damage	0·4	01/08–31/01††	1982–2002	0·012 (0·069)	0·230			Deutscher Jagdschutz-Verband
Hungary	34	1	Trophy, population control	0·5	01/09–31/01	1965–2002 (1969–2002)	0·050 (0·125)	0·010	0·36	0·39	Hungarian Game Management Database
Norway	66	2	Meat, recreation	4·8	10/09–15/11	1965–2002 (1977–2002)	0·062 (0·091)	< 0·001*	0·56	0·23	Statistics Norway
Poland	116	1	Trophy	0·3	M: 21/08–28/02 F: 01/09–15/01	1965–2002‡‡	0·029 (0·139)	0·148			Central Statistical Office, Warsaw¶¶
Scotland	41	4	Trophy, population control	1·3	M: 1/07–20/10 F: 21/10–15/02	1965–2002 (1965–2002)	0·031 (0·091)	0·024	0·48	0·14	Deer Commission for Scotland
Slovenia	7	1	Trophy, population control	2·0	M: 1/08–31/12 F: 1/09–31/12	1969–2002 (1969–2002)	0·041 (0·141)	0·052	0·46	0·44	Lovska Zveza Slovenije
Sweden	17	2	Recreation, meat	3·6	16/08–31/01	1965–2002	0·075 (0·216)	0·021			Svenska Jägareförbundet
Switzerland	16	1,3	Recreation, trophy, meat	0·4	01/09–31/01	1965–2002 (1965–2002)	0·035 (0·148)	0·082	0·57	0·19	Bundesamt für Umwelt, Wald und Landschaft

†Relative distributional range given as no. 50-km^2 occupied (Societas Europaea Mammalogica; Koubek & Zima 1999).
‡Management system as per Gill (1990) fig. 3·1, where 1: systems requiring detailed harvest plan; 2: systems where harvest is controlled by licence and land or hunting ground ownership; 3: system where harvest is controlled by licence only; 4: system where harvest is controlled by landowner only (Fig. 1).
§FACE (2004). Note data for Scotland not available so value for whole of UK is presented.
¶Season for yearlings begins 01/06, all dates vary ± 1 month between provinces.
††Season for yearling females 01/06–31/01, yearling males 01/06–28/02.
‡‡Missing data in 1977, 1986–89, 1991–93.
¶¶Statistical Yearbook of the Republic of Poland, Warsaw, 1965, 1968, 1970, 1975, 1981, 1985, 1997, 2002.
*H_r significantly greater than zero, assuming probability threshold of $P = 0{\cdot}0045$ after Bonferroni correction.

required to provide annual counts, detailed harvest plans and reports for an age- and sex-structured cull (management system 1; Fig. 1). In Scotland, individual landowners or groups of neighbouring landowners decide how many deer to hunt on their land (management system 4; Fig. 1). Further background information about the focal countries is given in Appendix S1 in the supplementary material.

French harvest data came from a total of 84 departments, ranging from 60 departments in 1973 to a peak of 81 in the late 1990s. Hungarian data came from the 19 counties, of which 13 had a red deer harvest in 1965 and all have harvested deer since 1979. In Norway, the number of municipalities harvesting deer increased from 93 in 1965 to 222 in 2002. The number of calves vs. adults in the harvest was available from 1966, with a full breakdown by age and sex from 1977. Scottish data came from the statutory cull returns for individual landholdings, grouped into blocks corresponding to Deer Commission for Scotland (DCS) counting areas. The number of blocks increased from 34 in 1965 to 74 in 2002. However, the total harvest was an underestimate because of a lag in reporting of shot animals on newly hunted landholdings (M. Daniels, personal communication). The total harvest within traditional red deer hunting areas was less subject to this bias. Red deer shot in commercial forestry plantations were included. The total number of hunting license holders per year (large and small game) in France (partial time series; Direction des Etudes et de la Recherche de l'ONCFS), Hungary (Hungarian Game Management Database) and Norway (from 1971; Statistics Norway) was used as an index of hunting effort, while the sum of areas of each region where harvesting occurred was used as an index of the red deer range in all focal countries.

STATISTICAL ANALYSES

Harvest growth rate

The harvest growth rate (H_r) was calculated for each country as the mean of the annual change in harvest size: $\log_n(h_{t+1}) - \log_n(h_t)$, where h_t is the size of the total harvest in year t. It is analogous to population growth rate (Caughley 1977), with which it appears to be positively correlated (S. Csányi & J.M. Milner, unpublished data), and as such is necessarily a temporary phenomenon. At a smaller spatial scale, harvest growth within focal countries was determined by calculating H_r for each region with at least 5 years harvest data. However, some regions had a zero harvest in years when no deer were culled, so 1 was added to enable natural logarithms to be taken (Sokal & Rohlf 1981). Regional H_r was therefore calculated as the average of $\log_n(h_{t+1} + 1) - \log_n(h_t + 1)$ for each region.

Comparison between countries

For each country, t-tests were used to assess whether H_r was significantly different from zero, making a Bonferroni correction for 11 tests (threshold P-value = 0·0045; Sokal & Rohlf 1981). Harvest growth rates were then compared between countries and management systems over time, fitting linear models using generalized least squares (GLS; see Appendix S2 in the supplementary material). These modelled both the mean and variance of the response variable (Pinheiro & Bates 2000) and allowed us to account for the observed unequal variances between countries (Bartlett's test, $T = 85{\cdot}98$, d.f. = 10, $P < 0{\cdot}001$) when comparing H_r. H_r was the response variable; year (covariable), either country (11-level factor) or management system (four-level factor), and the respective first-order interactions with year were entered as explanatory variables. The variances were allowed to differ independently according to the levels of the country factor. Finally, we checked the model adequacy, residual normality and homoscedasticity, against our data set graphically (Venables & Ripley 1999).

