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Boom and bust of a moose population: a call for integrated forest management

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Abstract There is increasing pressure to manage forests for multiple objectives, including ecosystem services and biodiversity, alongside timber production. However, few forests are currently co-managed for timber and wildlife, despite potential economic and conservation benefits. We present empirical data from a commercial Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) production system in southern Norway in which moose (*Alces alces*) are an important secondary product. Combining long-term hunting and forestry records, we identified temporal variation in clear-felling over the past five decades, peaking in the 1970s. Herbicide treatment of regenerating stands and a fivefold increase in moose harvest has lead to a reduction in availability of successional forest per moose of >90 % since the 1960s. Field estimates showed that spraying with the herbicide glyphosate reduced forage availability by 60 and 96 % in summer and winter, respectively, 4 years after treatment. It also reduced moose use and habitat selection of young spruce stands compared with unsprayed stands. Together these lines of evidence suggest that forest management led to an increase in moose carrying capacity during the 1970s and a subsequent decline thereafter. This is likely to have contributed to observed reductions in moose population productivity in southern Norway and is counter to sustainable resource management. We therefore call for better integration and long-term planning between forestry and wildlife management to minimise forest damage and the development of large fluctuations in ungulate populations.

Keywords Boreal forest · Clear-cut · Deer · Forest vegetation management · Multiple-use forestry · Multi-purpose forest management

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Introduction

Few temperate forests are truly co-managed for both timber production and wildlife, despite increasing human pressure on the environment necessitating that forest managers balance commercial objectives alongside the provision of ecosystem services and maintenance of biodiversity (Swanson and Franklin 1992; Nalle et al. 2004; Becker et al. 2011). Co-managing forests for wildlife products can add to the economic yield and provide revenue on a much shorter timescale than timber production. For example, game species have an economic value derived from recreational hunting and, in some areas, meat sales (McLaren et al. 2000; Ljung et al. 2012). Bio-economic modelling has shown that combined production of timber and moose in Norway is more profitable than managing these two commodities separately (Wam et al. 2005). By contrast, ignoring wildlife, particularly large herbivores, can exacerbate wildlife–forestry conflicts (Reimoser and Gossow 1996; Kuijper 2011).

Clear-felling has been the main forest harvesting strategy in northern coniferous forests over recent decades, with mixed benefits for wildlife (Keenan and Kimmins 1993;

Nalle et al. 2004). Controversy has arisen over habitat loss of old growth-dependent species (Swanson and Franklin 1992; Wittmer et al. 2007), while early seral species thrive (Becker et al. 2011). Following clear-felling, early successional forest with an abundance of highly nutritious, young, deciduous forage develops (Regelin et al. 1987; Wam et al. 2010; Boan et al. 2011). This causes two issues for forestry: (1) competition between the commercial (coniferous) crop trees and non-commercial deciduous and herbaceous species (Strong and Gates 2006; Ammer et al. 2011; McCarthy et al. 2011) and (2) attraction or population growth of large herbivores, particularly browsing species, into regenerating clear-cuts (Reimoser and Gossow 1996; Kuijper et al. 2009), which increases the risk of damage to commercial crops such as Scots pine, *Pinus sylvestris*, in Europe (Andrén and Angelstam 1993; Hörnberg 2001) and balsam fir, *Abies balsamea*, in North America (McLaren et al. 2000). The first issue can be tackled by post-harvest mechanical or chemical treatments. In northern commercial forests, herbicides, such as glyphosate, which promote conifer dominance through the suppression of deciduous and herbaceous species, are widely used (Raymond et al. 1996; McCarthy et al. 2011). Herbicides typically control hardwood re-growth for longer than mechanical cutting, which may stimulate the production of stump shoots and suckers within one or two growing seasons (Lund-Høie and Solbraa 1993; Hjeljord and Grönvold 1988). Management of the second problem tends to focus on ungulate population control, with mixed success (Hothorn and Müller 2010; Kuijper 2011). Whether browsing damage occurs, or whether selective browsing on competing non-commercial species is able to release the crop trees from competition, depends on a number of factors including the herbivore and tree species, their densities, site productivity and stand composition (Andrén and Angelstam 1993; Danell et al. 1991a, b; Reimoser and Gossow 1996). Nonetheless, browsing damage can cause major economic costs to forestry associated with reduced stocking densities or replanting and reduced timber quality in many regions (Lavsund 1987; McLaren et al. 2000; Hörnberg 2001; Côté et al. 2004).

