Bio-economic aspects of moose: forage interactions – gains and compromises of interdisciplinary research

Bio-økonomiske aspekter ved elg: beite interaksjoner – fordeler og ulemper med tverrfaglig forskning

Hilde Karine Wam

Norwegian University of Life Sciences
NO–1432 Ås, Norway
Phone +47 64 96 50 00
www.umb.no, e-mail: postmottak@umb.no

Hilde Karine Wam

Norwegian University of Life Sciences • Universitetet for miljø- og biovitenskap
Department of Ecology and Natural Resource Management
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Hilde Karine Wam

Department of Ecology and Natural Resource Management
Norwegian University of Life Sciences

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PhD supervisors

Olav Hjeljord
Department of Ecology and Natural Resource Management
Norwegian University of Life Sciences
Ås, Norway

Ole Hofstad
Department of Ecology and Natural Resource Management
Norwegian University of Life Sciences
Ås, Norway

Erling Johan Solberg
Norwegian Institute of Nature Research
Trondheim, Norway

Adjudication committee

Kjell Danell
Department of Animal Ecology
Swedish University of Agricultural Sciences
Sweden

Pekka Niemelä
Department of Biology
University of Turku
Finland

Eline Hågvar
Department of Ecology and Natural Resource Management
Norwegian University of Life Sciences
Ås, Norway

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CONTENTS

ABSTRACT

• Interdisciplinary research is a prerequisite for applied progress in natural resource management. Still, most relevant studies are done by economists alone, and not in collaboration with ecologists. I discuss the ideological reasons (**PAPER I**), and conclude that value-based practical compromises are inevitable for the two groups to team up. • Our bio-economic model for optimizing production of moose (*Alces alces*) versus timber (**PAPER II**) illustrates how the compromises can be implemented. It includes management restrictions based solely on ecology and/or ethics. These strongly influenced moose demography, but had negligible economic effects. Even with very favourable conditions for moose, timber was the main source of income (>69%) on a typical Norwegian forest property. The moose density (at intermediate to extreme damage levels) was kept 40-70% lower than if optimized without concern for tree browsing damage. Factors favouring moose were: a) a high market value of the hunt; b) lower proportion of pine in the forest; c) younger forest at start of planning period; d) lower soil fertility; and e) higher interest rate (not all relationships were linear). • The model work revealed a broad need for empirical studies of moose fitness: forage interactions. To obtain large gradients in these data within the short PhD timeframe, we allocated field work spatially (twelve Norwegian ranges, 58°45'N-63°32'N), rather than temporally. • The field work unintentionally provided an opportunity to compare how the two most-used methods for estimating ungulate diet apply to moose summer browse (**PAPER III**). Fecal analyses consistently deviated from field surveys of browsed vegetation, with lower diet content of birch (*Betula* spp.) and correspondingly higher contents of the more preferred browse species. Although we could not quantify each causative factor, fecal analyses apparently gave the less accurate diet depiction. The method is nevertheless needed to quantify forage other than browse, which may constitute a large part of moose summer diet (**PAPER IV**). • Several moose studies have shown that species composition of available forage may affect consumption, but none yet as comprehensively as in paper IV. Most importantly, we found that selectivity for (and not just diet content of) birch was negatively related to availability of more preferred species such as rowan (*Sorbus aucuparia*). Also, browse selectivity was overall less pronounced in summer than in winter (selectivity for rowan decreased, while for birch it increased when going from winter to summer). These findings will have bearings on our evaluation of the quality of summer and winter ranges, respectively. A dominance of birch compared to rowan will e.g. to a larger extent make the winter range "less good" than it will for the summer range. • Our study ranges turned out to comprise two ecologically distinct moose regions, which provided a unique opportunity to look closer at the 'range quality hypothesis' (**PAPER V**). This hypothesis states that moose with more preferred forage should have better fitness due to higher yields of energy and nutrients. Contrary, though, preferred species made up only 10% of the *per capita* browse availability in our high-fitness region, and 19% in the low-fitness region. Hence, abundant preferred forage is not a requirement for Scandinavian moose to obtain and maintain high fitness. In paper V, we also quantified what determined forage availability on these ranges, of which logging was the superior factor (e.g. 6.4 times as much birch shoot-cm/m^2 in young as in older forest, depending on soil fertility).

Recommendations: • Three explicit research needs emerged from the thesis: 1) Determine what caused the low utilization of birch by the moose on our low-fitness ranges, apparently a fitness disadvantage; 2) Quantify the link between moose diet and moose fitness; 3) Establish long term studies of qualitative effects of moose browsing damage on timber trees. • The thesis' most important applied findings are: 1) Differential plant selectivity makes carrying capacity for moose equivocal, and cautions against extrapolating such data across ranges or seasons; 2) Logging activity ought to be integrated to the moose management; 3) On many ranges, even the less preferred forage should be included when monitoring moose browsing pressure.

SAMMENDRAG

• Tverrfaglig forskning er nødvendig for å oppnå en bedre forvaltning av naturressursene våre. Likevel blir de fleste relevante studier utført av økonomer alene, og ikke i samarbeid med økologer. Jeg har sett nærmere på de ideologiske grunnene (**ARTIKKEL I**), og konkluderer med at verdibaserte praktiske kompromiss er uunngåelige om de to gruppene skal samarbeide. • Vår bio-økonomiske modell for å bestemme optimal produksjon av elg (*Alces alces*) versus tømmer (**ARTIKKEL II**) illustrerer hvordan kompromissene kan implementeres. Modellen innehar forvaltningsrestriksjoner basert helt og holdent på økologi og/eller etikk. Disse påvirket sterkt elgens demografi, men hadde minimal økonomisk effekt. Selv med gode forhold for elgjakt kom majoriteten av inntektene (>69%) på en typisk norsk skogeiendom fra tømmer. Tettheten av elg (ved middels til ekstremt skadenivå) ble holdt 40-70% lavere enn dersom optimalisert uten hensyn til beiteskade på tømmertrær. Faktorer som favoriserte elg var: a) høy markedsverdi på jakta; b) lav andel furu i skogen; c) yngre skog ved oppstart av planperioden; d) lav bonitet; og e) høy rente (ikke alle effekter var rettlinjet). • Modellen avdekket et bredt behov for flere empiriske studier av forholdet mellom elgens beite og dens kondisjon. For å oppnå tilstrekkelig gradient i disse dataene innenfor den korte PhD tidsrammen, fordelte vi feltarbeidet romlig (tolv norske studieområder, 58°45'N-63°32'N), og ikke over tid. • Arbeidet ga utilsiktet en mulighet for å sammenlikne de to metodene som er mest brukt for å estimere diett hos ville hjortedyr (**ARTIKKEL III**). Møkkanalyser avvek konsekvent fra felttaksering av beitet vegetasjon, med lavere diettinnhold av bjørk (*Betula* spp.) og tilsvarende høyere innhold av mer prefererte arter. Selv om vi ikke kunne kvantifisere hver medvirkende årsak, synes møkkanalysene å gi det minst presise bildet av den faktiske dietten. Metoden er likevel nødvendig for å estimere annet beite enn lauv og bar, hvilket kan utgjøre en betydelig andel av elgens sommerdiett (**ARTIKKEL IV**). • Flere studier har vist at artssammensetning av tilgjengelige beiteplanter kan påvirke elgens utnyttelse, men ingen så omfattende som i artikkel IV. Vi fant bl.a. at elgens seleksjon for (og ikke bare bruk av) bjørk var negativt relatert til tilgangen på mer prefererte arter (eks. rogn, *Sorbus aucuparia*). Elgen viste også mindre uttalt seleksjon blant lauvartene om sommeren enn om vinteren (seleksjonen for rogn var lavere sommerstid, mens det for bjørk var motsatt). Dette vil ha betydning for hvordan vi evaluerer kvaliteten på hhv. sommer- og vinterbeitene. En dominans av bjørk sammenliknet med rogn vil f.eks. i større grad gjøre vinterbeitet "mindre bra" enn det vil gjøre for sommerbeitet. • Våre studieområder viste seg å utgjøre to beiteøkologisk adskilte regioner, og det ga en unik mulighet til å se nærmere på 'beitekvalitets-hypotesen' (**ARTIKKEL V**). Denne sier at elg med mer preferert fôr forventes å ha høyere kondisjon pga. mer effektivt utbytte av energi og næringsstoffer. Vi fant derimot at preferert lauv utgjorde kun 10% av kvistmengden tilgjengelig per dyr i regionen med høy elgkondisjon (øst for Oslofjorden), og 19% i regionen med lav elgkondisjon (vest for fjorden). Stor tilgang til preferert fôr er således ikke en nødvendighet for at Skandinavisk elg skal oppnå og opprettholde høy kondisjon. I artikkel V kvantifiserte vi også faktorer som bestemmer elgens fôrtilgang i våre studieområder, og fant at hogst var den suverent viktigste faktoren (eks. 6.4 ganger så mye bjørkekvist i ung skog som den eldre skogen, avhengig av bonitet).