A similar procedure was used to investigate the influence of hunter numbers and range area (explanatory variables) on harvest size and harvest growth rate in the focal countries (excluding Scotland for analysis of hunter numbers). Here, ln(national harvest size) and H_r at the national scale were considered as the response variables, respectively, and country was fitted as an additional explanatory variable. Hunter numbers and range area were used to explain the observed time trend in ln(national harvest size) rather than fitting the covariable year, with which they were strongly correlated. Again, the variance was allowed to differ independently according to the levels of the country factor. Similarly, the influence of the proportion of females in the adult harvest on the annual rate of increase in harvests was explored using GLS models. Country, year and their interaction were fitted as covariables but none was significant.

Comparisons within focal countries

Within each focal country, regions were classified by hunting tradition as either traditional or non-traditional red deer hunting areas (two-level factor). In Hungary, Norway and Scotland, regions were classified as traditional if deer were harvested there from the beginning of the study period. In France, department-level data provided a poorer spatial resolution so traditional areas were taken as those in which red deer occurred in 1900 (Leduc & Klein 2004). The time series for each of the non-traditional areas began in the first year of harvesting.

Differences in H_r between traditional and non-traditional areas across countries were investigated within a mixed-model framework that accounted for the correlation structure arising at the country level because data were collected at the region scale. A linear mixed model was used, fitting country as a random effect on both the intercept and the regression slope and accounting for unequal variances between countries (Pinheiro & Bates 2000). Subsequently, comparisons within countries were made with linear models, having established that including region as a random effect did not significantly improve model fit (France, likelihood ratio 0·007, $P = 0{\cdot}932$; Hungary, L ratio 0·009, $P = 0{\cdot}923$; Scotland, L ratio = 0·003, $P = 1{\cdot}0$), except in Norway (L ratio = 8·547, $P = 0{\cdot}036$). Similarly, a mixed-model approach was taken to investigate the effect of proportion of females in the adult harvest, tradition and their interaction on regional H_r in the focal countries. Region was fitted as a random effect on both the intercept and the regression slope. In all these analyses, year was dropped as a fixed effect because it was not significant in any model.

Harvest composition

Changes in harvest composition (proportion of calves, males and females) were investigated in the seven countries for which composition data were available, and within traditional and non-traditional hunting areas in the focal countries. The dependent variables were binomial, treating number of calves as 1 and non-calves as 0, and, similarly, for the number of males (1) vs. females (0) in the total adult harvests. Binomial responses were analysed with generalized estimation equation (GEE) models (Diggle *et al*. 2002). We used a logit link function with a binomial error distribution and an 'exchangeable' matrix for the error correlation structure (Liang & Zeger 1986). GEE allowed us to handle the high degree of overdispersion originating from the spatial and temporal correlation structure of the data, for example country or region and year. For national models, linear and quadratic year terms, either country or management system and their interactions with year, were fitted as fixed effects, and country as the grouping factor. As there were marked differences in harvest composition between countries, the regional harvest of each focal country was modelled separately with tradition, year and their interaction fitted as fixed effects and region as the grouping factor. The effects of the explanatory variables were tested using the Wald statistic, based on naive *z* statistics and SE values, which follows a chi-square distribution with *k* degrees of freedom, where *k* is the number of parameters to be tested. All analyses were carried out using R 2·0·1 (R Development Core Team 2004).

Results

HARVEST GROWTH

Total red deer harvests had increased by 400–700% in most countries over the last 30 years. Exponential increases occurred in eight out of the 11 countries examined. The exceptions were Austria and Germany, which had stable harvests, and Poland, where a strong increase had been followed by a recent decline (Fig. 2). Harvest