The carrying capacity of moose (*Alces alces*), a large selective browser, is strongly associated with young successional forest (Stephenson et al. 2006; Wam et al. 2010). Following the introduction of clear-felling as the main forest harvesting practice in Scandinavia in the 1950s and 1960s, widespread forest regeneration allowed moose numbers to increase dramatically, i.e. the 'boom' period (Lavsund 1987). A corresponding increase in the moose harvest occurred, peaking in the 1980s in Sweden and during the 1990s in Norway (Lavsund et al. 2003). Forest stands felled during the 1960s and 1970s are now approaching mid-rotation, and the current area of newly

regenerating forest is low by comparison (Lavsund 2003; Lavsund et al. 2003; Danielsen 2001). Furthermore, herbicides, particularly glyphosate, have played a major role in vegetation management in Norwegian forestry (Lund-Høie and Solbraa 1993), affecting browse production and utilisation by moose (Hjeljord and Grönvold 1988; Hjeljord 1994). Consequently, the area of regenerating forest per head of moose has declined considerably over recent decades, i.e. the 'bust' period. We believe that this may have contributed to declines in both recruitment rate and autumn carcass weights of moose populations across southern Norway, west of Oslo fjord (Wam et al. 2010; Grøtan et al. 2009; Hjeljord and Histøl 1999). Density dependence alone cannot account for the observed trends (Grøtan et al. 2009; Herfindal et al. 2006). Here, using empirical data, we aim to demonstrate that in an area of southern Norway where moose population productivity has been declining (Milner et al. 2012, 2013), carrying capacity has decreased over the same timescale, due to an erosion of the natural forage base, both as a result of herbicidal treatment of regenerating stands and changes in the timber harvesting regime. Our approach involves combining long-term forestry and hunting records with field estimates of forage availability and habitat selection patterns of individually marked moose in relation to forestry management.

Methods

Study areas

Our study area was located in Siljan and Skien municipalities, Telemark county in southern Norway (59°N, 9°E; Fig. 1). The area is owned by two private forestry companies, Løvenskiold Fossum A.S. (330 km^2) and Fritzöe skoger A.S. (615 km^2). As such, the vegetation was primarily commercially managed coniferous forest (82 % cover) dominated by Norway spruce (*Picea abies* L.) and Scots pine (*P. sylvestris* L.), but some mixed deciduous stands of birch species (*Betula pubescens* and *Betula pendula*), rowan (*Sorbus aucuparia*), willow (*Salix* spp.) and aspen (*Populus tremula*) also occur (Løvenskiold Fossum A.S. and Fritzöe skoger A.S. unpublished data; see Fig. 2 for forest age structure). Elevation ranges from 20 to 800 m with the forest line at approximately 750 m. Less than 1 % of the area lies above the treeline, where subalpine birch woodland occurs. Abundant field layer species include bilberry (*Vaccinium myrtillus* L.), cowberry (*Vaccinium vitis-idaea* L.), raspberry (*Rubus idaeus* L.) and rosebay willowherb (*Epilobium angustifolium* L.).