Anbefalinger: • PhD-graden avdekket tre konkrete behov for videre forskning: 1) Bestemme årsakene til den lave utnyttelsen av bjørk i vest, tilsynelatende en ulempe for elgenes kondisjon; 2) Kvantifisere forholdet mellom elgens diett og dens kondisjon; 3) Etablere langtidsstudier på kvalitetsmessige effekter av beiteskader fra elg på tømmertrær. • Gradens viktigste anvendte funn er: 1) Varierende seleksjon for beiteplanter gjør det vanskelig å måle bæreevne for elg, og data bør ikke uten videre overføres verken mellom områder eller mellom sesonger; 2) Skogbrukets hogstaktivitet må integreres i elgforvaltningen; 3) I mange områder bør elgens beitepress på også mindre prefererte, og ikke bare høyprefererte, beiteplanter overvåkes.

LIST OF PAPERS

Paper I
Wam H.K. (2010). Economists, time to team up with the ecologists! *Ecological Economics* 69: 675-679.

Paper II
Wam H.K., Hofstad O. (2007). Taking timber browsing damage into account: a density dependant matrix model for the optimal harvest of moose in Scandinavia. *Ecological Economics* 62: 45-55.

Paper III
Wam H.K., Hjeljord O. (2010). Moose summer diet from feces and field-surveys: a comparative study. *Rangeland Ecology and Management* 63: 387-395.

Paper IV
Wam H.K., Hjeljord O. (2010). Moose summer- and winter diet along a large-scale gradient of forage availability in southern Norway. *European Journal of Wildlife Research* 00: 000-000- *in press*

Paper V
Wam H.K., Hjeljord O., Solberg E.J. (2010). Differential plant utilization makes carrying capacity equivocal for high density moose in Scandinavia. *Submitted manuscript*

Synopsis

FROM OPPOSITION TO COLLABORATION *(PAPER I)*

Interdisciplinary research involving ecology and economics is a prerequisite for progress in natural resource management, but as of today, still not very common. One notable example is found within the boreal forests of the northern hemisphere, where traditionally, ecologists and foresters study the same ecosystem, but rarely if ever engage in practical teamwork. The division in the research fields also reinforces a similar practice at the management level. Typically, the boreal forests are simultaneously managed by several parties that often have conflicting interests. The production of moose (*Alces alces*) at the expense of timber yield in Scandinavia is a long standing conflict (Lykke 1964; Solbraa 1998; Blennow & Sallnäs 2002) that clearly illustrates the economic counter efficiency of such management regimes (Wam et al. 2005).

The ultimate cause for the lack of research collaboration between foresters and ecologists is bipolarity in the researchers' pre-analytic visions (Wam 2010). In general, the ecologists strive for ecological achievements, while the foresters ultimately have economic goals. Of the various levels of potential oppositions between the ideology of ecology and the ideology of economics, the most pressing ones can be summarized as three prevalent maxims (in order of increasing severity): 1) the axiom of 'irreducible complexity of ecosystem functioning', which is held by many, though not all, ecologists; 2) the axiom of 'the precautionary principle', which is likely held by all ecologists; and 3) the economists' axiom of 'the tradability principle'. I argue, however, that in the majority of research scenarios relevant to natural resource management, none of these three fundamental oppositions presents a real hindrance for ecologists and economists to team up (**PAPER I**). This requires, though, that they are willing to accept value-based, practical compromises. In the first paper of this thesis I present the reasoning behind why I say such compromises are necessary.

Bio-economics has over the last two decades emerged as a potential meeting arena for ecologists and economists. It is a practice from the field of economics that may be epistemologically acceptable also to ecologists. Along with a diversification of neo-classical economics into more 'alternative' branches such as ecological economics (Söderbaum 2007), bio-economics has advanced to rather comprehensive approaches including complex techniques from not only economics, but also from ecology (Landa & Ghiselin 1999). As mathematical modelling of natural systems is in essence a practice of making compromises, it may be easier for ecologists and economists to meet in bio-economics than on other arenas. Our model for optimizing production of moose versus timber (**PAPER II**) may be taken as a proof that it can be done. More importantly, it illustrates how the aforementioned compromises can be implemented.

Prior to building the bio-economic model, we knew that quantitative data on moose fitness: forage interactions were scarce. The model work confirmed and clarified the details in this broad need for more empirical research. We therefore allocated much time and effort to field work in this PhD. In the synopsis I first present the bio-economic model, thereafter I take a critical look at the findings of the subsequent field studies, before returning to the model to compare how well its set parameter values actually fit the empirical data we ultimately obtained in the field work.

Empirical research needs ...and fulfilments

Sufficient empirical data and understanding of essential moose: forage relationships are fundamental to not only the bio-economics, but moose research and -management in general. Broadly summarized, these fundamental aspects comprise the three-way interaction between forage availability, forage utilization and animal fitness.

Most pioneer studies of wild animals start out by researching the animal's diet. This has been the case for moose as well, and a vast literature on moose diet accumulated up to and including the 1980's (Schwartz & Renecker 1998). Then the focus shifted to demography, although some notable research groups continued along the line of optimal foraging theory and plant growth strategy under varying browsing pressure (see Danell et al. 2006). Relatively little effort has been spent at comparing how plant: animal interactions relate to moose fitness and demography (but see McArt et al. 2009). Hence, there are still important gaps to fill in moose diet research.

The most basic question to answer in this regard is what constitutes moose diet given various forage availability, i.e. what we may call the moose' functional response *sensu* Holling's classic predation theory (1959). Though the subject turned out to be more complex than expected, with the data obtained in this PhD we were able to establish comprehensive explanatory models for moose diet in southern Norway (**PAPER III-IV**). Another basic question to address is to quantify the influence of diet on moose body mass and hence, the population productivity. While we did not find clear quantitative relationships in this regard, the field data obtained in the PhD did furnish some intriguing qualitative insights (**PAPER V**). Finally, there is the loop from moose utilization back to the forage plants. This reciprocal relationship is an integrated part of what constitutes the diet given various *per capita* forage availabilities. As such it is straightforward to measure empirically, but as is apparent in paper V, it may have complex mechanistic pathways. In regards to bio-economics, the relationship also includes browsing damage not measurable on timber trees until 50-100 years in time. Unfortunately no long term studies of these damages are available today. In the model, we therefore estimated the ultimate monetarily damage based on contemporary damage, for which we have rather extensive data concerning the most relevant timber species, i.e. pine (*Pinus sylvestris*) (Wam & Hofstad 2007).

BIO-ECONOMIC MODELLING OF MOOSE VERSUS TIMBER *(PAPER II)*

Model framework

The bio-economic optimization model we present in paper II is a deterministic matrix model including non-linear functions. A matrix base were chosen as the sex- and age distribution of moose as well as several aspects of the forest structure highly influence the dynamics of this herbivore: plant system. Although a simpler structure can capture much of the complexity (Wam et al. 2005), it is easier to keep track of in the matrix format. Non-linearity is inevitable when modelling complex multi-species systems, though it should be kept at a minimum in matrix models as it generally makes them less flexible for deterministic optimizations (Buongiorno et al. 1995). We therefore made the forest transition matrix stationary, which means that future timber trees followed a predetermined route with set probabilities for staying in a growth stage or moving into the next one. Furthermore, the density-dependency that was indeed necessary to include, was added as functions of aggregated variables, i.e. the sum of individuals in all stages, rather than modelled explicitly within the stage matrix itself.

A large school of scientists would probably feel that stochasticity is the one thing missing in our model framework. Stochastic events are generally considered to be of great importance in biological systems (Lande et al. 2003). Within the boreal forest it may have rather strong and long lasting consequences, e.g. through cohort effects in the moose population (Solberg et al. 2004; Solberg et al. 2008) or wind-throw of trees (see e.g. Lindroth et al. 2009), though not to the same extent as in more extreme ecosystems. We still opted for a deterministic model. I believe this is one of several

simplifications needed to comprehend the causal mechanisms in a nevertheless complex model. The time frame of our model is long (50-100 years), and hence, much of the stochastic influence will even out over the planning period. We must also keep in mind its ultimate applied purpose. As such it provides a planning tool, not a set of unbending management rules. The actual harvest of moose or timber may in any way be adjusted by the managers if stochastic events do occur.

As I see it, the one major technical limitation to our model framework is how we modelled moose browsing damage on potential timber trees. The latter was deducted as a monetary cost, but not allocated as damaged trees to the stage projections. Trying to include the damage in a more specific way would be guesswork at best, as there was an almost complete lack of data on moose selectivity in relation to species composition of available forage. I do believe, though, that our way of modelling the browsing damage was sufficient for the purpose of our paper (i.e. to illustrate the relative economic value of moose versus timber for a wide array of parameter values).

Ideological compromises

There is one aspect of our bio-economic model that sets it apart from most other related models, and that is the use of management restrictions based solely on ecology and/or ethics. This is a major compromise for the economist, as it is not in accordance with 'the tradability principle', which is likely the most important axiom of economics (as thoroughly discussed in paper I). As an ecologist who pledges biocentrism, I strongly believe that not all ecological principles or ethical concerns can be addressed by assigning a monetary value to them, or simply skipped if deemed too difficult to prize. The model thus has parameter restrictions that secure a minimum level of moose health, a minimum viable moose population level and a maximum for how skewed the moose sex-ratio can become as well as a ban on the orphaning of calves by hunting.