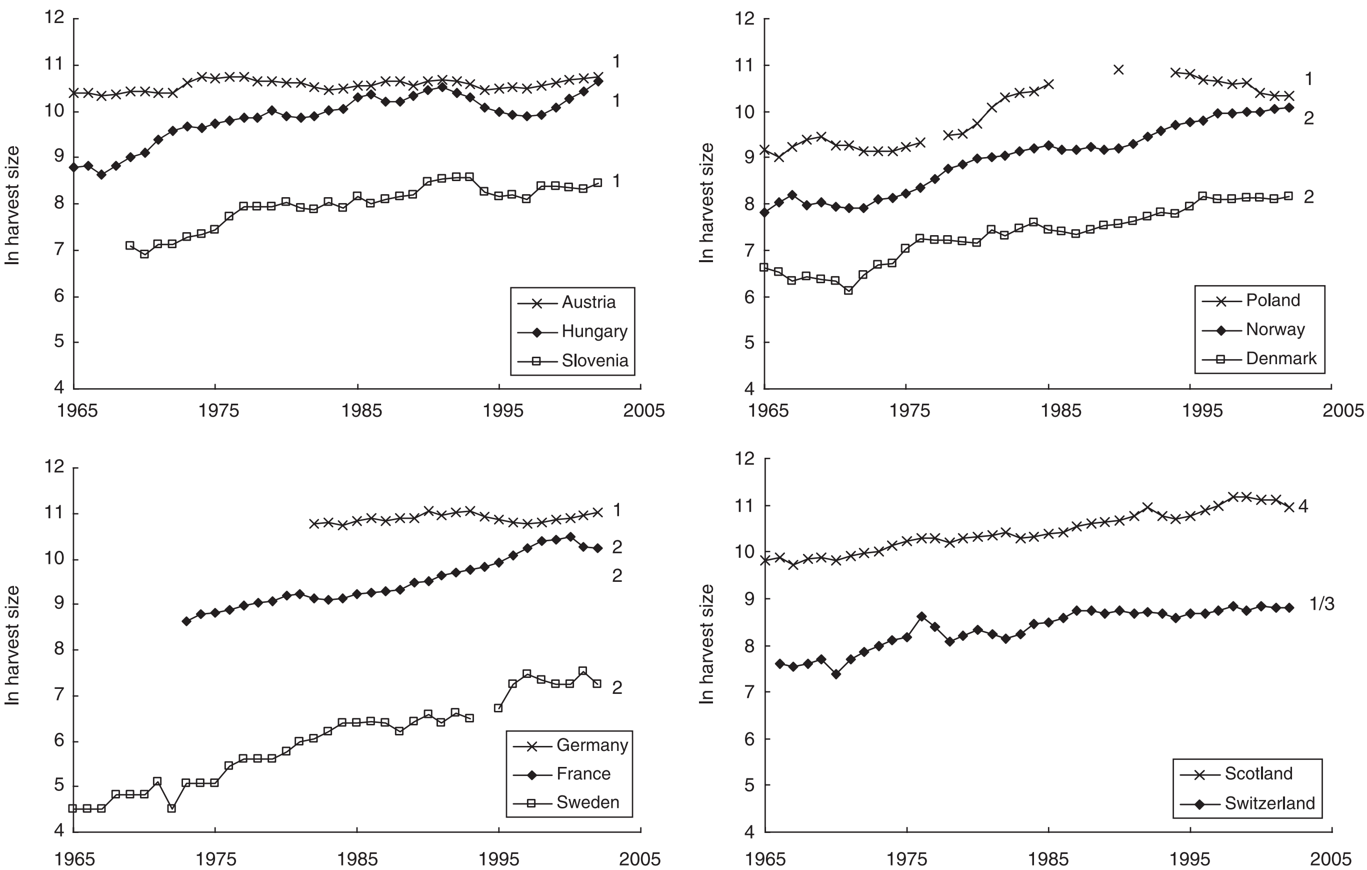

Fig. 2. Trends in size of the (ln) total red deer harvests in 11 European countries since 1965. For management systems, indicated by numbered labels, refer to Table 1.

growth rates varied from 0·009 in Austria, where the annual harvest fluctuated between 31 000 and 46 000, to 0·075 in Sweden, which had the smallest harvest, rising from around 90 red deer shot in 1965 to 1420 in 2002. However, harvest growth rates were only significantly greater than 0 in France and Norway after making a conservative Bonferroni correction for multiple *t*-tests (Table 1). During the study period, we found no evidence of a change in harvest growth over time in any country ($F_{1,365} = 1{\cdot}653$, $P = 0{\cdot}199$; see Appendix S2 in the supplementary material), suggesting that deer populations were growing at a faster rate than the harvests.

Differences in national harvest growth rates were not significant ($F_{10,356} = 1{\cdot}55$, $P = 0{\cdot}12$) because of high variability over time within countries. However, harvest growth rates differed significantly between management systems, being higher in countries where the harvest was controlled by licence and land or hunting ground ownership (management system 2; Fig. 1 and Table 1) than in countries with other management systems ($F_{1,365} = 9{\cdot}72$, $P = 0{\cdot}002$). Denmark, France, Norway and Sweden were also the countries with the highest percentage of inhabitants who were hunters in 2004 (average 3·5% of the population compared with 0·9%). Indeed, the percentage of hunters in the population explained nearly half of the variation in harvest growth rate between countries (slope = 0·009, $F_{1,10} = 7{\cdot}86$, $P = 0{\cdot}021$; Fig. 3a).

In support of prediction P2, harvest growth rate was significantly negatively influenced by the proportion of females in the adult harvest at the national level (Table 2a). Once the proportion of females in the adult harvest was fitted, the management system explained no additional variation ($F_{3,220} = 0{\cdot}367$, $P = 0{\cdot}777$), suggesting that this term accounted for much of the difference in harvest growth rate between management systems.

Within the focal countries there was, as predicted (P3), a positive relationship between ln(harvest size) and red deer range in all countries (Fig. 3c; $r^2 = 0{\cdot}82$–$0{\cdot}97$; see Appendix S3 in the supplementary material) and with hunter numbers in Hungary and Norway (Fig. 3b; $r^2 = 0{\cdot}83$–$0{\cdot}95$). However, harvest size in France increased despite a decline in hunter numbers (Fig. 3b; $r^2 = -0{\cdot}97$). Neither hunter numbers ($F = 0{\cdot}008$, d.f. = 1, $P = 0{\cdot}931$) nor range size ($F = 0{\cdot}244$, d.f. = 1, $P = 0{\cdot}622$) had any effect on harvest growth rates.

There was considerable spatial variation in harvest growth rates within focal countries (Table 3 and Fig. 4). The highest H_r values tended to occur in areas of recent colonization at the periphery of the red deer range (Fig. 4). The high variance between areas in France and Scotland was partly associated with a pronounced difference in regional harvest growth rates between traditional deer hunting areas and areas into which deer and deer hunting have expanded, being significantly faster in these non-traditional areas (Table 3). In contrast, there was no difference in the harvest growth rate between traditional and non-traditional areas in Hungary and Norway (Table 3). Thus prediction P1

