ORIGINAL ARTICLE

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Changes in bodyweight and productivity in resource-restricted populations of red deer (*Cervus elaphus*) in response to deliberate reductions in density

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Abstract

In resource-restricted populations of red deer, it is well-established that body size at maturity, female fecundity and calf survivorship are reduced, yet there are few formal studies documenting a reversal of these effects with reduction of density. In this paper, we consider changes in adult bodyweight and fecundity in populations of red deer in upland Scotland, before, during and after substantial reductions in population. Using generalised linear mixed models, we analysed changes in bodyweight and fecundity for 15,401 male and 21,053 female red deer culled from 9 different properties over periods from 9 to 35 years. After controlling for the effects of age, bodyweight in males showed a significant negative relationship with density and a significant positive relationship with the magnitude of reduction in density from that of the previous year as well as from population density recorded 2 and 3 years previously, implying that although main effects may relate to immediate reductions in density from that of the preceding year, increases in male bodyweight may be responding to cumulative reductions in densities as much as 3 years later. Analyses of female bodyweight yielded similar results with a direct and measurable effect of current density on age-related female bodyweight and significant effects of reductions in density in immediately preceding years. In this case, the model of best fit (lowest AIC score) is that incorporating a 3-year time lag, implying that bodyweight may be responding to the effects of cumulative culls over a preceding period of up to 3 years. Pregnancy rates among females were strongly influenced by bodyweight and prevailing (current) density (with females of higher bodyweight more likely to be pregnant), but there was no consistent effect of reduction of density on the probability of pregnancy of young females (aged < 4 years) or older animals (4 years or older). The probability of a lactating female becoming pregnant again in the same year was however significantly higher 1 year after a reduction in population density. While we focus in this paper on red deer, the results are applicable to other mammalian species where bodyweight is a major driver of fecundity. Our analyses suggest that some improvement in fertility and individual animal quality (bodyweight) may be expected where population densities of resource-limited populations are sufficiently reduced.

Keywords Red deer · Bodyweight · Fecundity · Effects of density · Effects of density reduction

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INTRODUCTION

Management of red deer in Scotland

As elsewhere within Europe (see for example Apollonio et al. 2010), management of red deer (*Cervus elaphus*) in the Highlands of Scotland offers a delicate balance of costs and benefits (Putman and Watson 2010). Although historically a woodland species, red deer are now found in a variety of habitats—on open moorland as well as in coniferous and deciduous forest; densities vary with quality and structure of the habitat. Densities of 5–40 km^{-2} occur in forestry plantations

and densities of 12–20 km^{-2} are typical for hill land (Staines et al. 2008). Scottish populations are currently estimated to be in the region of 300,000–350,000 (Putman 2010; Albon et al. 2017); in England, total populations have been estimated at 12,500 (Ward 2007; Putman 2010).

Red deer may be implicated in significant potential damage to commercial forestry (see for example Perez-Espona et al. 2009). Where they occur at high densities, there have in addition been increasing concerns expressed about suppression of regeneration of native woodlands and damaging impacts of grazing and browsing on heathland and other open moorland communities (Scottish Natural Heritage/Deer Commission for Scotland 2002; and see for example Reimoser and Putman 2011). At high densities and where deer have access to areas grazed by domestic livestock, deer may be implicated as vectors of disease (e.g. Ferroglio et al. 2011). Finally, there is growing concern about an increase in the number of road traffic accidents each year caused by or involving deer (e.g. Langbein et al. 2011; Putman et al. 2011). In response to these concerns in different areas, some management intervention is often indicated.

At the same time, deer represent an important economic resource in rural areas, through ecotourism (Bryden et al. 2010; Deer Commission for Scotland 2010), through the production of venison, and where estates may be able to 'let' the stalking (allow a third-party hunting rights for an appropriate fee). In the north of Scotland in particular, there has become established a very strong tradition of recreational stalking—especially of red deer on the open moorland which land is often unsuited to any other form of management or exploitation (e.g. forestry or agriculture). The lease of such stalking provides important revenue to private landowners and an important source of employment within local communities (PACEC 2006; Macmillan and Phillips 2008; Putman and Watson 2010). Over very large areas of the country, such recreational stalking is thus equally, if not more, important than shooting carried out to control damage (Putman 2010).

Management issues and management structure are described in Perez-Espona et al. (2009) and Putman (2010). However, in general terms, management of red deer populations in the Highlands of Scotland (in areas outside the public forest estate) is determined and carried out by private landowners over whose properties the deer population may range. Setting of management objectives, or management priorities, culling and other management is at the discretion of the landowner, although most landholdings belong to voluntary Deer Management Groups who coordinate management activity over the wider population range. At present, approximately 90% of the entire land area of Scotland is covered within one or other of over 50 of these voluntary Deer Management Groups. Beyond advisory input through the network of Deer Management Groups, the central government cannot generally influence management objectives or management practice,

with the exception that the statutory agency charged with responsibility for deer management, Scottish Natural Heritage, does have (limited) powers of intervention in situations where it may be demonstrated that deer are causing damage to agriculture, forestry or natural heritage interests, or pose a threat to public safety (under Section 14 of the Wildlife and Natural Environment Act 2012).

Resource limitation and demographic responses to density

In productive woodland environments, both male and female red deer reach sexual maturity as yearlings. It would be uncommon for yearling males to be successful in competing with heavier and more mature stags to gain access to females, and thus few males will begin to breed until perhaps 5 or 6 years of age (Staines et al. 2008). However, a high proportion of females will become pregnant as yearlings in woodland populations with, for example, around 75% of yearling females found pregnant in studies in the New Forest in Hampshire or in Exmoor, in southwest England (Langbein 1997; Putman and Langbein 1999) and 75% yearling pregnancy among forest populations even in Scotland (Ratcliffe 1984, 1987a, b).