Moose hunting is a secondary commercial product on both properties, contributing about 1/6th of the income of forestry on Fritzöe skoger (G. Nordtun, pers. comm.).
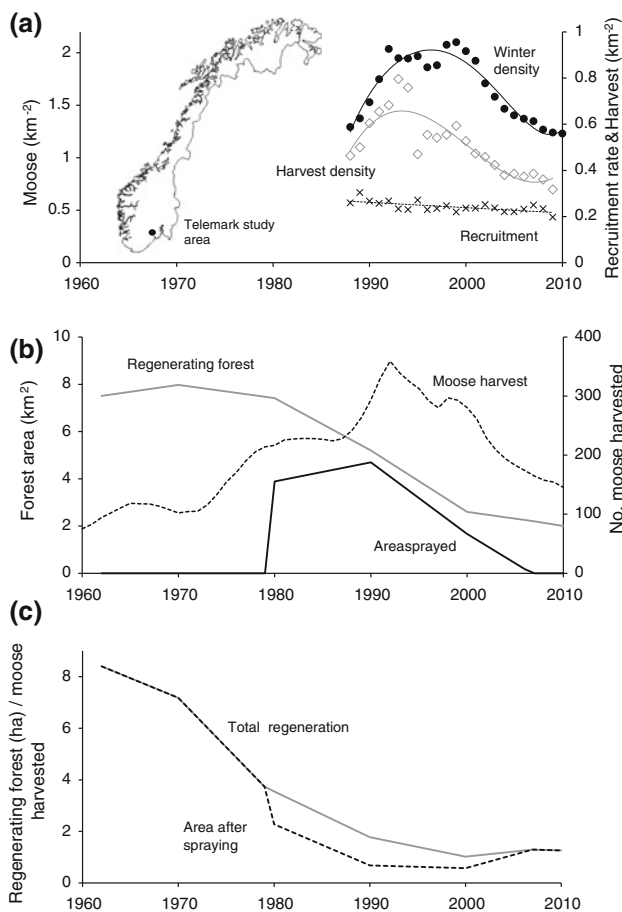
Fig. 1 Long-term trends in **a** estimated moose wintering density (moose km^{-2}), harvest density (moose harvested km^{-2}) and recruitment rate (proportion of calves among hunter observed moose) in our study area, in Telemark, southern Norway (1988–2010), **b** the total area of newly regenerating forest (km^2) created per year, area sprayed each year with glyphosate herbicide (km^2) and annual moose harvest (5-year running mean) on one property in our study area (Fritzöe skoger, 1960–2010), and **c** the area of newly regenerating forest (ha) per moose harvested (*solid line*) on Fritzöe skoger and the effective area available after spraying (*dashed line*), assuming forage production is reduced by 68 % in sprayed stands. In **c**, the moose harvest has been averaged over the time intervals at which forest data were available

Winter moose density (D) was estimated for the period 1988–2010, during which hunter observation data (Solberg and Sæther 1999) were available, using the equation:

$$D = \bar{h} \times \left[\frac{(R - M)}{(1 - R)} - \beta \right]^{-1} \quad (1)$$

where $\bar{h}$ was the average annual number of moose shot per km^2, R was the recruitment rate, M was the non-hunting mortality rate, and β was the discrete population growth rate, estimated from the equation $\beta = (e^r - 1)$, where r was the linear regression coefficient of $\log_n$ (moose seen per hunter-day) on year (Wam et al. 2010). R was estimated from the proportion of calves observed by hunters during
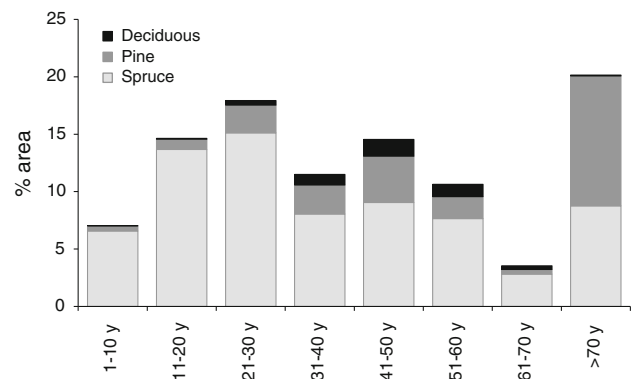

Fig. 2 The age structure of forest stands by area and dominant tree species, based on the digital stand maps from Fritzöe skoger in 2006

the hunting season but as this slightly under-estimates the proportion in the pre-harvest population, 0.02 was added (E.J. Solberg pers. comm.). M was assumed to be 0.05 (Solberg et al. 2005; Wam et al. 2010), which excluded predation mortality due to an absence of large carnivores. To produce a smoothed estimate of population density, a 5-year running mean was used. Red deer (*Cervus elaphus* L.) and roe deer (*Capreolus capreolus* L.) only occur to the south of the study area at densities of approximately 0.5 and 0.2 deer km^{-2}, respectively (S. Klasson pers. comm.).