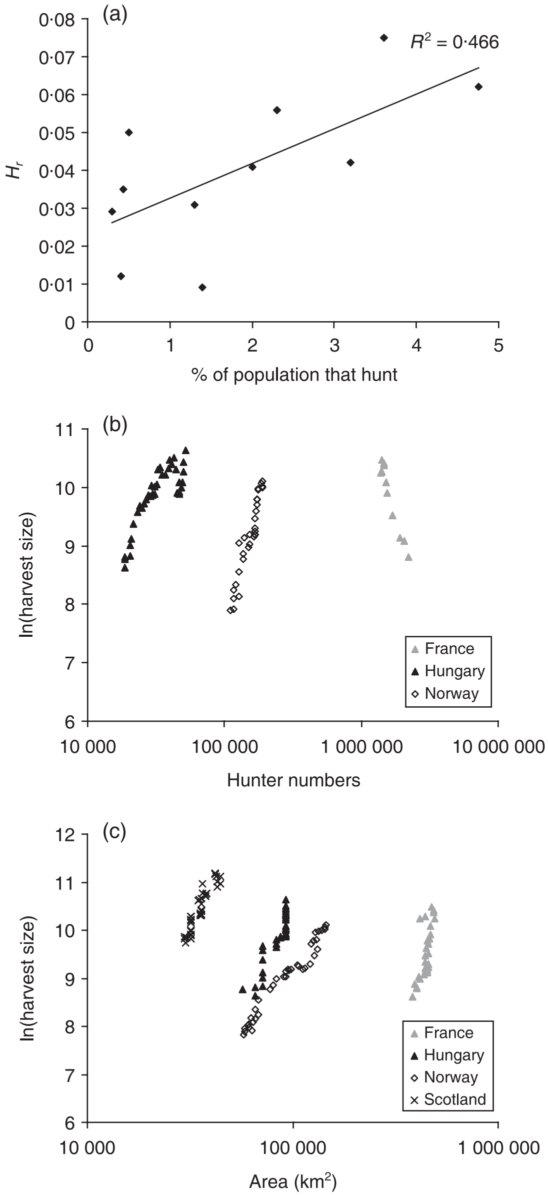

Fig. 3. Relationship between (a) harvest growth rate and the percentage of inhabitants that were registered hunters in 2004 in 11 European countries, (b) harvest size and hunter numbers in the focal countries and (c) harvest size and deer range area in the focal countries (note the log-scaled *x*-axis for b and c).

was only partially supported. The variability in harvest growth rate was greater in non-traditional than traditional areas in all countries (Table 3). In traditional areas, the harvest growth rate reflected an increase in harvest density (i.e. harvest per unit area) within regions, while in non-traditional areas it reflected a combination of both an increase in harvest density and an increase in the number of regions in which harvesting was carried out (Table 3). However, while the number of municipalities harvesting red deer for at least 5 years in Norway increased during the study period by 83%, the contribution of these new areas to the total harvest in 2002 was only 13% and, in Hungary, the non-traditional areas contributed only 3·6% to the 2002 harvest. In comparison, in Scotland the number of management blocks

Table 2. The effects of the proportion of females (PropF) in the adult harvest on the annual rate of increase in harvest in (a) the national harvest in seven countries (Austria, France, Hungary, Norway, Scotland, Slovenia and Switzerland) modelled by GLS, and (b) the regional harvest in each focal country together with the effect of hunting tradition and their interaction, modelled with a linear mixed model fitting region as a random effect on the intercept

			Estimate (SE)	*F*	d.f.	*P*	Random effect (95% CI)
(a)	National	PropF	−0·284 (0·096)	8·779	1	0·003	
(b)	France	PropF	−0·244 (0·095)	6·527	1,1235	0·0107	0·521 (0·377–0·719)
		Tradition*	−0·032 (0·017)	3·408	1,78	0·069	
	Hungary	*PropF*	*−1·243 (0·225)*	*12·01*	*1,544*	*< 0·001*	*0·422 (0·204–0·874)*
		Tradition	0·013 (0·243)	40·88	1,17	< 0·001	
		PropF–tradition	0·904 (0·432)	4·383	1,544	0·037	
	Norway	PropF	−0·032 (0·044)	2·467	1,4504	0·116	0·297 (0·227–0·388)
		Tradition	0·122 (0·033)	23·21	1,212	< 0·001	
		PropF–tradition	−0·166 (0·081)	4·167	1,4504	0·041	
	Scotland	PropF	−0·112 (0·139)	16·95	1,1632	< 0·001	0·403 (0·242–0·671)
		Tradition	0·177 (0·100)	5·014	1,55	0·029	
		PropF–tradition	−0·436 (0·187)	5·414	1,1632	0·020	

*Non-significant term, not included in the minimal model. *F*-value calculated as the change from the minimal model.

Table 3. (a) Linear mixed model showing the fixed effects of country and hunting tradition on the change in harvest between years, with region fitted as a random effect. (b) Mean harvest growth rates (H_r) in traditional and non-traditional red deer hunting areas, where n_i is the number of land units with red deer hunting in the initial year (1965 for Norway and Scotland, 1973 for France) and n_{max} is the maximum number of land units during the study period. Only land units with harvesting in at least 5 years were included

(a)		d.f.	F	P	
Intercept		1	347·6	< 0·001	
Country		3	4·693	0·003	
Tradition		1	5·833	0·016	
Country–tradition		3	3·594	0·014	
Residual		10254			
(b)		n_i	n_{max}	H_r (SD)	H_r range
France	Traditional	26	29	0·062 (0·248)	−0·006–0·111
	Non-traditional	34	52	0·119 (0·417)***	−0·058–0·418
Hungary	Traditional	13	13	0·075 (0·172)	0·040–0·110
	Non-traditional	0	6	0·075 (0·763)	−0·030–0·155
Norway	Traditional	92	92	0·061 (0·312)	−0·004–0·141
	Non-traditional	0	122	0·064 (0·543)	−0·154–0·260
Scotland	Traditional	34	34	0·037 (0·285)**	−0·008–0·155
	Non-traditional	0	22	0·096 (0·512)	−0·004–0·500

**$P < 0·01$, ***$P < 0·001$ significant difference in harvest growth rate between traditional and non-traditional areas within a country.

increased by 65% and non-traditional areas accounted for 21% of the 2002 harvest, while in France the number of departments in non-traditional areas increased by 25% and their contribution to the total harvest rose from 26% in 1973 to 50% in 2002. The increase in total size of the Hungarian and Norwegian harvests was therefore most influenced by an increase in harvest density in traditional areas, while in France and Scotland range expansion was an important contributory factor.