By contrast, among more resource-limited populations in habitats of poorer quality or where populations are at higher density, there is commonly a considerable delay in reaching reproductive maturity; growth is considerably slower under these conditions and females may not reach puberty until they are 2 or even 3 years of age. Even among adults, fertility is also suppressed and in extreme cases (such as in populations living in open moorland conditions in the uplands of Scotland), mature females may breed successfully only in alternate years, or at even lower frequency (e.g. Mitchell et al. 1977; Clutton Brock et al. 1982; Clutton-Brock and Albon 1989). Finally, there is also a reported density-dependent effect on winter survival of juveniles (for all these effects, see Clutton-Brock et al. 1985, 1987a, b; Putman et al. 1996; Coulson et al. 2004). The potential implications of such density-dependent responses for sporting harvests of red deer, and the effect of the skew in adult sex ratio which may result have been explored in the analyses of for example Clutton-Brock and Lonergan (1994) and Clutton-Brock et al. (2002).

Although responses in open-hill populations of Scottish red deer are extreme, similar density-dependent changes in productivity have been widely reported elsewhere (e.g. for red deer or the related North American wapiti *Cervus canadensis*: Forchhammer et al. 1998; Mysterud et al. 2002; Stewart et al. 2005; Rodriguez-Hidalgo et al. 2010; Borowik and Jędrzejewska (2018).

For more general review, see Fowler 1987; Bonenfant et al. 2009.

As a result of this suite of established density-dependent changes in population demography, Scottish Natural Heritage (and its predecessor the Deer Commission for Scotland), when discussing with managers optimal management strategies for the future, have argued that reduction in deer densities may be advantageous even for those managing deer populations purely as a sporting resource, because it will result in an increase in productivity and an increase in the quality of calves born into that population. It is argued that in populations which are resource-limited to some degree, a reduction in density will result in increases in bodyweight, reproductive rates and calf survival and decreases in age at first breeding. However, while from a purely theoretical standpoint, this might be expected, the empirical evidence that it does occur is sparse and somewhat contradictory. Although Bonenfant et al. (2002) report clear differences in bodyweight, female fecundity and calf survival for red deer in a forest environment in northeastern France, when comparing between two time periods of higher and lower density, by contrast, Langvatn and Loison (1999) found no effects of sustained harvesting on survival rates and reproductive performance in a red deer population in central Norway, noting that the population appeared to be primarily limited by stochastic fluctuation in recruitment parameters (juvenile survival and age at first breeding; Loison and Langvatn 1998). Nor is it clear how large a reduction of density is required to release this density-dependent brake on population growth or whether, if some response to reductions in density is apparent, the sequence of responses will be symmetrical with those reported as density increases (e.g. Eberhardt 1977; Fowler 1987).

Over recent decades, there have been a series of separate attempts to reduce substantially the density of deer populations on a number of different landholdings in the Scottish Highlands for a variety of different reasons, most commonly to encourage regeneration of native woodlands or reduce damaging impacts of grazing and trampling on Natura sites (sites designated nationally or internationally as of especial conservation interest). Where detailed population information has been maintained for a period of years before, during and after such management intervention, it is possible to explore population responses to changes in density or resource availability.

Using count data and larder records (for all animals shot) from nine different estates where reductions in population density have been effected and monitored, we seek to explore

i)   what is the effect of different levels of reduction of effective density on adult bodyweight of males and females; age-specific pregnancy rates of females and age at first reproduction; breeding frequency of adult females; and as an overall measure of productivity, population recruitment rates (calf-hind ratio in late winter counts)?

ii)   what level of reduction of density is required before any such changes may be observed at all (and indeed, are the changes of density applied in Scottish hill situations enough to release the brake of density-dependence/resource limitation at all or do densities still remain above levels at which such responses would become evident)?

iii)   Is there a time lag before any such effect becomes apparent? It is perhaps unlikely that mature body weight, or reproductive performance of existing adults will change dramatically; it is more likely that more significant change might be expected among cohorts of animals born in to the better conditions (see Albon et al. 1987) and that in consequence the effect will not be noticeable at a population level until sufficient of those 'better' cohorts have entered the adult population.

Materials and methods

In this paper, we have investigated the effects of age, density and reduction in population density on:

1)   male and female bodyweight
2)   pregnancy rates of females aged ≤ 3 years. If age at first reproduction decreases as a result of reductions in density, this should be reflected in an increase in the number of younger females found to be pregnant
3)   pregnancy rates of mature females aged ≥ 4 years
4)   rate of females recorded as simultaneously pregnant and lactating (thus supporting a calf born the immediately previous season
5)   overall recruitment rate is estimated as the number of surviving calves counted in end of winter counts per 100 hinds of mixed age (see below).

The data available for this project have been collated from nine privately-owned estates in the Scottish Highlands. Data available included information on animal numbers (thus densities) derived from ground, or aerial counts and total numbers of animals culled each year (separately males, females, calves). On most Scottish estates, counts are carried out, in late winter, at least every 3 to 5 years by helicopter; on many estates, additional counts are carried out in intervening years either by helicopter or as ground counts (see for example Daniels 2006).

Such counts are carried out after the end of the normal cull season in any year, before the commencement of the next year's stag cull. As well as returning estimates of numbers, where all animals are fully classified as stags, hinds and calves of the year, an estimate of average annual recruitment to the population may be derived. This is generally presented as the number of surviving calves reported in end of winter counts as

a proportion of the number of mature hinds counted (> 1 year old).

Since counts are traditionally carried out at the end of winter (typically, in March or April) such counts show the net recruitment of calves to the adult population after both natural and imposed (cull) mortality have been taken into account. In effect, this *recruitment rate* integrates over time the separate demographic components of actual calving rate (birth rate), neonatal, summer mortality (see for example Guinness et al. 1978; Clutton-Brock et al. 1985) and both natural (Clutton-Brock et al. 1985, 1987a, b) and imposed mortality over the winter. For the estates considered in this paper, counts were generally available for every year.