Forest management

Detailed, long-term records of forest stand management practices were available for Fritzöe skoger A.S. These were used to determine forest harvesting patterns and usage of glyphosate herbicides in relation to trends in the moose population from 1959 to 2010. As moose density was not available for the whole period, we used moose harvest data as an index of moose population size. Variation in the number of moose harvested per year has previously been shown to be correlated with variation in moose abundance (Solberg et al. 2004; Wam et al. 2010) and was highly correlated for our population for the period 1988–2010 ($r = 0.710$; Fig. 1). Forestry records were only available as 10-year blocks of aggregated data from 1965 to 2004, with shorter intervals covering 1959–1964 and since 2005. We divided variables by the number of years in each interval to provide annual estimates of the average area of forest felled and glyphosate treated. Clear-cut spruce stands were re-planted, while pine stands were allowed to regenerate naturally. We grouped both together to give the area of newly regenerating forest (felling class I of the Norwegian National Forest Inventory). Herbicide treatments ("Roundup") were applied between 1979 and 2006 by manual spraying or from a tractor or helicopter at application rates of 1.7–4.0 l ha^{-1}.

Forage availability in relation to herbicide treatment

We measured moose forage availability within 2 stands, which were sprayed with glyphosate in October 2002, nearly 4 years before field sampling in July 2006, on one half, while the other half was left unsprayed as a control. One stand (430 m altitude, 6.5 ha), which had a field layer dominated by bilberry indicative of low to medium soil productivity (forest vegetation type A4; Fremstad 1997), had been clear-felled in 1997. The other (600 m altitude, 8.8 ha) was felled in 1999 and had a field layer dominated by small ferns, indicative of medium to high soil productivity (A5; Fremstad 1997). Both stands had a north-westerly aspect. In each half of each stand, 30 plots (5 m²) were laid out in a grid, giving a total of 120 plots. Within each plot, we counted all trees by species and measured their height, crown depth and crown diameter. The height and percentage cover of the principle field layer species were also recorded. Available summer and winter forage biomass were then estimated using seasonal species-specific multiple regression equations derived as part of another study in the same area (see van Beest et al. 2010c for full details). The regression equations related vegetation measurements to seasonal biomass of tree and field layer species. With only two stands sprayed according to the treatment versus control approach, we limited our statistical analyses to paired t tests with 2 replicas.

Moose habitat use and selection

A total of 34 adult female moose, each accompanied by a calf, were captured in January 2007 and 2008 using established techniques (Arnemo et al. 2003). Each was fitted with a global positioning system (GPS) collar (Tellus Remote GSM, Followit AB, Lindesberg, Sweden), programmed with a 1-h relocation schedule. All GPS locations collected within 24 h of capture, as well as erroneous positional outliers identified using moose movement characteristics, were excluded (van Beest et al. 2011). The average GPS collar fix rate while on the moose was 94 % (range 76–100 %), and the mean GPS location error estimated during field trials (see van Beest et al. 2010b for full details) was 29.9 m (range 8–49 m). GPS locations were collected between January and autumn with a median data collection period of 9.5 months per collar (range 2–12 months; $n = 15$ in 2007 and $n = 17$ in 2008). Two individuals were excluded due to early collar failure and winter mortality.