As at the national level, the proportion of females in the adult harvest also had a negative effect on regional H_r in all focal countries, adding further support to prediction P2. However, the relationships differed between traditional and non-traditional areas in all cases except France (Table 2b), being stronger in non-traditional than traditional areas in Hungary but only significant in traditional areas in Norway and Scotland (Table 2b).

HARVEST COMPOSITION

Calf harvest

The composition of the harvest has changed dramatically over recent decades in the seven countries for which data were available (Fig. 5). In particular, there was a strong increase in calf harvesting in all countries, many of which prohibited or rarely practised this before the early 1970s. Averaged across countries, the proportion of calves in the harvest increased more than fivefold, from 5% in 1965 to 29% in 2002, although in recent years it had reached a plateau in several countries (Fig. 5a). By 2002, calves accounted for between 14% (Scotland) and 44% (Slovenia) of the harvest (Table 1). The change in the proportion of calves in the harvest over time differed significantly between countries (country–year interaction, $\chi^2 = 108·11$, d.f. = 6, $P < 0·001$; country–

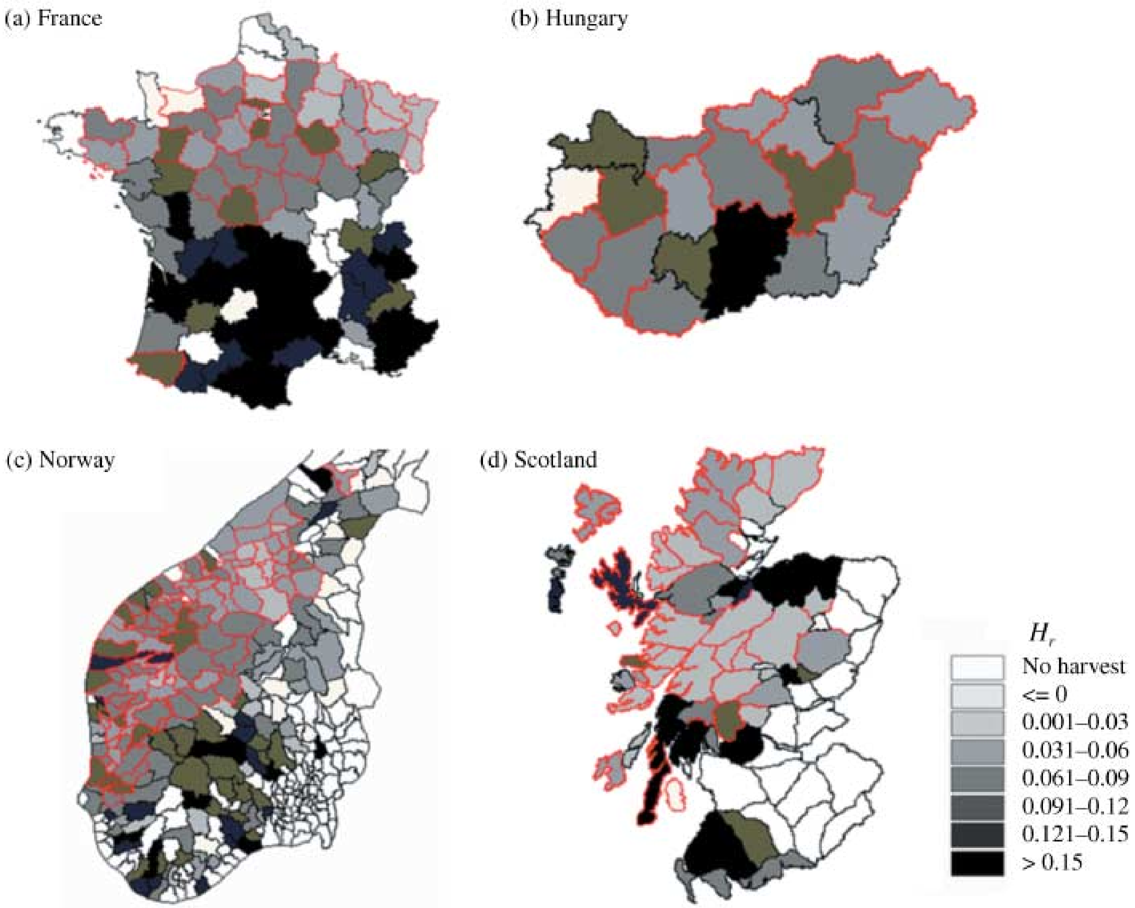

Fig. 4. The spatial variation in the rate of growth in harvest size in (a) France at the department scale, (b) Norway at the municipality scale and (c) Scotland at the scale of management blocks. Traditional hunting areas are outlined in red. Areas with no harvest include those areas where the total number of deer harvested over the study period was less than 50 or where harvesting took place in fewer than 5 years.