As expected, the management restrictions strongly influenced moose demography, but as it turned out, they had negligible economic effects. At the base scenario (i.e. with parameters values set at what we considered to be the most realistic), the effect was hardly noticeable as it reduced the net property value with less than 2%. When we maximized moose profit rather than the joint profit of timber and moose, the management restrictions still only reduced the property value with approximately 5%. Obviously, the less economic impact, the easier it will be for the ecologist to persuade the economist to include such restrictions in a bio-economic model.

Moose or timber - or rather both?

Over the last decade there has been considerable optimism for commercializing the moose hunting in Scandinavia. Although the timber in the same period had a market value eight to nine times the meat value of moose (Gåsdal & Rysstad 1999), there is a much higher potential for income from moose hunting than what is presently realized (Mattson 1990; Storaas et al. 2001). Nevertheless, in our bio-economic model, timber provided the dominating proportion of the total net value (>69%) of a typical Norwegian forest property - *even* when conditions were set very favourably for moose hunting. That does not mean, however, that there is always an economic gain in reducing browsing damages, and that the moose density therefore should be kept at the very minimum. At intermediate to extreme browsing intensity (300-2000 trees browsed per winter per moose) on our sample property, the model kept the moose density 40-70% lower than if optimized without concern for tree browsing damage (the reduction was adjusted so that the proportion of trees that were damaged was kept constant).

Moose browsing damages on potential timber trees in Fennoscandia are mainly a concern relating to the production of pine (though see e.g. Viherä-Aarnio & Heikkilä 2006). Clearly, there are properties where it is beneficial to let some or even all pine saplings be browsed by moose rather than growing into timber trees. Our model shows that the main factor governing this decision is the proportion of pine in the forest. Other factors favouring moose over timber in our scenarios were (not arranged in order of importance): a) obviously, a high market value of the hunting; b) younger forest at start of planning period; c) lower soil fertility; and d) higher interest rate. The effects of these factors were not all linearly, though. The part of the income stemming from moose was e.g. the highest for some intermediate proportions of pine in the forest. Another example is that low soil fertility favoured moose relatively to timber more than high soil fertility, but it also reduced the moose' overall potential carrying capacity. Thus, the highest number of moose was not kept at the lowest soil fertility.

The preceding examples show how complex the interactions can become in a dynamic bio-economic model, even when the number of parameters is kept relatively low. Although this level of complexity posed some challenges as to reporting the model results, interpreting them was relatively straightforward. I therefore see no need to make future bio-economic models addressing the same issue less complex. Rather I recommend adding further to the complexity, by separating the year into a winter- and summer period, respectively (for reasons discussed in the next section). Another, albeit not essential, improvement would be to make the model spatially explicit, so that it would also apply to properties where moose move between seasonal ranges and/or across property boundaries. The latter is a source of much local conflict among Norwegian forest owners (Skonhoft 2005).

DISENTANGLING THE MOOSE: FORAGE INTERACTIONS *(PAPER III-V)*

A range level approach to field studies

To obtain sufficient gradients in the needed data within the short PhD timeframe, we allocated field work spatially, rather than temporally. Our study area comprised twelve Norwegian moose ranges from 58°45'N to 63°32'N. Thus, we took a range level approach rather than conducting a traditional study at the level of individual moose. Historically, research on moose foraging has focused on the mechanisms of its functional response (i.e. intake or encounter, bite or chew) (Searle et al. 2005; Shipley 2007), which are most easily observed by following individual moose. The latter method is extensively time consuming to do in natural settings. A range level approach, on the other hand, may provide substantial data within reasonable time, aptly illustrated by the fact that the field work carried out in relation to this PhD constitutes one of the spatially most extensive foraging studies ever done on moose. We comprehensively gathered data on moose consumption and availability of all forage species, both in the tree/shrub-layer ('browse') and in the field layer ('herbaceous forage').

Three different field studies (Jul-Aug 2005-2008) were conducted in order to get an inclusive view of moose diet in relation to forage availability: 1) A plot survey, where we obtained data on moose forage availability, as well as the winter use of browse species. In total, we surveyed 8.539 plots (106.738 m²), and counted 55.738 trees, of which 26.757 had been browsed by moose. Detailed measurements on shoot availability and utilization were taken on 9.380 sample trees; 2) A belt survey, where we obtained data on the summer use of browse species. We walked 547 km and counted 143.722 trees, of which 26.369 had been browsed by moose; and 3) Microhistological analyses of moose feces, where we obtained data on the use of

herbaceous forage during summer. We collected a total of 219 fecal samples, and identified 97.583 epidermal fragments. The fecal analyses were required as use of herbaceous forage is difficult to quantify in field, and in any way cannot be measured with the same index as browse. Only survey 1) and 3) were originally intended, but these provided insufficient sample sizes for estimating summer selection of browse.

Scrutinizing the methodology *(PAPER III)*

No method exists that can measure the true moose diet with absolute precision (Ortmann et al. 2006; Wam & Hjeljord 2010), but a comparison of parallel methods may provide valuable insights as to their relative value for diet approximation. Although the microhistological analyses of feces in our study were conducted to look at herbaceous forage, it naturally also provided data on browse. Thus, we could compare how the two most-used non-invasive methods for estimating animal diet apply to moose summer browse. **PAPER III** is the first ever such study done on moose.

The fecal analyses consistently deviated from the field surveys of browsed vegetation, with lower diet content of birch (*Betula* spp.) and correspondingly higher contents of the more preferred browse species rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and willow (*Salix* spp.). The discrepancies were too consistent to simply be artefacts of our sampling procedure. Furthermore, we thoroughly checked the sample sizes for both methods, and found sufficiently low standard errors for all the main forage groups. We see four possible explanations for the discrepancies: **(a)** different time span of foraging; **(b)** differential digestibility of forage species; **(c)** bias in biomass ingested per browsed tree; and **(d)** bias in epidermal fragmentation. Apparently, none of the postulated factors could singly explain all the discrepancies:

Different time span of foraging **(a)** and differential digestibility **(b)** applied to our data, though they can only explain small portions of the discrepancies. **(a)** The feces reflected the diet in July-August, while the field survey included browsing from May-August. Previous studies of moose in the area have found that the ratio of browsed birch trees to browsed rowan trees declines over the summer, although only slightly so (Hjeljord et al. 1984; Hjeljord et al. 1990). Also, the possible bias from early summer browsing on birch is likely to be partially counteracted by birch re-foliation (Bergstrøm & Danell 1995). **(b)** Fecal analyses in general overestimate the less digestible diet portions (Cuartas & Garcia-Gonzalez 1996), though none has specifically looked at moose forage. Birch foliage would have to be several times *more* digestible than rowan foliage in order to balance the fecal and field estimates. With certainty, winter twigs of birch are *less* digestible than those of rowan (Hjeljord et al. 1982; Shipley et al. 1998). Even its summer foliage (*B. pubescens*) seems less digestible than for rowan (23% less in Hjeljord et al. 1990; 7% less in Wam & Hjeljord 2010).

Bias in the estimated biomass ingested per browsed tree may explain a larger portion of the discrepancies **(c)**. When moose browse on birch, they typically do not strip the shoot for leaves completely. By calculating various correction factors, we found that a >75% biomass reduction for birch was necessary to balance the fecal and field estimates. That means moose should have ingested less than half as much foliage per browsed tree of birch compared to rowan, which does not seem realistic in view of the low biomass available per rowan tree on these ranges. Thus, other factors must have contributed as well, such as bias between species in epidermal fragmentation **(d)**. Leaves of birch have more strength than e.g. rowan leaves (pers. obs), and may thus disarticulate in larger fragments during ingestion and digestion. Although samples were sieved to <0.2 mm, there was still some variation in the fragment sizes, possibly

causing underestimation of birch as the diet content was calculated as proportion of the number of identified fragments

Although we could not precisely quantify each causative factor, we conclude, based on previous field studies of moose foraging in the area (reviewed by Hjeljord & Histøl 1999), that fecal analyses gave the less accurate browse diet depiction. After traversing so many miles of forest land looking for moose browsing, my subjective feeling is also that birch cannot possibly have contributed so little to the herbivore's diet as depicted by the fecal analyses. The latter method still has its use, though, as it is the only practical way to obtain data on moose foraging in the herbaceous layer.

Moose diet *(PAPER IV)*

The moose diet study conducted in this PhD contributes new knowledge on moose forage selectivity (**PAPER IV)**. First and foremost it shows that the selectivity is not as straightforward as many, particularly among the hunters and managers, seem to believe. Realizing that there is no uniform selectivity codex applying to all moose ranges is important. Even if a selective feeding provides only a minor change in quantity or quality of food intake, it may cause a substantial multiplier effect on animal performance (White 1983).