We assessed the forest stand classification accuracy of digital forest maps provided by the forest owners at 180 sites (94.8 % accurate; van Beest et al. 2010b). Then, within a geographic information system (GIS), we determined the felling class and dominant tree species (spruce,

pine or deciduous) at each forest GPS location used by moose (van Beest et al. 2010b), as well as whether the stand had been sprayed with glyphosate within the last 10 years. For the purpose of this study, we grouped the forest types into 3 habitats: sprayed young spruce stands, young spruce stands that had not been sprayed and all other forest types. Habitat use was calculated for each moose as the proportion of time (i.e. GPS fixes) spent in each habitat type. Proportions were normalised by an arcsine transformation for analysis by linear regression (Crawley 2007), with habitat type, season and their interaction fitted as explanatory variables. This was followed by post hoc paired Tukey's HSD tests. Habitat selection, which quantifies the relationship between use and availability, was determined using Jacob's modification of Ivlev's electivity index (Jacobs 1974). The index, J_D, was calculated for each individual as follows:

$$J_D = \frac{(r - 2p)}{(r + p - 2rp)} \qquad (2)$$

where r was the proportion of a habitat type used, based on GPS fixes, and p was the proportion of the habitat type available within each individual's home range. This was estimated from the mapped area of each habitat type within a 95 % minimum convex polygon of locations used throughout the study period by each individual (van Beest et al. 2010c). Negative J_D indices correspond to habitats that are avoided, while positive values correspond to selected habitats. We tested whether moose selection or avoidance of forest types was significant by using a t statistic to compare the Jacob's index with an index of zero, expected if the habitat was used in proportion to its availability (Revilla et al. 2000). An analysis of habitat selection using a more powerful technique, such as a resource selection function (RSF), was not possible due to high zero counts in the sprayed stands.

Results

Changes in moose population and forest management

Moose winter population density peaked in the mid-1990s at around 2 moose km^{-2}, while moose harvest density peaked a couple of years earlier (Fig. 1a). The recruitment rate, in terms of the proportion of calves of all moose observed by hunters during the hunting season, declined significantly from a peak of 0.30 in 1989 to 0.19 in 2009 ($F = 15.87$, $P < 0.001$; Fig. 1a). Although moose density and recruitment could not be estimated further back in time, the annual moose harvest on Fritzöe skoger land increased fivefold between 1960 and its peak in 1993, while the area of forest felled per year peaked in the 1970s

and subsequently decreased to a quarter of the peak (Fig. 1b). Consequently, the area of newly regenerating forest per harvested moose declined by 88 % from 8.4 ha per harvested moose in 1959–1974 to a minimum of 1.0 ha per harvested moose in the period 1995–2004 (Fig. 1c). Furthermore, in the period from 1979 until 2006, 50–90 % of all regenerating forest was sprayed with herbicide. As herbicide has the effect of reducing annual moose forage biomass by around two-thirds (0.68), the effective area of regenerating forest producing moose forage was reduced to a minimum of 0.57 ha per harvested moose in 1995–2004 (Fig. 1c). This implied a 93 % reduction in carrying capacity between the highest and lowest points. In addition, the species composition of forest has shifted towards a greater dominance of spruce amongst the youngest stands (Fig. 2), and there was a steady and significant increase in the mean altitude of stands felled across the study area since 1959 ($F = 133.3$, $P < 0.001$). Fritzöe skoger stopped spraying in 2007, which together with a lower moose population size, meant that the area of new regenerating forest per moose harvested started to increase again after then.