year^2, $\chi^2 = 107{\cdot}02$, d.f. = 6, $P < 0{\cdot}001$), management systems (management system–year interaction, $\chi^2 = 38{\cdot}32$, d.f. = 2, $P < 0{\cdot}001$; management system–year^2, $\chi^2 = 37{\cdot}9$, d.f. = 2, $P < 0{\cdot}001$) and, within focal countries, between traditional and non-traditional areas (see Appendix S4 in the supplementary material). Differences between countries are likely to reflect in part biological differences, such as calving rates being lower in Scotland (Clutton-Brock & Albon 1989; Milner, Alexander & Griffin 2002), than in countries with high female productivity (Langvatn *et al*. 1996, 2004; Bonenfant *et al*. 2002). In contrast, differences between management systems are more likely to reflect cultural factors related to harvesting strategies. For example, central European countries (management system 1) harvested a significantly higher proportion of calves than countries where harvesting was controlled by licence and ownership (management system 2), which showed the fastest increase in calf harvesting and in turn harvested a greater proportion of calves than other countries (Table 1 and Fig. 5a; main effect of management system, $\chi^2 = 732{\cdot}92$, d.f. = 2, $P < 0{\cdot}001$). Calves generally accounted for a higher proportion of the harvest in traditional than non-traditional areas of focal countries, with lower year-to-year variability (see Appendix S4 in the supplementary material).

Adult harvest

As a consequence of an increased calf harvest, adults accounted for a smaller proportion of the total national harvests in later years in all countries. However, within the adult harvest, the proportion of males shot remained relatively stable, at just below 50% in most countries, although there were considerable periodic fluctuations in many cases (Fig. 5b). Norway was the only country with a strongly male-biased harvest. The trends at either extreme were a significant decline in the proportion of males shot in Slovenia, from 0·53 in 1969 to 0·46 in 2002 ($\chi^2 = 16{\cdot}77$, d.f. = 1, $P < 0{\cdot}001$), and a small but significant increase in France, from 0·46 in 1983 to 0·48 in 2002 ($\chi^2 = 4{\cdot}27$, d.f. = 1, $P < 0{\cdot}001$). The proportion of males in the adult harvest differed significantly between countries and over time (country–year interaction, $\chi^2 = 14{\cdot}11$, d.f. = 6, $P = 0{\cdot}028$; year^2, $\chi^2 = 9{\cdot}37$, d.f. = 1, $P = 0{\cdot}003$). Contrary to P4, there was no evidence of a

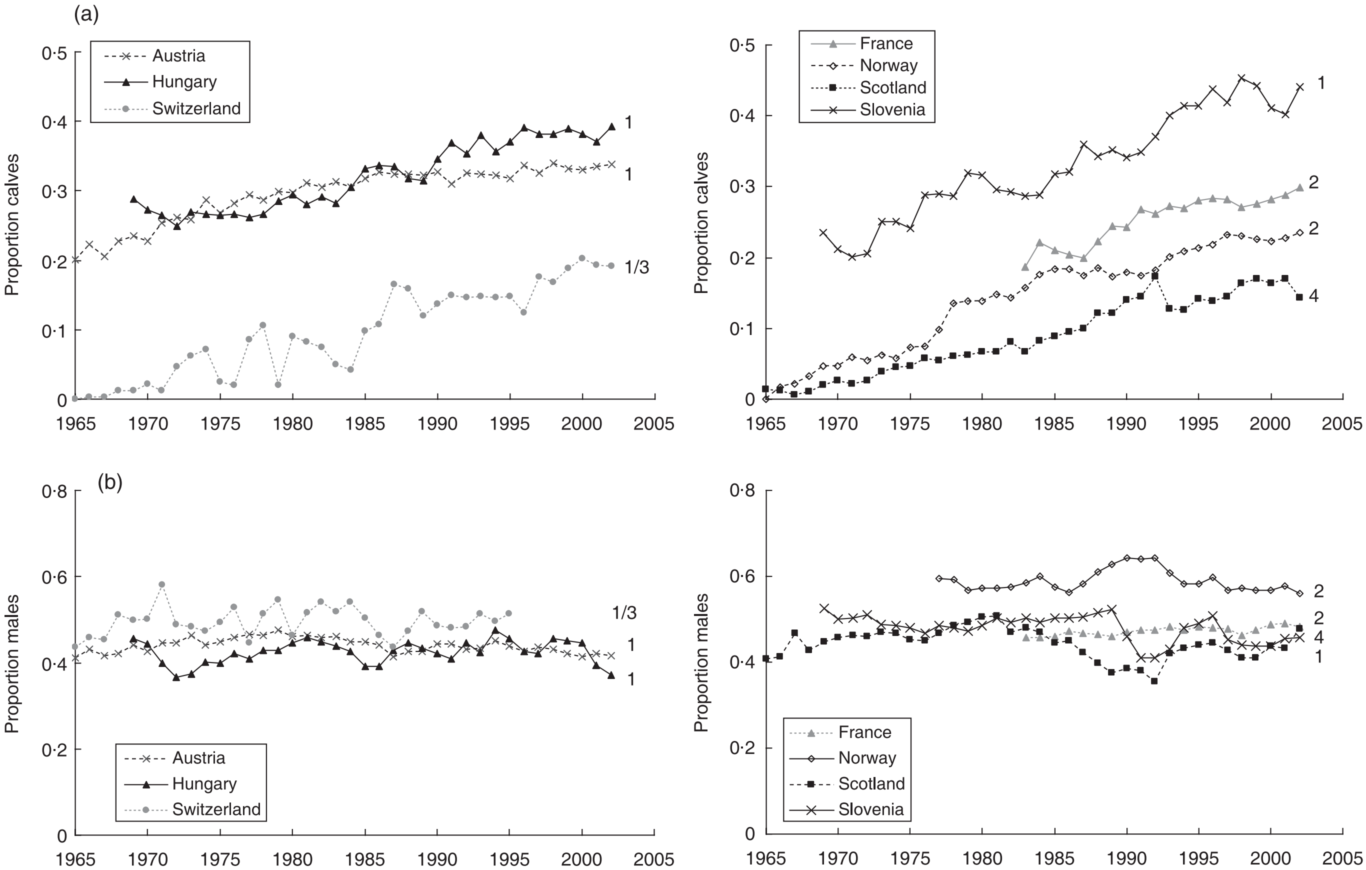

Fig. 5. Changes in harvest composition in terms of (a) the proportion of calves in the total harvest and (b) the proportion of adult males in the total adult harvest. Yearlings are included with adults in all cases. For management systems, indicated by numbered labels, refer to Table 1.

relationship between the proportion of males in the adult harvest and trophy hunting culture (Table 1).