The forage selectivity of our study moose was a complex product of quantitative forage availability in relation to species composition. Multiple models with availability of several plant species were therefore superior to single species models in explaining the diet content of all main forage species. In other words, the moose showed non-linear dietary functional responses. Birch was the most abundant browse on the ranges, with a shoot availability that far surpassed that of the next most common browse (pine, *Salix* spp. and rowan, in that order). Moose most strongly selected for rowan, thereafter for *Salix* spp. and then aspen, but this varied with range and season. For birch, the selectivity increased with availability, and was negatively related to availability of rowan, aspen and *Salix* spp. together, more strongly so in winter than in summer. Overall, browse selectivity was less pronounced in summer than in winter (selectivity for birch increased, while it decreased for rowan, when going from winter to summer).

The less pronounced selectivity in summer suggests that in this season, the intra-specific differences in plant nutritional content may to some extent override the inter-specific differences. Accordingly, the moose' search for nutritious plant tissue will be less linked to plant species (Hjeljord et al. 1990). Our study has thus not identified a lower need for nutritious forage in winter compared to in summer, although such a relationship is expected due to lowered metabolism (see e.g. Gaillard et al. 2000; Cook et al. 2004). Irrespectively of its proximate pathway, though, the less pronounced selectivity in summer has bearings on our evaluation of the quality of summer and winter ranges, respectively, and hence, of their relative influence on population productivity (Klein 1970). A dominance of birch compared to rowan will e.g. to a larger extent make the winter range "less good" than it will for the summer range.

In retrospect of paper IV, I advocate more application of a range level approach in order to obtain sufficient empirical data on forage species composition for herbivores. As paper IV shows; moose forage selectivity - and consequently its diet - is likely to vary with species composition of available forage as well as time of the year. I therefore also caution against indiscriminately extrapolating data between ranges or seasons.

Putting it all together *(PAPER V)*

We could not establish clear relationships between moose fitness and forage availability

(**PAPER V**), but our data did provide important insights to the matter. First and foremost, we got a unique opportunity to look into the 'range quality hypothesis' (Hjeljord & Histøl 1999). Our study ranges turned out to comprise two distinct regions in regards to forage availability and moose fitness. The 'range quality hypothesis' states that, provided forage selectivity is positively related to nutritional quality, animals with higher availability of preferred species are expected to have higher fitness (Sæther & Heim 1993, Schwartz & Renecker 1998).

The high-fitness region in our study (east of the Oslofjord, calf body mass 70.6 ± 1.22 kg) had 41% more total browse available per moose, but 15% less quality browse (i.e. rowan, aspen and *Salix* spp.) than the low-fitness region (west of the Oslofjord, calf body mass 57.4 ± 2.87). While the lightly browsed birch was the far most abundant browse available in both regions, it dominated the diet only in the east. There were clear relationships between moose fitness and accumulated browsing intensity (% of twigs browsed), but the moose densities at the time of study were not related to the forage availability. Consequently, there was no association between moose fitness and *per capita* forage availability, neither within nor across the regions. Although the study does not give reason to generally reject the hypothesis, it does show that preferred forage at least is not a pre-requisite for moose to obtain and maintain high fitness.

One particular intriguing question emerged from paper V: the western moose' utilization of birch seemed disproportionably low given the animals' low fitness. Birch constituted more than half of the *per capita* browse availability, but only 12 ± 3.5 (winter) and 24 ± 5.8 % (summer) of the browse diet (versus 44 ± 6.8 and 68 ± 7.6 % in the east). Allegedly, a higher utilization of birch would have increased the moose' foraging rates, and hence, possibly improved its fitness (see e.g. Vivås & Sæther 1987; Sæther & Andersen 1990; Nicholson et al. 2006; Bremset Hansen et al. 2009). Two likely explanations for the seemingly contradictive relationship are: **(a)** Nutritionally deviating birch; and **(b)** Cohort effects. The latter may have long lasting consequences for individual fitness in ungulates (Gaillard et al. 2003; Solberg et al. 2004; Solberg et al. 2008). The effect may also be transmitted between generations if smaller mothers produce smaller calves (Albon et al. 1987; Beckerman et al. 2002). For moose, though, there are indications that compensatory processes reduce the transmission between generations (Sæther & Heim 1993; Solberg & Sæther 1994; Histøl & Hjeljord 1995; Solberg et al. 2004). Despite the moose density in the west being almost halved since the peak in the early 1990s, it was nevertheless very high (2.0 ± 0.18 moose/km^2 in summer). Thus, cohort effects may still have influenced the fitness in this region.

The nutritional value of birch may differ between regions (see e.g. Haveraaen & Hjeljord 1981; Danell et al. 1997; Ohlsson & Staaland 2001; McArt et al. 2009). Since the geo-climatic relations were fairly similar in the two regions, a nutritional difference in birch would likely stem from soil characteristics. A lower proportion of (the more selected, Månsson et al. 2007) *B. pendula* than *B. pubescens* in the west was ruled out. In the west there was more than twice as much land with high soil fertility than in the east. In general, plant growth rates are higher on more fertile soils (Wilson 1988), and according to the theory of 'carbon-nutrient balance' (Bryant et al. 1983), the plants should thus be more palatable. However, the carbon-nutrient hypothesis has been substantially criticised for its simplicity (e.g. Hamilton et al. 2001), and we cannot rule out a different relationship before explicitly testing it.

In order to achieve a sustainable management we must be able to make prognoses about the future. Even so, very few studies have tried to quantify what determines moose forage availability. Our field data provided clear, comprehensive findings in this regard. As expected (Thompson & Stewart 1998; Hjeljord et al. 1990; Månsson

2009), the most important factor was the effect of logging on forest age structure (amplifying the overall browse availability about four times compared to in the older forest). While the effect of soil fertility was mostly negligible for browse availability in the older forest, it significantly augmented the effect of recent logging (the magnitude was e.g. doubled for birch on the richer soils). Furthermore, moose favoured the young forest when foraging: an almost 1/3 higher proportion of browsed trees was found in younger forest than expected from their availability. Also the accumulated browsing pressure was an important determinant of forage availability on our study ranges, and even this effect depended on soil fertility.

THE BIO-ECONOMIC MODEL IN RETROSPECT

Specifically, there were five moose: forage interaction parameters in the model that were set based on rather scarce empirical knowledge (Table 1). The subsequent field work successfully provided data on four of these five parameters.

In the model, browse availability for moose was expressed directly as the number of moose sustained and hence, are not directly comparable to the forage availabilities calculated in paper V (i.e. shoot-cm/m^2). However, the relative contribution of young and older forest can be compared. The model base scenario value (i.e. what we considered to be the most realistic) of moose forage in young forest was approximately 3.6 (pine) and 1.9 (birch) times that of the older forest. While the set effect of recent logging on pine availability was well in accordance with the observed value, the set effect on availability of birch was clearly underestimated (see Fig. 3 in paper V). Although this discrepancy has no bearing on the finding that timber is the main source of income in most Norwegian forests, the more economic potential there is in moose, the more important these parameter values become. In retrospect, the gathered field data will enable us to model the effects of recent logging on moose browse availability with more sophistication and precision than was actually done in paper II.

Although we have not yet looked empirically into the timber browsing damage, we can make a rough comparison of the parameter values in the model versus those observed in field (bear in mind that the species composition in the forest was quite different in the base scenario model compared to in our study area: 70% of the model forest was set to be pine, while pine was only found on 27% of the plots in the study area). Approximately 265 (accumulated browsing) and 50 (summer browsing only) trees/km^2 (all browse species included, not just potential timber trees such as pine) had been browsed by moose on our study ranges. With a moose density of 1.7 animals/km^2 (the average between the western and eastern region), this equals 150 and 30 trees/animal. In the model base scenario, 300 additional trees (all being either pine or birch) were browsed by moose each year (i.e. in addition to those browsed in previous years). This value thus seems largely overestimated for forests in southern Norway.

On the other hand, the values of α and β, which regulated the proportion of browsed trees that were actually damaged, must have been underestimated: At the model base scenario, about 5% of all available pine and birch trees together (within moose browsing height) were damaged to the extent they lost all their monetary value (at a moose density of 0.7 animals/km^2). These damage levels are not far from what we observed: 12% and 2% (Wam, unpublished data) of the sample trees of pine and birch respectively, were completely damaged by moose browsing (i.e. dead or dying). If we weight these figures after the relative species composition at the model base scenario, the average percentage is 10%. Thus, the combined effect of over- and underestimating these parameters mean we nevertheless modelled with quite realistic

Parameter	Empirical study	Model vs. observed	
Browse availability in older forest Kb (7)	Data provided	{	Effect of logging
Browse availability in young forest ε_s (7)	Data provided	{	underestimated
Effect of moose density on fitness η_k (8)	Not determinable	- - -	
No of trees browsed/moose/year tb (11)	Data provided	Overestimated	
% of browsed trees damaged a and β (11)	Data provided	Underestimated	

Table 1. Parameters[1] in need of more empirical quantification, as identified in a bioeconomic model for optimizing production of moose versus timber, as well as the outcome of subsequent field work collection and analyses of such data.