Cull data are similarly presented as numbers (separately) of stags, hinds and calves shot in each season. The normal close seasons for red deer in Scotland prohibit the killing of males (stags) between 21st of October and 30th of June and prohibit the killing of females (hinds) between 16th of February and 20th of October; exemptions may be granted where it can be shown that deer are causing significant damage to agriculture, forestry or the natural heritage. For clarity, it should be recognised that this cull year runs from May each year to the following April (formally 1st of May, in any given year, t, to the end of April, year $t + 1$). For the purposes of our analyses here, estates also made available full data on each individual animal shot. Data provided included date, location, sex and estimated age as well as weight and (in the case of females) data on reproductive status (whether or not the individual was pregnant, lactating or not).

Specifically, although the form and degree of detail varies, larder sheets generally record: date, location, sex, estimated age (largely determined by tooth eruption and wear (after, for example Ratcliffe 1977, 1987a, b) and generally report two estimates of weight: hill weight and larder weight. Hill weight records the full weight of the carcase minus viscera (which are traditionally removed before the carcase is retrieved); larder weight is a subsequent measure taken after the removal of the head, the distal part of the legs and other internal organs (heart, lungs, liver) (e.g. Mitchell and Crisp 1981; Staines et al. 2008). Our analyses in this paper are throughout based on this latter measure of larder weight. For males, the number of tines on each antler is usually recorded, and for adult females, (as above) data record whether or not a foetus is present on visual examination of the uterus and whether or not the animal was supporting a current year's calf, based again on visual examination of the teats accompanied usually by manual expression of milk between the thumb and the forefinger.

Estates in our analyses included those in which management has aimed at maintenance of approximately stable population size year on year ('Control' sites) and those where deliberate efforts have been undertaken to effect a substantial reduction in population number ('Treatment sites'). In all treatment sites, larder data were available for a period before, during and after the period of population reduction. Control sites were selected as far as possible to provide matched pairs for treatment sites, drawn from the same deer management area and as far as possible similar to their 'partner site' in topography and vegetation cover. In our studies, initial densities varied from 4.92 to 18.50 deer km^{-2}; densities were maintained on control sites, but reductions carried out on treatment sites were from 18.50 to 14.81 deer km^{-2}, 12.53 to 11.30 deer km^{-2}, 11.29 to 5.36 and 4.92 to 1.17 deer km^{-2}.

Altogether, data were available for a total of 12,293 individual carcases from control sites (5454 males; 6839 females) and 24,161 carcases from treatment sites where reductions had been carried out (9947 males; 14,214 females). While analyses of the effects of density on bodyweight were carried out on the entire database, analyses of female fecundity (pregnancy rates) were restricted to females culled after 1st of January in any cull season since before this time embryos may be small and not reliably detected, leading to a risk of animals being falsely recorded as non-pregnant when the foetus is missed.

Statistical analyses

We developed a series of mixed effect models to explore effects of age, density and density reduction on the following six demographic measures: body weight in males, body weight in females, pregnancy rate in young females, pregnancy rate in adult females, rate of females simultaneously pregnant and lactating and end of winter recruitment rate.

We modelled body mass (formally that metric reported as 'larder carcase weight') in males using a generalised linear mixed-effect model, with density, reduction in density and their interaction as predictor variables. Bodyweight was of course expected to change with animal age, as well as potentially with changes in density. We therefore included age of each individual in the candidate explanatory variables, as both a linear and a quadratic effect, and its interaction with density. Analyses of the effects of density and reduction in density on female body weight may also be confounded by the established fact that females lose weight consistently through the winter period as they draw on stored energy reserves (e.g. Mitchell et al. 1976). To account for this, in analyses of female body mass we used a generalised mixed effect model (GAM), and we included (in addition to the same variables included for males) a smooth function of a continuous variable indicating the date through the legal culling season from the 21st of October. This adjustment was not considered necessary for males, since the majority of males are shot in a brief period of 5–6 weeks in the autumn.

Pregnancy rate, for models of young and fully mature females, was treated as a binomial response variable (1 if a female was pregnant, 0 otherwise). For females simultaneously pregnant and lactating, we subset all lactating females and ran again a binomial model (1 if female was pregnant and

lactating, 0 if it was just lactating). In such models, we included as explanatory variables body weight, density, reduction in density (and their interaction), age (but we excluded the quadratic term in the analysis of young females, since we were not anticipating any plateau effect in relation to age) and the following additional interaction terms: age*density, age*bodyweight, density*bodyweight. As already noted, analyses on pregnancy rates were restricted to females culled on or after the 1st of January in any year.

Recruitment rate, assessed as the ratio between the number of surviving calves in end of winter counts and the total number of females, was modelled using a binomial distribution, and we included density, reduction in density and their interaction as predictor variables.

Our analyses rely on data collected across a number of different sites. In any lateral comparisons of this sort, it is clear that there may be individual properties of different sites which may affect parameters of interest—such as differences in habitat quality, altitude and climatic conditions. We made allowance for such effects of site by including random intercept and slope according to estate in relation to both density (D|Estate) and reduction in density (Red|Estate).

It was not possible directly to include climatic variables since in many cases the closest meteorological stations were as much as 100 km from the estate concerned and/or at significantly different altitude. In addition, because of the sparse distribution of such met. stations across Scotland, for many properties, the nearest met. station was the same for all properties.

The calendar years over which population reductions were taken on treatment sites also, and inevitably, dates of population reduction, also differed between properties. Since, in consequence, density and larder data for different estates were collected over different spans of calendar year, a further random intercept was included to take account of variation due to calendar year (1|Year).