Herbicide treatment

A total of 279 stands have been sprayed with glyphosate across the two properties during the period 2002–2010 of which >90 % were young spruce stands. The total area amounted to 1,027 ha. Within the two half-sprayed stands, spraying with glyphosate reduced the average annual standing biomass of available moose forage by 56 %, 4 years after spraying (Fig. 3a). We estimated that annual forage availability of birch and rowan was 99 % lower (50.2 and 41.4 kg DM ha^{-1}, respectively) and willow 34 % lower (2.3 kg DM ha^{-1}) on sprayed than unsprayed areas. In addition, biomass of bilberry was 85 % lower (90.7 kg DM ha^{-1}) and raspberry 51 % lower (57.5 kg DM ha^{-1}). Despite a 169 % higher biomass of rosebay willow herb in sprayed areas, the total summer forage biomass available was 60 % (153.2 kg DM ha^{-1}) lower on sprayed than on unsprayed areas (101.5 ± 60.1 kg ha^{-1} compared with 254.7 ± 18.4 kg ha^{-1}; $t = 150.42$, $P = 0.004$), while winter forage biomass was 96 % (72.3 kg DM ha^{-1}) lower (3.2 ± 2.5 kg ha^{-1} compared with 75.5 ± 10.3 kg ha^{-1}; $t = 9.28$, $P = 0.068$). Spraying with glyphosate reduced the density of regenerating deciduous trees (Fig. 3b), although the difference was not statistically significant ($t = 3.91$, $P = 0.159$). However, spraying did not increase the density of regenerating coniferous crop trees, with an average stem density of 1,367 pine and spruce trees ha^{-1} on the sprayed part of the stands compared with 1,300 stems ha^{-1} on the non-sprayed parts (Fig. 3a).
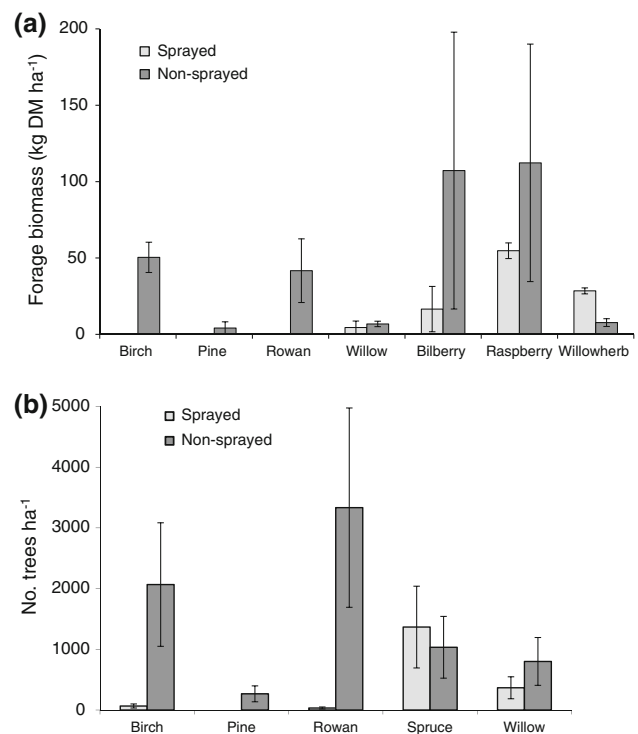

Fig. 3 a Mean annual available forage biomass (kg DM ha^{-1} ± SE) of trees and important shrub and herbaceous species and **b** mean tree density (trees ha^{-1} ± SE) in herbicide-treated and herbicide-untreated Norway spruce stands ($n = 2$), 4 years after spraying

Moose habitat use and selection

Of the 32 collared moose, 19 used sprayed stands within their home range at some point during the study period, 6 moose had sprayed stands within their home range but never used them, and 7 had no sprayed stands within their home range. The moose that used sprayed stands spent only 0.78 % (median; range 0.05–7.91 %) of their time in these stands during the study period while sprayed stands accounted for 1.52 % (median; range 0–3.72 %) of the area of home ranges (Fig. 4). Habitat use differed significantly between habitat types ($F = 769.8$, $P < 0.001$), with moose on average, spending 25 % of their time in young unsprayed spruce stands and 74 % of their time in the more widely available other forest types (Table 1). Habitat use also differed significantly between seasons ($F = 7.658$, $P < 0.001$; Fig. 4), with a lower use of non-sprayed young stands in winter compared to other seasons (Tukey's HSD: $P < 0.05$ in all cases) and a parallel increase in use of other forest types in winter (Tukey's HSD: $P < 0.02$ in all cases). Use of sprayed stands did not differ significantly between any seasons (Tukey's HSD: $P > 0.25$ in all cases).