[1] Number in parentheses refers to equation line in Wam, H.K., Hofstad, O. 2007. Ecological Economics 62: 45-55.

damage levels. The fact that the browsing damage values so strongly affected the optimal moose density in the model (see Fig. 5a in paper II) underlines the need to conduct further studies of the browsing: damage mechanisms.

CONCLUDING REMARKS

This PhD thesis proves that economists and ecologists can in fact collaborate in research related to natural resource management. However, more important than simply answering whether the teamwork can be done, is to question to what extent it is beneficial. These aspects are not straightforward to measure, as 'beneficial' does not constitute the same meaning to the various parties involved. For the economists (and the anthropocentric oriented public), the beneficial gains of interdisciplinary teamwork with ecologists lie primarily in achieving a broader acceptance of the work among non-economists. Additionally, there may be the practical benefit of more efficiently obtaining the needed biological data, and hence, possibly building a better model. For the ecologists (and the biocentric oriented public), the benefit simply lies in achieving more influence, which may far surpass that of "working against" the economists when the economy nevertheless sets the bottom line.

RESEARCH NEEDS AND APPLIED RECOMMENDATIONS

The PhD uncovered the following needs for future research:

1) Determine, e.g. by using chemical and possibly also genetic analyses, what caused the apparently disadvantageously low selectivity for birch by moose in the western (low-fitness) region of our study area.
2) Quantify the link between moose diet and moose fitness, using large scale studies in order to cover the high variance in the relationship as revealed by this PhD.
3) Establish long term studies of qualitative effects of moose browsing damage on timber trees.

The following applied recommendations emerged from the PhD:

1) Differential plant selectivity makes range quality for moose equivocal, which cautions against extrapolating such data across ranges or across seasons.
2) Logging activity should be integrated with the moose management.
3) On many ranges, even the less preferred, and not just the most preferred, forage should be included when monitoring moose browsing pressure.

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Paper I

Commentary

Economists, time to team up with the ecologists!

Hilde Karine Wam *

Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Box 5003, 1432 Ås, Norway

ABSTRACT

Bioeconomic modeling is an increasingly relevant meeting arena for economists and ecologists. A majority of the growing literature, however, is written by economists alone and not with ecologists in true interdisciplinary teamwork. Physical distance between research institutions is no longer a reasonable justification, and I argue that, in practice, neither do the more fundamental philosophical oppositions present any real hindrance to teamwork. I summarize these oppositions in order of increasing magnitude as: 1) the axiom, held by many ecologists, of 'irreducible complexity of ecosystem functioning', which is avoided simply because the ecological 'whole' (as opposed to its 'parts') is not an element of most realistic modeling scenarios; 2) the axiom, also held by many ecologists, of 'the precautionary principle', which mainly surfaces at the applied end of natural resource management, and thereby should not prevent economists and ecologists from jointly building the models necessary for the final decision making; and 3) the economists' axiom of 'the tradability principle', which is harder to overcome as it demands value-based practical compromises from both parties. Even this may be solved, however, provided the economists accept non-marketable components in the model (e.g. by using restriction terms based on ecology), and the ecologists accept a final model output measured in terms of monetary value. The easiest candidates for interdisciplinary teamwork in bioeconomics are therefore researchers who acknowledge ethical relativism. As bioeconomics presently functions mainly as an arena for economists, I say the responsibility for initiating interdisciplinary teamwork rests most heavily on their shoulders.

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1. In Opposition

Traditionally, ecology and economics are bipolar research fields. Practitioners from the two fields often study the same natural resources, but tackle their task from quite opposite ideological and practical perspectives. Still, with today's widespread consensus on the ideal of sustainable management ("*Meeting the needs of the present without compromising the ability of future generations to meet their own needs*", WCED, 1987), it is inevitable that the two groups have to interact. The anticipated "times of energy scarcity" makes the interaction even more pressing (Day et al., 2009). One increasingly relevant meeting arena for economists and ecologists is bioeconomic modeling, a practice from the field of economics that may be principally and epistemologically acceptable to both parties. The literature on the subject is growing: the search string 'bio-economic* OR bioeconomic*' in the ISI Web of Knowledge[SM] database brings up 307 references pre-dating the year 2000 (7.0 per year, starting in 1956) and 572 published in the present millennium (60.2 per year, as of June 2009). Unfortunately, however, only a minority of the publications are the results of true interdisciplinary collaboration. Most seem to be written by economists, not by teams of economists

and ecologists. Why the lack of teamwork? Although there likely are far more economists than ecologists in the world, the latter group is not so scarce that this can be a major limiting factor.

One simple proximate cause may be that the two groups seldom are represented within the same research departments. It takes more effort to initiate collaboration with someone working at a physical distance from you. In the few institutions that do interdisciplinary teamwork on a regular basis, economists and ecologists normally work side by side within the same corridors (but see e.g. Sweden's Beijer Institute of Ecological Economics, which collaborates extensively with researchers across several fields and institutions). Nevertheless, in today's information era, physical distance is no longer a reasonable justification for absence of teamwork. Distant communication is both fast and easy, and the flow of information between institutions may be as instant as the flow within the institute corridor.

I believe the ultimate cause of lack of collaboration between ecologists and economists, is the bipolarity in what Joseph Schumpeter [1883–1950] would call their "pre-analytic visions". A pre-requisite for researchers from bipolar fields to collaborate productively is to acknowledge such eventual oppositions. Although there are various levels of potential oppositions between ecologists and economists, arguably the most relevant are those stemming from the following three prevalent field-specific maxims (here summarized in increasing order of magnitude): 1) the axiom, held by many ecologists, of

* Tel.: +47 64 96 57 72; fax: +47 64 96 58 01.
E-mail address: hilde.wam@umb.no.

'irreducible complexity of ecosystem functioning'; 2) the axiom, also held by many ecologists, of 'the precautionary principle'; and 3) the axiom, held by economists, of 'the tradability principle'. In this paper I argue that in the majority of bioeconomic modeling scenarios none of these oppositions are incommensurable hindrances to interdisciplinary teamwork among ecologists and economists, provided those involved are willing to compromise.

2. Recent Roots, Early Divergence

Both ecology and economics are relatively new research fields, even though ecological and economic principles were already being discussed by early philosophers, e.g. Aristotle [384–322 BCE] on economy in his work *Politics* (Jowett, 2000), and Aristotle's student Theophrastus [370–c.285 BCE] on ecology in his various works on botany (Ramalay, 1940). Ecology as a scientific term was founded by the German biologist Ernst Haeckel [1834–1919] and the Danish botanist Eugenius Warming [1841–1924] in the 1860s (Goodland, 1975). Adam Smith [1723–1790] is broadly referred to as the originator of economics (Pressman, 1999), specifically his 1776 series *The Wealth of Nations*, which has been labeled "the effective birth of economics as a separate discipline" (Blaug, 2007). Ecology and economics both evolved at the time when science parted from philosophy and the 'scientific method' emerged with fairly broad consensus (Butterfield, 1965). Accordingly, neither can claim superiority over the other on the grounds of historical maturity.

From their literal identities alone, it seems at first that ecologists and economists have more in common than not. The indiscriminate *eco* forms the terminological basis of both terms. *Eco* stems from Greek and is typically translated as *household* in the English language. Thus, ecologists and economists both include in their name a metaphor that implies they are involved with systems (as opposed to isolated elements)[1]. With the suffixes of 'ecology' and 'economics', however, the common metaphor diverges into different actions: *-logy* and *-nomy* are typically translated by ecologists and economists themselves to *knowledge* and *manage*, respectively. Although the rational interrelationship between knowledge and management (one who wishes to manage must also have knowledge) is acknowledged by both ecologists and economists, an opposition emerges through the syllables' value associations. These represent the core of the contrasting ethical beliefs of the majority of the two fields' practitioners. Ecologists and economists tend to be positioned relatively far apart on the anthropocentric–biocentric ethical axis.

3. Viewing the World from Different Centers

Arguably, in Western cultures anthropocentric ethical views are, both historically and currently, more widely distributed than biocentric views. 'Arguably' because centrisms do change over time. Today there is a wide range of anthropocentric ethics, from traditional utilitarianism to newer environmentalism bordering biocentrism (like the *Deep Economy*, McKibben, 2007). Within anthropocentrism, an illustrating example of starkly contrasting views on man's role in relation to other species, is Peter Singer [1946–] versus the Kantian ethics, i.e. the divergence between assigning intrinsic value to animals other than humans versus assigning values to these animals only on the grounds of their worth to us.

Biocentrism, on the other hand, is relatively recently defined in the western cultures, originating as late as the Victorian era 1837–1901 (Worster, 1994). Although not yet as diverse, biocentrism still has branched off from several sources, e.g. the 'deep ecology' of Arne Næss

[1912–2009] and the 'Ehrfrucht vor dem Leben' of Albert Schweitzer [1875–1965]. In its purest form, biocentrism equals the value of all life[2]. Most branches of biocentrism also consider abiotic factors integral to the ethics on living organisms, but there are variations in emphasis on individual life versus holistic ecosystem functioning (the latter exemplified by 'Gaia', Lovelock, 1979). What all branches of biocentrism have in common, and which differentiates them from anthropocentrism, is the fact that they do not consider benefit to humans or humanity to be the ultimate criterion for ethical decisions.