Finally, in order to assess the effect of any time lag in response to density and reduction in density, we compared the goodness of fit, in each case, of four models using, as covariates, density at year t, t-1, t-2 and t-3 (D_t, D_{t-1}, D_{t-2}, D_{t-3}), and stepwise reductions in densities (Red$_{t-1}$, Red$_{t-2}$, Red$_{t-3}$). These latter covariates were calculated as difference between $D_{t-1}-D_t$, $D_{t-2}-D_t$, $D_{t-3}-D_t$. We then selected the best model that minimised Akaike's information criterion (AIC) (Akaike 1973) to identify the time lag best fitting the data. Information criteria such as AIC are based on likelihood function, which in turn depends on sample size. Comparison of models based on AIC, therefore, need models themselves to be fitted exactly on the same samples. In our case, there were occasional gaps in recording of population size/density, so that the available data at, for example, year t could be different than data at year t-1. To deal with this, we selected, for each analysis, the minimum subset of data that allowed us to include exactly the same records for the four time-series models to make the AIC-

based comparison feasible. After the model selection, however, we fitted the models on the full dataset.

All analyses were carried out in R (R Core Team 2014) using the package 'lme4' (Bates et al. 2015).

Results

Effects of age

Results from GLMMs with age and age^2 included as covariates showed significant effects of age on bodyweight (as recorded larder carcase weight in kg). For males, weight increased until an estimated age of around 10–11 years, showing subsequent decline (Fig. 1 a). For females, bodyweight showed a similar pattern of increase followed by decline, although with lower recorded weights at any given age than those recorded for males and with, in this case, maximum weights reached at approximately 8–9 years of age (Fig. 1 b).

Among females, we also observe a positive effect of linear term of age on fecundity and a negative effect of the quadratic term. This indicates that as females mature, the probability of being pregnant increases, before beginning to decline at around 9 years (see Fig. 2 a). At the same time, the probability of conceiving at the autumn rut in a given year, while supporting a calf from the same year (and thus lactating), shows an accelerating decline with mother's age, immediately after first reproduction (Fig. 2 b).

Effects of density and density reduction

Effects of density on male bodyweight

When no time lag information is included in the model (density data for previous years), our model shows a significant negative effect of density on bodyweight as might be anticipated, showing that high densities are associated with lower body weights and conversely that lower densities are associated with higher bodyweight ($p < 0.001$; Table S1, time lag = 0).

In the model of best fit, density in the previous year (year prior to the year of death; D_{t-1}) and reduction in density from year t-1 to year t showed, respectively, a negative and a positive coefficient, indicating that both low density in the previous year and a reduction in density from the previous year are associated with increased bodyweight in males (Table 1). This negative influence of density and a positive relationship with density reduction is retained in all models. If we consider 2- and 3-year time lags, although such models were worse in terms of fit, all show again a significant negative effect of density and positive effect of reduction in density (Tab. S1, time lag = 2, 3). This implies that although main effects may relate to immediate reductions in density from that of the immediately preceding year, increases in
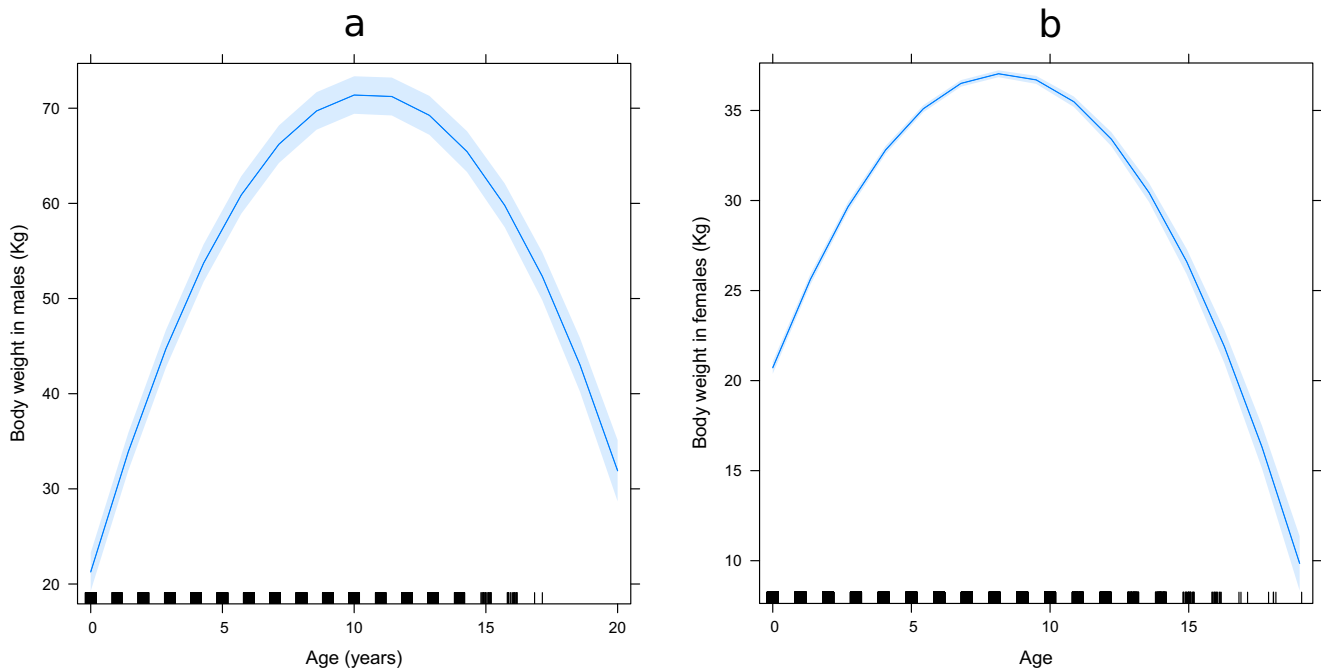
Fig. 1 Effects of age on bodyweight in Scottish red deer. The figure shows changes in body weight (larder carcase weight) with estimated age for **a** males and **b** females

male bodyweight may be responding to cumulative reductions in densities as much as 3 years later.

Effects of density reductions on bodyweight were detected even for the most modest annual or overall level of reduction. Although there were clearly significant time lags before full responses were completed, there did not appear to be any critical threshold density to which populations had to be reduced before increases in bodyweight began to become apparent.