Differences in the proportion of males in the adult harvest between management systems were less pronounced than differences in calf harvesting. Generally, countries with management systems 1 and 3 had a lower proportion of males in the harvest than countries in other systems. However, differences in the proportion of males in the harvest in Norway and France, both under management system 2 (Fig. 5b), were too extreme to make a comparison between management systems meaningful. Within the focal countries, males accounted for a larger part of the adult harvest in non-traditional than traditional deer hunting areas in all countries, with harvest composition tending to be more variable from year-to-year in non-traditional areas (see Appendix S4 in the supplementary material).

Discussion

Harvesting has a fundamental influence on the population dynamics of ungulates, often accounting for the majority of mortality (Langvatn & Loison 1999) and increasing adult female mortality, the vital rate with the highest elasticity (i.e. the factor in which a given variation affects dynamics the most; Gaillard, Festa-Bianchet & Yoccoz 1998). However, in contrast with the huge body of theoretical and empirical literature of other key processes such as density dependence and climate (Fowler 1987; Sinclair 1989; Lande, Engen & Sæther 2003; Turchin 2003), there are extremely few empirical studies addressing how different harvesting strategies have affected the development and composition of ungulate populations (Gordon, Hester & Festa-Bianchet 2004; but see Fryxell *et al*. 1991; Langvatn & Loison 1999; Solberg *et al*. 1999; McCullough 2001). As a preliminary step towards addressing this, we have shown the extent to which red deer harvests have increased across Europe as a result of both biological and cultural factors, including increasing deer range and hunter numbers in at least some countries (P3). Harvest growth rates and harvest composition differed between management systems across Europe. Although variation in the harvest of adult females explained part of this (P2), differences were not related to hunting objective in terms of meat vs. trophies (P4), and were only partially related to differences in harvest growth rates between traditional and non-traditional areas (P1). While harvest growth rates do not reflect population growth rates perfectly, the continued growth and apparent sustainability of the harvests over time is indicative of steadily growing red deer populations in many European countries, despite differences in the cultural aspects of management. Such increases are indicative of an underestimation of population sizes (Csányi & Tóth 2000; Gaillard, Loison & Toïgo 2003) and/or underharvesting, particularly of females (Clutton-Brock, Coulson & Milner 2004; Giles & Findlay 2004), but appear to be independent of the red deer management system.

HARVEST GROWTH AND COMPOSITION: THE CULTURAL COMPONENT

Across Europe, harvest growth rates of red deer were highest in management systems where the harvest was controlled by licence and land or hunting ground ownership (management system 2; Fig. 1). Differences between systems are more likely to reflect differences between groups of countries with similar hunting cultures and general approaches to management, than to be a direct result of the system for controlling harvesting. The intensity of harvesting, i.e. harvesting rate, is likely to strongly influence harvest growth and may differ between management systems, but in the absence of population data it is not possible to identify the extent to which this occurred. Based on available data, harvest composition was partly responsible for the higher harvest growth of management system 2 countries (although Norway harvested more males than Denmark, France and Sweden), but these countries also showed a strong hunting culture, indicated by a high percentage of inhabitants who were hunters. Hence harvesting rates may be higher and management more focused towards satisfying hunters' demands. For example, management practises such as introducing new deer populations in France in the 1950–60s (Leduc & Klein 2004) and taking a male-biased harvest in Norway (Langvatn & Loison 1999) were taken to increase population size and hence hunting opportunities in low-density areas.

Harvest composition is strongly influenced by cultural factors, including management strategies, hunting traditions and economic considerations, as well as by biological factors. Changes in calf harvesting strategy during the study period were at least partly the result of legislative and management policy changes. In terms of the adult harvest, this was female-biased in all countries except Norway. Contrary to prediction P4, the proportion of males in the harvest was unrelated to trophy hunting objectives, unlike the harvesting of many African ungulates (Ginsberg & Milner-Gulland 1994). As is typical for Scandinavia, meat rather than trophies was the major hunting objective in Norway, yet the harvest was more male-biased than in many primarily trophy-hunting countries. While large males may be targeted by meat hunters for their higher yield, this does not account for the female bias in other countries. However, trophy size is strongly influenced by age (Kruuk *et al*. 2002), so trophy hunters tend to be reluctant to shoot young males, which make up most of the male population. Consequently relatively few animals are shot as trophies even in areas where trophy hunting is the most economically important management objective. For example, in Scotland, the sporting cull accounts for only 25% of the total harvest (Reynolds & Staines 1997). In addition, managers may harvest males suboptimally to avoid overharvesting (Milner-Gulland, Coulson & Clutton-Brock 2004). Good-quality trophies are generally achieved at lower population densities, requiring female numbers to be controlled. As a result, secondary management objectives, such as meat yield or population control, often account for the greater proportion of the total harvest. Furthermore, many populations of dimorphic ungulates are female-biased (Clutton-Brock & Lonergan 1994), so despite near parity in the harvest a greater proportion of the males in the population may none the less be harvested. Indeed, in Scotland, where the total red deer harvest is female-biased, approximately 16% of males compared with 14% of females were harvested during the 1990s (Deer Commission for Scotland, unpublished data).