The personal ideological views of ecologists and economists influence both their selection of research topic in the first place, and their choice of factors to include or emphasize in their actual research. Consequently, two models for the same basic natural resource problem built by the two individual parties may turn out to have nothing more common than having the same subject under study. That practically sums up why the society needs practitioners to work interdisciplinarily.

4. Bridging the Gap with Bioeconomics?

Bioeconomics is an interdisciplinary methodology that draws on both the natural and social sciences by combining economic and ecological theories in the study of biological resource dynamics. Although Malthus [1766–1834] may be the one who (unconsciously) initiated bioeconomics in the first place (Tullock, 1999), the methodology was not formally established until the 1950s by fishery economists (Gordon, 1954, Scott, 1955, Schaefer, 1957). The first approaches involved mostly mathematics and not much economics, and typically were single-species models with no higher-order ecological relations. Over the last three to four decades, however, bioeconomic modeling has advanced to relatively comprehensive approaches that include complex techniques from both economics and ecology (Landa and Ghiselin, 1999).

Within the bioeconomic tradition, ecological economics emerged as a distinct field with an emphasis specifically on sustainable development through interdisciplinary practice (Söderbaum, 2007). The International Society of Ecological Economics (ISEE) was founded in 1989, and its peer-review journal *Ecological Economics*, has in its twenty years of existence contributed significantly to interdisciplinary exchanges between economy and ecology. Originally, ecological economics was not intended to lean more heavily on either field (Constanza, 1989). However, as Constanza said in his founding editorial, "Ecological economics will, in the end, be what ecological economists do". Bioeconomics (hitherto ecological economics) is still largely represented by economists collaborating with each other, not economists collaborating with ecologists. While the economists may no longer so clearly be labeled 'pure economists' in that they, to a lesser degree, represent traditional neoclassical economics, few would likely disagree that involving more of the 'pure ecologists' nevertheless would be beneficial in order to make progress (leaving it for the reader to define what constitutes progress).

What, then, are the hindrances? It is often said of bioeconomics that it is an attempt to bridge the empirical culture of biology and the theoretical culture of economics. That clearly describes a pertinent practical challenge to ecologists and economists meeting interdisciplinarily in bioeconomic modeling. The former comes from a predominantly empirical school, while the latter comes from a largely theoretical school. The debatable question is: how much empirical data are needed to obtain adequate knowledge? When allocating scarce research funds for theoretical model building and empirical fieldwork, respectively, a disagreement is likely to arise between two

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[1] By this I do not imply that all ecologists and economists are holistic. A few may pledge reductionism, while many do both (they have a complementary view on holism and reductionism).

[2] The majority of these are likely to acknowledge that the cognitive abilities of *Homo sapiens* are unsurpassed by any other species, and that our culture sets us morally apart (under the notion that moral duties and deficiencies are solely for humankind).

such methodologically different practitioners. In the long history of science, ecologists and economists who team up are still pioneers in their fields. Since the theory-empirics dilemma is practical, not ideological, I optimistically choose to believe it will be solved within a reasonable period of time of interdisciplinary practice. I will therefore turn to the three, more fundamental philosophical oppositions between economists and ecologists which may explain their reluctance to team up.

4.1. Irreducible Complexity

Building system models, be they biological or economic, means finding the right balance between simplicity and complexity. When a bioeconomic model is built in interdisciplinary collaboration, the trade-off discussions as to which parameters to include will be more pressing than if the same model is built by one of the parties alone. An element that particularly complicates these discussions is the axiom, held by many ecologists, of 'irreducible complexity of ecosystem functioning'. Although many ecologists have a complementary view on reductionism versus holism, i.e. they see it as necessary and rational to reduce ecosystems in order to obtain knowledge about them, some also believe that "the whole is more than the sum of its parts" (Tancred-Lawson, 1998). These ecologists may deem it difficult, though possible, to describe 'the parts' with economic language, but they may find it practically and philosophically impossible to do so for 'the whole'. Fortunately, in practice this potential opposition is seldom a non-solvable challenge in bioeconomic model building. As all modeling is simplification of reality, for most natural resources the 'whole' will not be part of a realistic modeling scenario. One exception may be models that directly addresses ecosystem functioning per se, but so far their relation to economics remains largely unexplored (Hooper et al., 2005).

4.2. 'Precautionary Principle'

The ethical element over which 'pure ecologists' and 'pure economists' most often have collided in the past is the axiom broadly accepted by ecologists of 'the precautionary principle'. It basically says that if we do not know the consequences of our actions, we shall refrain from them. More specifically it applies to actions that may do 'harm' (including actions that is not considered harmful today, but possibly considered so in the future). An essential application of this principle is that in the absence of scientific consensus on the effects of actions, the burden of proof falls on those who advocate taking the actions. It is much-quoted in politics, as exemplified by this communication from the European Commission as of February 2, 2000: "The precautionary principle applies where scientific evidence is insufficient, inconclusive or uncertain and preliminary scientific evaluation indicates that there are reasonable grounds for concern that the potentially dangerous effects on the environment, human, animal or plant health may be inconsistent with the high level of protection chosen by the EU".

In natural resource management it is traditionally the economy that drives potentially 'harmful' actions (i.e. development of land, rural employment and economic subsistence). Although few economists rhetorically dismiss 'the precautionary principle' (e.g. in their risk analyses), their approach to it is almost exclusively anthropocentric and thereby fundamentally different from that of the ecologists. This also holds for most of the economists involved in ecological economics, the subfield of economics that for the last two decades has specifically addressed sustainability. For ecologists the concept typically may include, in addition to anthropocentric precautions, the ethical responsibility towards intrinsic values of all life and the maintenance the aforementioned 'whole' of ecosystems. To use everyday language, ecologists have more reasons to be precautious,

and where economists see possibilities for human exploitation, ecologists see limitations to it.

At first thought, therefore, one would think that the 'precautionary principle' opposition creates considerable difficulties for ecologists and economists who try to collaborate. While this may occasionally be so (e.g. when particularly strong-headed researchers are involved), in my experience the opposition mainly surfaces at the applied end of natural resource management, not in the actual model building process. In this context, building the model is actually the 'easy' part; while it is harder for the managers/politicians later to implement the model findings. In the actual process of building the model, 'the precautionary principle' may create the same allocation dilemma as already discussed for model parameters in general. However, typically it is mainly the precautions that draw the two groups into collaboration in the first place, and consequently, the researchers involved more or less have *a priori* agreement on which broad-scale elements to include. The real challenge lies in how to measure them, which is an opposition that is more difficult to overcome.

4.3. 'All Things Tradable'

A central axiom in economics is that most resources can be sold in a market, and therefore assigned a monetary value (hereafter referred to as 'the principle of tradability'). Within the majority of schools of thought in economics, prices are principally set on the convergence of supply and demand. Most economists acknowledge that it is difficult to put a price on non-material goods such as mental values (hitherto personal, cultural and religious), while they also see it as a rational necessity in order to make decisions. While economists may have several approaches to the problem of pricing non-material goods, they basically all use people's or societies' willingness to pay either by revealed or stated preferences (Whitehead et al., 2008), with the preferences being subject to supply and demand.

For some ecologists the tradability axiom may be an 'incommensurable' opposition, to phrase it with the liberally used term and concept of Thomas Kuhn [1922–1966]. Kuhn said of incommensurability that it "…causes fundamental problems in communication between proponents of different paradigms…This problem cannot be resolved by using a neutral language for communication…" (Kuhn, 1970). The challenge of linguistic incommensurability between ecologists and economists should be negligible. It only demands a willingness to be each others' 'translators' (Kuhn, 1970), which I personally see as my moral duty rather than as my choice when involved in research funded by the society.

Kuhn (1969) clearly stated that scientists with incommensurable theories should in no way shun communicating with each other. According to Kuhn, it is this particular communication that may lead to scientific progress. While Kuhn basically treated paradigms within disciplines in his work on scientific revolutions, his theories of incommensurability may also apply interdisciplinarily. This is not to imply that interdisciplinary bioeconomic modeling necessarily leads to scientific progress, although it may lead to applied progress such as a more comprehensive land use management.

What distinguishes a bioeconomic model from purely ecological or purely economic models is the combination of biological entities and monetary values. Every input parameter must be assigned a value, either a cost or a benefit which negatively or positively influences the output measurement. Indirectly, the prices do not have to be monetary values. Forage for wildlife for example can be valued as the number of animals sustained per entity. Likewise, the value of a reduction of biodiversity in a national park can be impacted by a decrease in the number of visiting people. Ultimately, however, these entities are valued in terms of money in the model's output statement (another numéraire may be used, e.g. energy (Gilbert and Braat, 1991, p. 41), though see Månsson, 2007).