Effects of density on female bodyweight

Similar analyses of female larder carcase weight suggest that, in the same way, there is a direct and measurable effect of current density on age-related female bodyweight with lower densities associated with higher bodyweight ($p < 0.001$; Table S2, time lag = 0) and that again there are also significant effects of reductions in density in immediately preceding years. In this case, the model with the lowest AIC score is that
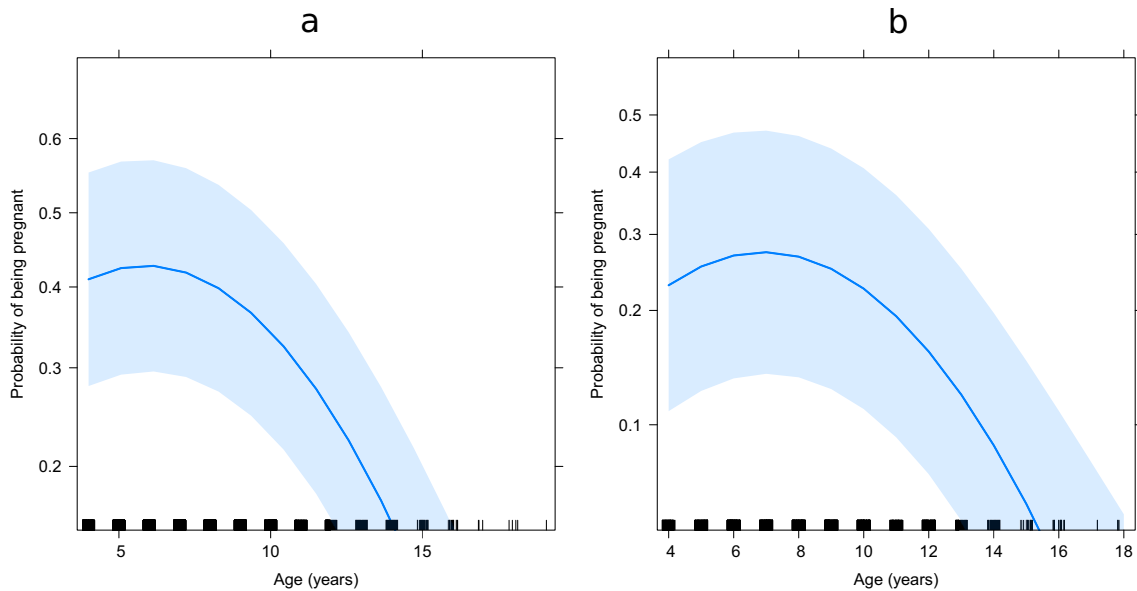

Fig. 2 Effects of age on female fecundity in female Scottish red deer. The figure shows changes with estimated age in **a** the probability of a female becoming pregnant and **b** the probability of a female already lactating in

support of a current calf conceiving in the following rut (thus simultaneously lactating and pregnant with a new calf)

Table 1 Summary of the effect of age, density and reduction of density on bodyweight in male red deer in Scotland in the model of best fit (with a time lag of 1 year). Full results of all models (time lags 0–3 years) are included in supplementary materials Table S1

Time lag (years)	Variable	β	se	p	ΔAIC
1	(Intercept)	23.28	1.973	< 0.001	0.00
	Age	8.42	0.289	< 0.001	
	Age^2	− 0.38	0.022	< 0.001	
	D_{t-1}	− 0.19	0.121	0.129	
	D_{t-1}*age	0.09	0.045	0.094	
	D_{t-1}*age^2	− 0.01	0.009	0.201	
	Red$_{t-1}$	0.98	0.297	0.001	
	D_{t-1}*red$_{t-1}$	− 0.05	0.023	0.340	

incorporating a 3-year time lag, again implying that bodyweight may be responding to the effects of cumulative culls over a preceding period of up to 3 years (Table 2, Red$_{t-3}$ $p < 0.001$).

Effects of density on probability of pregnancy among females aged 3 years or less

While it was not possible explicitly to explore age at first breeding, if age at puberty were reduced as a consequence of decreased density, the proportion of females aged 3 years or younger in our samples ($N = 1901$) which were found to be pregnant would be expected to increase. While in all models, we observe a significant effect of density and bodyweight (with females of higher bodyweight more likely to be pregnant), there was no consistent effect of reduction of density. The model of best fit (Table 3, time lag = 0) relates pregnancy within these younger females solely to bodyweight and current density.

However, the positive effect of the interaction between density and age indicates that, when density is higher, 3-year-old females are relatively more likely to be pregnant

Table 2 Summary of the effect of day, age, density and reduction of density on body weight in female red deer in Scotland, in the model of best fit (with a time lag of 3 years). Full results of all models (time lags 0–3 years) are included in supplementary materials Table S2

Time lag (years)	Variable	β	se	p	ΔAIC
3	(Intercept)	16.44	1.111	< 0.001	0.00
	Age	2.73	0.202	< 0.001	
	Age^2	− 0.16	0.017	< 0.001	
	Density	0.33	0.148	0.111	
	Density*age	0.10	0.086	0.193	
	Density*age^2	− 0.01	0.030	0.332	
	Red$_{t-3}$	2.25	0.139	< 0.001	
	Density*red$_{t-3}$	− 0.16	0.011	< 0.001	

Table 3 Summary of the effect of body weight, age, density and reduction of density on pregnancy rate in young female male red deer (age ≤ 3), in the model of best fit (relating to current density; time lag = 0). Full results of all models (time lags 0–3 years) are included in supplementary materials Table S3

Time lag (years)	Variable	β	se	p	ΔAIC
0	(Intercept)	− 5.84	2.717	0.032	0.00
	Bodyweight	0.31	0.054	< 0.001	
	Age	0.23	0.869	0.794	
	D_t	− 0.68	0.279	0.015	
	D_t*age	0.29	0.056	< 0.001	
	D_t*bodyweight	0.00	0.005	0.440	
	Age*bodyweight	− 0.08	0.021	< 0.001	

compared with younger ages; while, when density is lower, a higher proportion of younger females may be observed pregnant (Fig. 3).