FEEDBACK BETWEEN BIOLOGICAL AND CULTURAL PROCESSES

Deer and hunter populations are both dynamic entities that are constantly interacting (Brown *et al*. 2000). Feedback between cultural factors, hunting traditions and biological processes are likely to be involved in the development of game populations. For example, hunting culture (including a mixture of facts and beliefs) will influence size and composition of yield, which will affect population growth rates and consequently management decisions (Fryxell *et al*. 1991; Côté *et al*. 2004; Gordon, Hester & Festa-Bianchet 2004). These may in turn feed back into hunting culture. In addition, the hunting methods allowed will influence the ability to harvest selectively (Martinez *et al*. 2005). For example, in Hungary driven-shooting of male cervids is prohibited by law in order to ensure that the goals of selective male harvesting will not be jeopardized.

In North America, with declining numbers of hunters and growing deer populations, it is now questionable whether sport hunting can reliably control deer numbers (McShea, Underwood & Rappole 1997; Brown *et al*. 2000; Côté *et al*. 2004). A similar situation is likely in parts of Europe, such as France, although in Norway and Hungary hunter numbers have risen and it may be that increased availability of game has stimulated the recruitment of new hunters.

SPATIAL PATTERN OF HARVEST

Deer harvests have risen both as a result of increased harvest densities (reflecting population densities) within existing ranges, and as a result of considerable expansion of the range of red deer throughout Europe (Gill 1990). Consequently, national harvests hide much interesting spatial variation. Within the focal countries there has been extensive range expansion around many discrete introduced populations in France (Leduc & Klein 2004) and in Alpine areas, while in Norway there has been a primarily southerly and easterly expansion since 1920 (Langvatn & Albon 1986; Mysterud *et al*. 2002). The establishment of commercial forestry plantations in Hungary, UK and western parts of Norway has also allowed red deer to move into new areas (Clutton-Brock & Albon 1989; Csányi 1999; Fuller & Gill 2001). However, the influence of deer range expansion on total harvest size was much greater in France and Scotland than in Hungary and Norway. Environmental constraints such as snow depth or the duration of snow cover in winter may limit the rate of colonization of inland ranges in Norway. In addition, hunting in new areas of Norway often starts as soon as red deer establish because of fears of agricultural or forest damage, which may severely restrict population growth. In contrast, in France there is frequently a considerable time lag between population establishment and the start of hunting (Bonenfant & Klein 2004). Much of the spatial variation in France and Scotland was associated with differences in harvest growth between traditional and non-traditional areas (P1). Particularly large increases in harvest size occurred in non-traditional areas at the edges of the deer distribution (Fig. 4). In these areas, harvest growth rates were often higher than the maximum possible population growth rate for red deer, assuming a finite rate of population increase (λ) for red deer of 1·25–1·35 (Gaillard *et al*. 2000). It is unlikely that dispersal could account for all of this (Clutton-Brock *et al*. 2002), suggesting that cultural factors associated with the expansion of hunting interest or improvements in hunting competence must have been involved, as well as the predicted biological factors related to rapid growth during colonization. In the traditional hunting areas of France and Scotland, it is unclear whether the lower rate of increase in harvest size reflected a slower increase in deer numbers, as a result of either density-dependent factors or differences in harvest off-take. However, in Norway, where population density is generally well below carrying capacity (Mysterud *et al*. 2001), and in Hungary, where population growth rate is almost at the maximum possible (Csányi 1992), harvest growth rates were similar in traditional and non-traditional areas. Alternatively in traditional areas in France and Scotland, there may be a greater lag in keeping abreast of population growth. For example, in Scotland the size of the cull is often set on the basis of what it has always been (Buckland *et al*. 1996) and a tendency to target the female cull towards old rather than the most productive hinds (Trenkel *et al*. 1998) could exacerbate problems of population control.

CONCLUSIONS

Red deer numbers have increased considerably throughout Europe over the last 30 years, regardless of management system and cultural hunting traditions. Our findings suggest that deer population growth has been faster than harvest growth. Changes in harvest size and composition coincided with changes in management policies, hunter numbers and red deer range. Further shifts can be expected in the future as the social impacts of high deer numbers become increasingly felt (Fuller & Gill 2001; Côté *et al*. 2004; Gordon, Hester & Festa-Bianchet 2004) and as an awareness of the need for population control develops (Gordon, Hester & Festa-Bianchet 2004). The increase in calf harvesting is an indicator that control efforts are being made in many countries, but changing the adult harvest is more problematic because hunting traditions and economic considerations often conflict with population control objectives.

An important challenge for the future management of red deer in Europe is to improve the availability and quality of population data on which management decisions are based. Despite being one of Europe's largest and most economically important mammals, with a wide distribution and a probable population size of 1–2 million animals, sound data on red deer populations and their dynamics are patchy, scarce or inconsistent. Against this background, harvesting must balance changing hunting requirements and capabilities with the increasing social and economic impacts of deer and other ungulates.

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Supplementary material

The following supplementary material is available as part of the online article (full text) from http://w.w.w.blackwell-synergy.com.

Appendix S1. Harvest management in the focal countries.

Appendix S2. Changes in harvest growth rate over time in the 11 study countries.

Appendix S3. GLS models of harvest size in relation to hunter numbers and red deer range area in the focal countries.

Appendix S4. Harvest composition within the focal countries.

Figure S2. Harvest growth rate over time in the 11 study countries.

Figure S4a. The proportion of calves in the harvests of traditional and non-traditional areas in the focal countries.

Figure S4b. The proportion of males in the adult harvests of traditional and non-traditional areas in the focal countries.

Table S2. GLS model of harvest growth rate.