For ecologists particularly the pricing of non-material goods may be ideologically challenging (Rappaport, 1993). Economists have tried to acknowledge intrinsic value e.g. through the concept of 'existence value' (Aldred, 1994), which may broadly be defined as value of an object apart from human use of it. While some mental values, such as to know that a species will exist in the future, are probably acknowledged by many ecologists to fall within the concept of existence values, the majority of ecologists will principally object to the pricing of intrinsic values per se (see e.g. Attfield, 1998 versus Aldred, 1994). This is a vast debate not necessary to reiterate here, suffice it to say that the objection centers on the paradox of evaluating non-human value with human measures.

Likewise, 'non-tradable' ecological processes and principles cannot be straightforwardly quantified. When faced with this problem in bioeconomic modeling, I find that the solution is to include the elements as restrictions terms. For example when modeling production of moose versus timber (Wam and Hofstad, 2007), we were challenged by the biological fact that sex ratios of moose must not exceed a certain skewness in order for cows to find adequate mates (Solberg et al., 2002). We put no direct monetary value on the sex-ratio principle, but rather included it simply as a model restriction term. Although it would be philosophically more demanding to do the same for intrinsic values per se, in practice it can be done quite easily (e.g. by applying the principles of minimum viable populations as model restriction terms). Such non-priced restriction terms mean the economists have to compromise regarding their 'tradability principle'. Such philosophical compromises demand relativism, i.e. an open mind and a willingness to view one's own knowledge[3], beliefs and values not as absolute truths.

5. Inevitable Relativisms

Relativism versus absolutism has probably been the object for more philosophical thought than any other issue throughout man's existence. It has caused much debate, from Platon's [c. 424–348 BC] innate knowledge versus the Sophists (like Protagoras [490– 420 BC]) to the 20th century "Science war" with participants such as Paul Feyerabend [1924–1994] and Alan Sokal [1955–]. The more recent controversies center much on scientific method, where relativism by some has even been aligned with anarchism: "The displacement of the idea that facts and evidence matter by the idea that everything boils down to subjective interests and perspectives is – second only to American political campaigns – the most prominent and pernicious manifestation of anti-intellectualism in our time" (Laudan, 1990). However, even the perception of being a relativist is relative. For a relativist it is not illogical to be an ethical relativist, and simultaneously have a (more) absolute view on scientific knowledge.

"Wilderness is the raw material out of which man has hammered the artefact called civilization... To the labourer in the sweat of his labour, the raw stuff on his anvil is an adversary to be conquered. So was wilderness and adversary to the pioneer. But to the labourer in repose, able for a moment to cast a philosophical eye on his world, that same raw stuff is something to be loved and cherished, because it gives definition and meaning to his life" (Leopold, 1949). As the American naturalist Aldo Leopold [1887–1948] wrote of wilderness in his Sand County Almanac: "How we perceive and value something is individual". This particular quote illustrates relativism in all its philosophical senses; cognitive, ethical and aesthetical. When it comes to management of natural resources (and hence, bioeconomic modeling), cognitive, ethical and aesthetical relativism all matter. In this particular context the cognitive and aesthetical becomes part of the ethical. The ethics concerned involves taking into consideration anthropocentric values such as human happiness and experiences of

mastering and identity, of which in all the aesthetical is an integral part (Hågvar, 1999). With the cognitive here becoming part of the ethical relativism, I address the (to me) fact that what individuals see as objects in this context (i.e. natural 'resources'), is so influenced by our values that we may see differently. Physically a tree is a tree, but for reasons reflected in the oppositions discussed throughout this text, our translation of a tree into a 'resource' is relative. A collaborative bioeconomic model is therefore ethical relativism in practice, an exercise in making ideological compromises and finding the "least common denominator". Compromise, however, is not automatically negative. Under the moral norms of ethical relativism, compromise might in fact be the right thing to do!

6. Conclusions

I have argued that the three potentially incommensurable oppositions between the traditionally bipolar research fields ecology and economics, may all be overcome (in the context of bioeconomic modeling): 1) the axiom, held by many ecologists, of 'irreducible complexity of ecosystem functioning' is of no real hindrance as the ecological 'whole' (as opposed to its 'parts') is seldom an element of most realistic modeling scenarios. 2) The axiom, also held by many ecologists, of 'the precautionary principle' mainly surfaces at the applied end of natural resource management, and should not prevent researchers from building the underlying, interdisciplinary models. 3) The economists' prevalent axiom of 'the tradability principle' is an opposition of fundamental character, but can be solved with a willingness to compromise by both parties: the economist must accept non-marketable components (e.g. use of restrictions terms based on ecology) in the model, and the ecologist must accept a final model output measured in terms of monetary value. The easiest candidates for interdisciplinary teamwork in bioeconomics are therefore researchers who acknowledge ethical relativism. As bioeconomics currently functions mainly as the economists' arena, I say the responsibility for initiating interdisciplinary teamwork rests most heavily on their shoulders.

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[3] Knowledge as what we personally perceive to know, not concerning undisputable scientific facts, see section 5.

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Paper II

METHODS

Taking timber browsing damage into account: A density dependant matrix model for the optimal harvest of moose in Scandinavia

Hilde Karine Wam*, Ole Hofstad

Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, 1432 Ås, Norway

A B S T R A C T

At present there is a growing optimism in commercializing the moose hunting in Scandinavia. We developed a deterministic, dynamic bio-economic model to examine the optimal management of land with both moose and timber as potential sources of income. We show that most forest owners should target their moose commerce towards increased quality of the hunt rather than quantity. Due to the inherent complexity of moose: forest interactions we ran the model for a wide array of parameter values to check its sensitivity. Although it was the combined production of timber and moose that gave the highest net value in all run scenarios, timber was the major source of income (69% or more). The main single-factors favouring moose over timber was: low timber productivity of the soil and high moose prices in the market. Also factor synergies can strongly increase the relative value of moose. Our model may serve as a decision tool for choosing the economically optimal moose levels in populations with no across-border migration. It highlights the following need for further studies: I. Quantifying the relationship between browse availability (forest state, moose density) and moose condition (weights, fecundity). II. Quantifying the relationship between browse availability and timber browsing damage.

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1. Introduction

There is currently a conclusive need for integrating the management of timber and moose production in Scandinavia. While some forest owners still view the moose as a great threat to their income (Blennow and Sallnäs, 2002), there is also a growing number that highly value it both for recreational and economic reasons (Storaas et al., 2001). Depending on the preferences of forest owners involved, the number of moose is seldom adjusted to neither the ecological nor the economic carrying capacity.

Partly the lack of co-ordination is due to a distinct separation of decision-makers. Although Scandinavian land-owners hold the right to both trees and wildlife on their property (and may extensively influence its management), traditionally few engage in the active management of both resources. In forestry, landowners individually decide how much timber to cut at any time, given the laws' sustainability criteria are respected. The moose harvest in Norway is decided by a board of county authorities and representatives for the hunting units, the latter typically are elected hunters with or without land property rights. The majority of hunting units involve several properties. Prior to 2002 landowners had considerable less influence on the moose harvest. Hunting quotas were then decided by municipality authorities, while county authorities had some responsibility for deciding the

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* *Corresponding author.*
  E-mail address: hilde.wam@umb.no (H.K. Wam).

quotas' sex- and age structure. The involvement of hunters/ landowners varied from absent to dominating in different areas.

Even modelling work on moose and timber production has been kept separate, despite their highly potential inter-relationship. There now exists an extensive literature on forest yield models (for recent reviews, see Porté and Bartelink, 2002; Sedjo, 2003). Although a lot fewer, also moose yield models are assembling (e.g. Sylvén, 1995; Moen et al., 1998; Sæther et al., 2001). Models that combine the two, however, stem from a comparatively new practice and are not yet very comprehensive (Nersten et al., 1999; Kalén, 2004; Skonhoft, 2005; Wam et al., 2005).

Different modelling paradigms between wildlife biologists and forest economists are the major reason for the lack of (comprehensive) moose-timber yield models. With bio-economic modelling, though, the two groups can meet on more common grounds (Clark, 1976). Here we present a bio-economic model for optimizing the moose and timber harvest when both have potential income value. While the optimization in our model is done mainly from an economic perspective, it also includes biological concerns that are usually viewed as difficult to address in terms of monetary value.

2. Model development

Our model is developed for forest planning over a variable number of years on properties with only one decision-maker (a single owner or several owners joined). We assume that the property is large enough for the across-border migration of moose to be negligible. Consequently, we do not address distribution issues related to the costs and benefits of migratory moose and different right holders (for such a discussion see Olaussen and Skonhoft, 2002).