Habitat selection also differed between forest stand types, with moose showing highly significant avoidance of sprayed stands throughout the year (Table 1). Jacob's
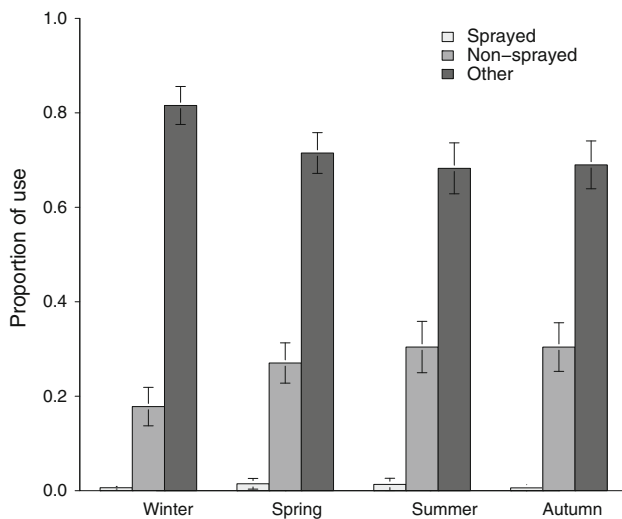
Fig. 4 Seasonal use of sprayed young spruce forest stands (sprayed), non-sprayed young spruce forest stands (non-sprayed) and all other forest stand types (other)

index of selectivity was positive for non-sprayed young spruce stands, with moose using them significantly more than expected from their availability (Table 1). Moose used other forest types significantly less than expected from their availability (Table 1).

Discussion

Our study showed a marked reduction in the absolute and per capita area of newly regenerating forest available to moose over the last 50 years. The per capita decline arose from a combination of a reduction in the total area of forest felled annually, high usage of herbicides throughout the middle of the study period and a concurrent increase in the moose population size. In addition, a shift in forest composition in younger stands away from Scots pine, an important winter forage species for Scandinavian moose (Andrén and Angelstam 1993), and the increase in mean altitude of felled stands have reduced the availability and accessibility of forage during winter. Other studies showing the effect of recent logging on subsequent forage

production have highlighted the importance of young forest in supporting wildlife populations (e.g. Visscher and Merrill 2009; Wam et al. 2010). Together these lines of evidence indicate that forest management led to an increase in moose carrying capacity during the 1970s and a subsequent decline thereafter. Similar reductions in ungulate carrying capacity are occurring throughout managed European forests (Kuijper 2011). Furthermore, Fig. 1a showed that despite the decline in moose density over the last decade, there has been no evidence of a recovery in recruitment rates, as should be expected from the theory of density dependence (Bonenfant et al. 2009). A low availability of winter browse in relation to population size has been implicated in declining calving rates within the study area (Milner et al. 2012, 2013). Unfortunately, data showing temporal changes in browsing damage to regenerating stands were not available.

Managing forests for timber and wildlife requires a long-term planning perspective, due to long rotation times and the inherent lag between vegetation successional development and ungulate population responses (Nalle et al. 2004; Visscher and Merrill 2009). The current poor demographic performance observed in southern Norway may at least partly be a lagged cohort effect from a period of more severe food limitation in the past (Wam et al. 2010). Figure 1c suggests that a particularly chronic period of limitation may have occurred during the 1990s, potentially leading to the birth of several cohorts of small individuals with poor subsequent reproductive performance.

As long as the management of timber production and moose production is not integrated, neither will be optimal (Wam and Hofstad 2007). Long-term maintenance of high-density herbivore populations supported by clear-felling is not desirable due to forest damage (McLaren et al. 2000; Côté et al. 2004) and other impacts on ecosystem functioning (Hobbs 1996; Gass and Binkley 2011). The subsequent declines due to populations tracking forest development are also undesirable from the perspective of maintaining stable harvests and steady income to the rural economy. Well-integrated wildlife–forestry production systems should therefore avoid the type of boom and bust scenario we have observed. By smoothing out the peaks