Effects of density on probability of pregnancy among mature females aged 4 years or more

If we restrict consideration to animals past puberty ($N = 6633$), once again it is clear that female bodyweight is a major factor influencing the probability of pregnancy. There is a clear and significant (negative) effect of current density ($p < 0.001$; Table S4; time lag = 0). The model of best fit in terms of population reduction was that incorporating a time lag of 2 years (Table 4); in this model, the clear negative effect of density was retained, indicating that adult females in lower density areas have a higher probability of being pregnant, but there emerged no significant effect of population reduction. Results for models with other time lags suggested a similar effect (negative effect of density and a positive effect of density reduction), although they were worst in terms of overall fit (Table S4).

Effects of density on probability of pregnancy among lactating females

One of the first responses to restriction of resources among adult female red deer is that the demands of lactation in support of a current calf are so great that the female is unable to regain adequate bodyweight and condition to ovulate at the time of the following rut, resulting in a pattern of pregnancies in alternate years. If density is artificially reduced, does this result in a higher probability that females lactating in support of a current calf may also have managed to conceive a new foetus in the current year?

Results show clearly that the probability of a lactating female, aged 4 years or older, being simultaneously pregnant is positively related to a reduction in density, with a stronger effect when considering a 1-year time lag ($p = 0.002$;
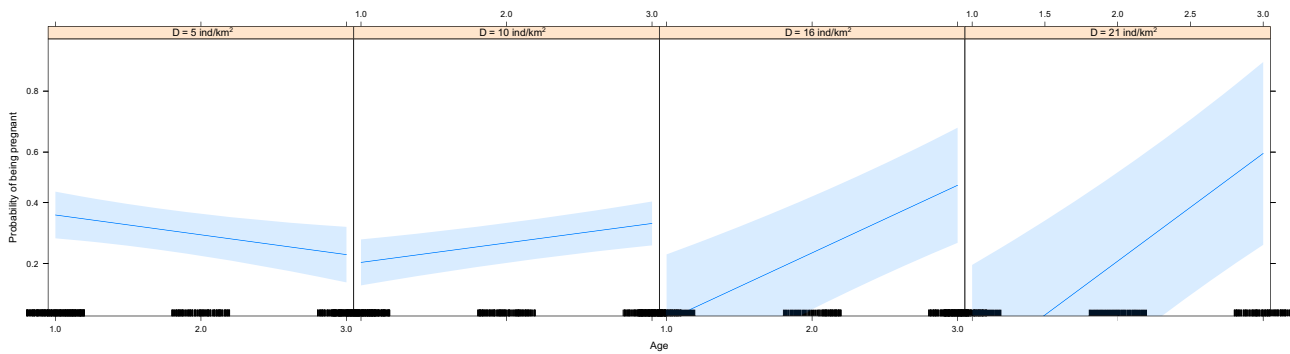
Fig. 3 Effect of the interaction between age and density on the probability of a young female Scottish red deer (age < 4) becoming pregnant. Plots from left to right show how the effect of age varies with the increase of density

Table 5); thus, the probability of a lactating female becoming pregnant again is significantly higher 1 year after the density reduction. The model also showed an overall positive effect of bodyweight, indicating that lactating females with higher weight have a higher probability of being pregnant again.

Effects of density on overall recruitment rates

The net effect of all these changes in female fecundity are reflected in overall recruitment rates observed in populations at the end of winter. Such end of winter assessments of the number of calves surviving per 100 mixed-age hinds also take account of overwinter mortality of young calves—something we cannot easily measure directly. In the model of best fit (time lag = 3), we found a significantly positive effect of density reduction ($p = 0.002$; Table 6); an effect of reduction of density was also apparent in the model for time lag of a single year ($p = 0.002$; Table S6), indicating that if we reduce density, we expect an immediate increase overall in the number of surviving calves recruited to the population (relative to

number of hinds) in the year following that reduction of density, but that the full effect of reduction of density may not be realised until up to 3 years after the commencement of reduction culls.

Discussion

Our retrospective analysis rely on data collected over a wide span of years, by different subjects with (probably) different training and background. Any incidental lack of consistency between data collection methods is likely to be a source of bias. However, with this dataset, we had a unique opportunity to explore effects of reductions in population density from a very large amount of data. We are confident that the limitations of having some 'second-hand' data, without any information for example about the variability of density estimates, are well-compensated by the large sampling. Indeed, the fact that relatively clear signals emerge, despite the potential

Table 4 Summary of the effect of body weight, age, density and reduction of density on pregnancy rate in mature female male red deer (age > 3), in the model of best fit (with a time lag of 2 years). Full results of all models (time lags 0–3 years) are included in supplementary materials Table S4

Time lag (years)	Variable	β	se	p	∆AIC
2	(Intercept)	− 1.86	1.515	0.219	0.00
	Bodyweight	0.04	0.028	0.166	
	Age	0.24	0.032	< 0.001	
	Age^2	− 0.12	0.023	< 0.001	
	$D_{t\text{-}2}$	− 0.21	0.101	0.037	
	$D_{t\text{-}2}$*age	0.02	0.019	0.315	
	$D_{t\text{-}2}$*age^2	0.00	0.001	0.254	
	$D_{t\text{-}2}$*bodyweight	0.00	0.002	0.100	
	Age*bodyweight	0.00	0.002	0.451	
	Red$_{t\text{-}2}$	0.11	0.100	0.275	
	$D_{t\text{-}2}$*red$_{t\text{-}2}$	0.00	0.007	0.684	

Table 5 Summary of the effect of body weight, age, density and reduction of density on rate of pregnancy among lactating female red deer, in the model of best fit (with a time lag of 1 year). Full results of all models (time lags 0–3 years) are included in supplementary materials Table S5