Table 1 Proportional moose habitat use and availability in Telemark forest stands and habitat selection measured with Jacob's index (mean ± SE; $n = 32$)

Stand type	Used	Available	Jacob's index	t	P
Sprayed	0.010 ± 0.004	0.011 ± 0.001	−0.498 ± 0.10	−4.96	<0.001
Non-sprayed	0.254 ± 0.016	0.206 ± 0.010	0.111 ± 0.04	2.74	0.010
Other	0.736 ± 0.016	0.783 ± 0.010	−0.108 ± 0.04	−2.72	0.011

A positive Jacob's index indicates greater use than expected from relative availability, while negative values indicate lower use. The t statistic compares the Jacob's index with an index of zero (the habitat is used in proportion to its availability). Habitat types are sprayed young spruce forest stands (sprayed), non-sprayed young spruce forest stands (non-sprayed) and all other forest stand types (other)

and troughs in forage availability, a more temporally even distribution of animals at intermediate densities could be maintained throughout the forest rotation (the even-flow timber-cutting scenario of Visscher and Merrill 2009). This is achieved by creating an even forest age structure, unlike that observed in our study area (Fig. 2). Alternatively, the boom and bust could be managed by mirroring fluctuations in forage availability with fluctuations in herbivore population size, controlled by pulsed hunting about 15 years after timber felling (Wam et al. 2005). The short-term provision of supplementary forage during restricted time periods in mid-rotation may also be an option, but we warn of the implications for localised forest damage due to long-term feeding (van Beest et al. 2010a) and stress that it will not reduce forest damage if used as a tool to increase ungulate wintering densities (Milner et al. 2012).

We only measured the effect of herbicide on short-term changes in forage biomass (4 years after application), and, as expected, biomass was lower on sprayed than on unsprayed control areas (Hjeljord and Grönvold 1988; Raymond et al. 1996; Strong and Gates 2006). Similarly, use and selection of recently sprayed sites by moose was lower than for other habitat types, as observed elsewhere (Hjeljord and Grönvold 1988; Eschholz et al. 1996). However, the duration of herbicide effects varies and depends on site characteristics, herbicide type and application rate (Raymond et al. 1996), as well as plant species, with for example, rowan being more sensitive than birch (Hjeljord and Grönvold 1988). Consequently, over the longer term (7–30 years, corresponding to the period of peak palatable biomass production (Visscher and Merrill 2009)), browse biomass on sprayed sites may be lower (Hjeljord 1994; Boan et al. 2011), similar (Raymond et al. 1996) or higher (Newton et al. 1989) than on unsprayed areas or the effect may vary with season (Strong and Gates 2006). Nonetheless with public pressure to reduce use of chemical herbicides (McCarthy et al. 2011), and voluntary restrictions on herbicide use now common in Europe (Ammer et al. 2011) including Norway (Living Forests 2007), the effects of herbicide treatment on ungulate forage availability are likely to be less of an issue in the future. However, competing vegetation will still need to be controlled using alternative methods or silvicultural techniques associated with, for example, stand manipulation and canopy management (Ammer et al. 2011; Wiensczyk et al. 2011). A variety of cost-effective silvicultural manipulations are currently being tested in eastern Norway to determine their implications for landscape-scale moose forage availability and subsequent browsing effects (C. Skarpe, pers. comm.).

Our study has shown the repercussions for wildlife of an abrupt change in forestry policy decades earlier. Although providing a sound forage base for ungulates need not be mutually exclusive to the commercial production of timber (Visscher and Merrill 2009), a better understanding of how animals respond to changes in forest harvesting regimes is needed in order to design appropriate wildlife–forest co-management plans for multi-objective forestry. We therefore call for better integration and long-term planning between forestry and wildlife management, including the assessment of herbivore forage production within forestry plans, to minimise forest damage and the development of large and potentially damaging fluctuations in ungulate populations. Such integration would ensure that wildlife and commercial land-use practices can produce sustainable benefits at the same spatial scale while anticipating changes over a long temporal scale.

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