Time lag (years)	Variable	β	se	p	∆AIC
1	(Intercept)	− 7.64	2.263	0.001	0.00
	Bodyweight	0.11	0.049	0.023	
	Age	0.50	0.206	0.015	
	Age^2	− 0.02	0.010	0.010	
	$D_{t\text{-}1}$	0.09	0.150	0.558	
	$D_{t\text{-}1}$*age	− 0.01	0.011	0.585	
	$D_{t\text{-}1}$*age^2	0.00	0.001	0.733	
	$D_{t\text{-}1}$*bodyweight	0.00	0.003	0.755	
	Age*bodyweight	0.00	0.004	0.749	
	Red$_{t\text{-}1}$	0.59	0.191	0.002	
	$D_{t\text{-}1}$*red$_{t\text{-}1}$	− 0.04	0.130	0.198	

Table 6 Summary of the effect of density and reduction of density on recruitment rate in red deer in Scotland, in the model of best fit (with a time lag of 3 years). Full results of all models (time lags 0–3 years) are included in supplementary materials Table S6

Timelag (years)	Variable	β	se	p	ΔAIC
3	(Intercept)	-0.55	0.368	0.137	0.00
	D_{t-3}	-0.02	0.045	0.676	
	Red$_{t-3}$	0.09	0.030	0.002	
	D_{t-3}*red$_{t-3}$	0.00	0.002	0.643	

'noisiness' of the data, gives us confidence that relationships emerging from our analyses are generally robust.

Previous analyses of population level changes in fecundity and survival with increasing density emphasise the potentially confounding effect of changes in population age structure (e.g. Bonenfant et al. 2009). In our individual-based studies, age structure of the population is not in itself a confounding effect, but indeed our analyses do confirm clear changes in bodyweight and female fecundity with individual age, with weights and fertility rates increasing to a maximum and then showing significant decline, as shown previously in the detailed analyses of Challies (1978) or Clutton-Brock and Albon (1989). Our analyses here do, however, suggest a slightly longer time of body growth before it reaches a maximum. Data summarised by Clutton-Brock and Albon (1989) suggest that Scottish red deer hinds can continue to increase in bodyweight until their fifth or sixth year, stags until they are six or seven (where we found maximum weights achieved at 10–11 years in males, 8–9 years in females). Analyses of skeletal frame size in a sample of 4200 red deer shot in New Zealand showed a similar pattern of increase, with skeletal size reaching maximum size in females at 4 or 5 years old in females and at 6–7 years in males (Challies 1978). Clutton-Brock and Albon note a decline in reproductive performance of older females, but suggest that fecundity does not begin to fall until hinds pass their 12th year; whereas, our analyses record some decline from age 13 years. In this context, however, we should recognise that in all our data, reported ages are those presented by stalkers as estimates only, and it is not improbable that these consistently overestimate age of animals culled although the general trends are clear. Subsequent analyses correct for possible effects of age on male and female bodyweight and on female reproductive parameters. Because there is some concern about the accuracy of ages estimated by stalkers from tooth wear, we repeated all analysis with animals simply assigned to age-classes; results were broadly very similar and we elect to report results in relation to estimated actual age here.

In their longitudinal studies of changes in vital parameters of red deer in the Petite Pierre National Reserve in northeast France, comparing between periods of high and low population density, Bonenfant et al. (2002) found that both male and female body mass increased when population density decreased, but male mass changed to a greater extent than female mass. We also found clear evidence for a relationship between male carcase weight and density with significant increase in age-related carcase weights in populations where densities were artificially reduced; the model of best fit emphasises population reduction from the immediately preceding year, but effects of reduction of density were apparent with time lags of up to 3 years following reduction. Analyses of factors affecting female carcase weights suggested that there is also a direct and measurable effect of current density on age-related female bodyweight with lower densities associated with higher bodyweight, and that again there are also clear effects of density and cumulative reduction in density from up to 3 years prior to the year of death. What is notable is that responses to reductions of density were apparent and significant, whatever the initial population density (starting density) and even in relation to the most modest annual or overall level of reduction. Although there were clearly significant time lags before full responses were completed, there did not appear to be any critical threshold density to which populations had to be reduced before increases in bodyweight began to become apparent.

Over the range of densities with which we have worked, there did not appear to be any clear effect of density reduction on age at first breeding (as reflected in the number of young females pregnant) where probability of pregnancy was most closely associated with female bodyweight and current density. These results are in agreement with those reported by Langvatn and Loison (1999) from central Norway who noted no effects of density reduction on either survival rates or reproductive performance following sustained culling, suggesting that variation in both juvenile survival and age at first breeding was primarily due to stochastic fluctuation (Loison and Langvatn 1998; Langvatn and Loison 1999). By contrast, the studies reported by Bonenfant et al. (2002) showed that pregnancy rates of primiparous females increased markedly with decreasing density.

These latter authors however noted that pregnancy rates of adult hinds were fairly constant and unrelated to density. Again, by contrast, our models suggest a significant effect of reduction in population density on pregnancy rates of mature females; although, this becomes apparent only after a time lag of 2 or 3 years (Table S4). Differences between our results here and those reported by Bonenfant et al. may indeed be due to the time lag in response, or explained more simply if in fact, in a more productive, forested environment, pregnancy rates among Petite Pierre hinds, even at the highest densities, had not declined from maximum levels as substantially as those among our females in open moorland, leaving little room for any significant improvement.

In addition to direct effects of reduction in density on pregnancy rates of mature females, we found clear effects on the number of females simultaneously pregnant and lactating within the cull sample. The fact that numbers of mature hinds simultaneously pregnant and lactating increased in response to a reduction of density is almost certainly related to an increase in body weight of adult females. Once past the age of puberty, females much reach a critical threshold of body mass and condition in order to return to oestrus for the autumn rut (see Albon et al.1983; Putman et al. 1996). In resource-restricted populations, the demands of lactation in support of a current calf may be sufficient to prevent females gaining sufficient condition to return to oestrus by the time of the following rut (Mitchell et al. 1976; Albon et al. 1986). The observed increase here of the proportion of mature females simultaneously pregnant and lactating is almost certainly a result of an increase in female bodyweight and condition as a result of reduced density, allowing lactating females nonetheless to regain sufficient condition before the following rut in order to ovulate and conceive successfully (Albon et al. 1983, 1986).

As noted previously, overall recruitment rates calculated as the number of calves counted at the end of winter in relation to the total number of hinds (of all ages) offer a convenient 'integration' of both natality within the population as a whole and subsequent calf survival/mortality without need to dissect out the separate contributing elements. In our analyses, recruitment rate showed significant relationship with density and significant increase with density reductions over all time-periods, indicating that if we reduce density, we expect an immediate increase overall in the number of surviving calves recruited to the population (relative to number of hinds) in the year following that reduction of density, but that the full effect of reduction of density may not be realised until after the cumulative effect of up to 3 years of density reduction. We should note however that for this measure (as for other measures of female productivity) increases reported with reductions in overall population density are increases in *per capita* productivity. Such increases will not necessarily and inevitably translate into an increased productivity at the level of the whole population if reductions have been such that increased *per capita* rates of production are multiplied by a significantly reduced population of breeding females. We will pick up on this point further, below.

In almost all parameters considered, we found evidence of a considerable time lag in delivery of the complete response to reductions in population size, such that while there might be an immediate response to body weight or fertility to reductions in density, maximum responses were observed only in relation to the overall cumulative reduction in density achieved over a 2- or 3-year period. There might be a number of reasons for this time lag in response. Vegetational recovery following reduction of deer density is known to be delayed for some considerable period after reduction of grazing pressure (Albon et al. 2007;

Tremblay et al. 2007); while animals surviving after reduction culls may benefit immediately from reduced competition for forage resources, they will not benefit fully from increased availability and quality of forage resources until after a considerable recovery period. There may in addition be significant cohort effects, as reported by Albon et al. (1987) such that changes, particularly in reproductive performance, may become apparent among the mature female population only once animals born into the better conditions experienced at low density have themselves reached maturity. Such cohort effects are pervasive in large vertebrates (Beckerman et al. 2002, 2003; Gaillard et al. 2003) and affect several demographic parameters and phenotypic traits (body growth, body mass, survival, fertility, litter size; Bonenfant et al. 2009).

What is apparent however is that there would appear to be some asymmetry in the sequence of responses in demographic parameters to artificial reductions in density, by comparison to the widely-reported sequence of changes associated with increasing density or resource restriction (Eberhardt 1977; Hanks 1981; Fowler 1987) according to which increasing density should sequentially affect juvenile survival, reproductive rates of primiparous females, reproductive rates of adults and lastly, adult survival. This lack of symmetry was also noted by Bonenfant et al. (2002) who found that pregnancy rate of primiparous females, rather than juvenile survival, was the most sensitive trait to variation in density. Indeed, in the Petite Pierre red deer population, the first response to reduced density was in survival rates of male calves, followed by pregnancy rates of first time breeders, then adult male survival, female calf survival and lastly, pregnancy rates and survival of adult females. Although in our analyses, it is difficult to dissect out the effects of time *per se* from those of the increased overall (cumulative) reduction in population density through time, increases in male bodyweight and the proportion of lactating females returning to oestrus and conceiving in the rut immediately following parturition, respond most strongly to population reductions carried out in the immediately preceding year, while the proportion of mature females actually pregnant responds most strongly in our models to a cumulative reduction in density over a 2-year period. Responses in female bodyweight and in overall recruitment rates to the population accrue over a longer period still, responding most strongly to cumulative reductions of density over the full 3-year period considered in our analyses.

It is also evident that clarity in response may be further confused by changes in landscape-level dynamics of deer populations and the fact that, in response to reductions in density on some target property, there is increased immigration to that population from the surrounding area. A response to such heavy and sustained culling by increased immigration from surrounding properties is well-documented (e.g. Putman 2012; Wäber et al. 2013). After initial reductions, subsequent culls will thus inevitably include a proportion of recent

immigrants as well as established residents, and that proportion of recent immigrants in culls will increase the greater the reduction in resident populations (Putman 2012). This would dilute the strength of the signal revealed by our analyses since the demographic traits characteristic of those immigrants would be unaffected by density reductions on-site and influenced far more by the conditions experienced on the home site from which they have been drawn. In consequence, there may be through time an increasing distortion or dilution of the effects of population reduction on the home population because the cull contains an increasing proportion of such immigrants and the distortion will be greater, the greater the reduction achieved in the resident population. In the limit, where resident populations are reduced to near zero, culls will be composed almost entirely or recent immigrants (e.g. Putman et al. 2005). This dilution effect as a result of immigration will have a greater effect in masking the effects of density reduction on population productivity in those parameters with longer time lags of response to prevailing density.

Applicability to other species and implications for management

While we focus in this paper on red deer, many of the results are probably applicable to other species, especially where body mass is a major driver of fecundity. Our analyses suggest that the established density-dependent changes observed with increasing density of ungulate populations may be reversed to some degree where densities are subsequently artificially reduced. While there is a significant time lag in response and the sequence of recovery of the different elements of female fertility is not symmetrical with that in which productivity is suppressed with increases in density, our analyses suggest that some improvement in fertility and individual animal quality (as expressed through body weight) may be expected where population densities of resource-limited populations are sufficiently reduced.

We would emphasise again however that the responses described in this paper are responses at the individual level and, even if productivity rises *per capita*, this does not necessarily imply an increase in productivity from the population overall, since this higher individual productivity may be multiplied by a significantly smaller population of breeding females. Managers should thus remain cautious in expecting major increases in production at the population level in response to substantial reductions of the reproductive female population.

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