2.1. Model structure

Trees and moose are projected at one-year intervals, assuming discrete reproduction and mortality. The number of individuals is counted after harvest, immediately before reproduction. A suitable model for the growth of both trees and moose is a modified stage-version (Usher, 1966, 1969) of the basic Leslie matrix model (Leslie, 1945). If $\mathbf{M}_t$ is the number of moose present in the forest at time t, then:

$$\vec{\mathbf{M}}_{t+1} = \mathbf{M} \cdot \vec{\mathbf{M}}_t - \vec{\mathbf{H}}_t \tag{1}$$

where $\vec{\mathbf{M}}_t$ is the vector of population stage structure at time t, $\vec{\mathbf{H}}_t$ is hunting stage structure and $\mathbf{M}$ is the population projection matrix, which is given as:

$$\mathbf{M} = \begin{bmatrix} 0 & 0 & 0 & f_4 & 0 \\ \frac{s_1}{2} & 0 & 0 & 0 & 0 \\ \frac{s_1}{2} & 0 & 0 & 0 & 0 \\ 0 & s_2 & 0 & s_4 & 0 \\ 0 & 0 & s_3 & 0 & s_5 \end{bmatrix} \tag{2}$$

where f is calves produced per cow per annum (primary fecundity, not influenced by density, see later for density effects), and s is the probability for animals in one stage to

survive until next year. Reflecting what is recognizable for the hunters, we have five stages of moose: 1=calves (0–1 years), 2 and 3=female and male yearlings (1–2 years), 4 and 5=older cows and bulls (2+ years). Only cows 2+ years may reproduce. For simplicity we assume that calves contribute 50:50 to the male and female yearling segment, although in reality this ratio may be skewed (see Andersen and Sæther, 1996 for a discussion).

Likewise, though slightly more complicated, we can make an Usher–Leslie matrix for the trees. Let $F_{t,s}$ be the number of trees in stratum s at time t. A stratum is composed of two variables: tree species and soil productivity. Hence, one particular stratum is made up of all trees of a certain tree species growing on land with the same level of soil productivity. The development of each stratum is modelled as:

$$\vec{\mathbf{F}}_{t+1,s} = \mathbf{F} \cdot \vec{\mathbf{F}}_{t,s} - \vec{\mathbf{U}}_{t,s} + \vec{\mathbf{R}}_{t,s} \tag{3}$$

where $\vec{\mathbf{F}}_{t,s}$ is the vector of stratum stage structure at time t, $\vec{\mathbf{U}}_{t,s}$ is harvesting stage structure and $\vec{\mathbf{R}}_{t,s}$ is recruitment stage structure (stemming from timber harvest, recruitment only to stage I, no recruitment across strata). The stratum projection matrix $\mathbf{F}$ is given as:

$$\mathbf{F} = \begin{bmatrix} (1-g_1)q_1 & 0 & \cdots & 0 \\ g_1 q_1 & (1-g_2)q_2 & \cdots & 0 \\ 0 & g_2 q_2 & \cdots & 0 \\ \vdots & & & \vdots \\ 0 & 0 & \cdots & (1-g_i)q_i \\ 0 & 0 & \cdots & g_i q_i \end{bmatrix} \tag{4}$$

where q_i is the probability for trees in stage i to survive until next year and g_i is their probability to grow into the next stage. Trees are allowed to move a maximum of one stage at each projection interval. We have ten different stages of trees, I–X. Stage I are trees fully covered by snow in winter and not available to moose (0.0–0.5 m). Stages II and III are trees within all-year moose browsing height (0.5–3.0 m). The remaining stages are trees with their crown fully above moose browsing height.

Note that in our model the volume growth of individual trees is not density dependant, i.e. our forest matrix is stationary. A stratum follows a pre-scheduled development through the growth stages, where natural and selective thinning is included in the mortality factor (as a set constant for each stage). A tree is considered mature (it no longer increases in volume) when it reaches stage X. Harvest may take place in all stages but the first three.

Most interactions between moose and its forage are largely density dependant, so we want to introduce non-linearity to our basic Leslie models, although matrix models with non-linearity are less flexible for deterministic optimization (Buongiorno et al., 1995). In order to retain as much of the linearity as possible, we include density dependance through functions of aggregation variables, i.e. the weighted sum of all individuals in all stages. The general form for including such functions to our moose projection is:

$$\vec{\mathbf{M}}_{t+1} = \vec{\mathbf{M}}_t + D(M_t) \cdot (\mathbf{M} - \mathbf{I}) \cdot \vec{\mathbf{M}}_t - \vec{\mathbf{H}}_t \tag{5}$$

where $\mathbf{I}$ is the identity matrix of $\mathbf{M}$, and $D(M_t)$ is the density dependant function we want to include. In our model moose

fecundity, moose weights and moose browsing depend on population density:

Moose fecundity is made density dependant by letting the logistic function:

$$D(M_t) = 1 - M_t/Km_t \tag{6}$$

operate on recruitment of moose to the first stage (calves). Moose carrying capacity Km has two components: (a) Primary carrying capacity (Kb), defined as the number of moose in the winter population sustained (surviving) if all forest stratums were in the mature stage (stage X). Moose browse must then come from a patch mosaic of vegetation underneath and in-between mature trees. (b) Added carrying capacity stemming from trees within moose browsing height (stages II and III). Mathematically:

$$Km_t = \sum_{s=1}^{S} [Kb + \varepsilon_s \cdot F_{t,s}], \quad s \in \{II, III\} \tag{7}$$

where ε_s is a species-specific constant that transforms trees into nutritional value for moose in terms of an added number of animals to the primary carrying capacity.

A number of moose is hunted each year ($h_{t,k}$), and the hunt is traded in the marked. The income from one moose consists of: (a) a per kilo meat price (pm) which depends on the weights of the animals (wm_k). (b) a sex- and age-specific hunt price per animal hunted (ph_k), that does not depend on the individual weights. The latter may reflect for example the recreational value of the hunt. Total moose income (πm) is:

$$\pi m = \sum_{t=1}^{T} \sum_{k=1}^{K} \delta^t \cdot [ph_k + pm \cdot wm_k \cdot [1 - M_t/(\eta_k \cdot Km_t)]] \cdot H_{t,k} + MEV \tag{8}$$

where the constant η_k adjusts the density influence on animal weights (a stronger influence on calves and yearlings than for older animals). δ^t is the discount factor and MEV (moose expectation value) is the net present value of all future moose hunting on the property counting from the end of the planning period. The MEV will contribute to determine the final size, sex- and age structure of the moose population at the end of the planning period. There exists no established tradition for calculating expectation values for moose, but a simplified parallel to forest theory is:

$$MEV = \delta^T \cdot \left[\sum_{k=1}^{K} [ph_k + pm \cdot wm_k \cdot (1 - M_T/(\eta_k \cdot Km_T)) \cdot (1 + \varphi \cdot M_{T,k})^{-1}]/r \right] \tag{9}$$

where r is the interest rate and φ is a constant that regulates the economic effect of having more or less moose present in the forest at the end of the planning period. With Eq. (9) we assume that all future huntings will be stationary and on an annual basis.

Trees are harvested at various stages in each stratum, and sold as timber. The total profit (πf) is:

$$\pi f = \sum_{t=1}^{T} \sum_{s=1}^{S} \delta^t \cdot (pf_s \cdot u_{t,s} - cf_s - cr_s - af - cM_t) + FEV \tag{10}$$

where δ^t is the discount factor, pf_s is the net price per m^3 of timber cut in stratum s, $u_{t,s}$ is the m^3 cut at time t in the stratum (all trees of the same stage in a stratum have the same volume), cf_s is fixed cutting costs in the stratum, cr_s is the costs of recruiting new forest after cutting in the stratum and af is the administrative costs of managing the entire property. Fixed cutting costs are zero as long as no timber is cut. For large properties administrative costs may operate even without any timber harvest. cM_t is the costs of having moose in the forest in terms of browsing damage on trees in stages II and III, which depends on the number of moose in relation to its carrying capacity at time t:

$$cM_t = \delta^{T_H} \cdot pf \cdot tb \cdot \sum_{k=1}^{K} (M_{t,k} \cdot b_k) \cdot \frac{\alpha \cdot \exp^{\beta \cdot M_t \cdot Km_t^{-1}}}{1 + \alpha \cdot \exp^{\beta \cdot M_t \cdot Km_t^{-1}}} \tag{11}$$

where δ^{T_H} is the discount factor T_H years in time, which corresponds to the time it takes for the average tree of stages II and III to reach the mature stage. The monetary value of this average tree is pf. The constant tb is the number of trees browsed by an average moose annually (assuming that moose re-browse trees (Lÿttyniemi, 1985; Bergqvist et al., 2003), while the age-specific constant b_k adjusts the relative browsing influence of the different moose categories. The two constants α and β regulates the proportion of browsed trees that are completely damaged, i.e. loose all their monetary value. The proportion will be higher when the moose population is close to its carrying capacity.

In Eq. (10) FEV (forest expectation value) is the present net value of all future rotations on the property counted from the end of the planning period, calculated by Svendsrud (2001) as:

$$FEV = \delta^T \cdot \sum_{s=1}^{S} \sum_{n=1}^{N} \left[\delta^{n-T} \cdot \left(H_{n,s} + \frac{H_{n,s}}{\delta^{-n}-1} \right) - c_s \cdot \frac{\delta^{-T}}{\delta^{-n}-1} \right] \tag{12}$$

where $H_{n,s}$ is the net income from harvesting the stratum at age n, and c_s is the cost of recruiting new forest on the site after harvest. In Eq. (12) we assume that no thinning is undertaken.

When reporting results we express profit in terms of the numerical denominator PTU (pine timber unit), defined as the market value paid to the forest owner for 1 m^3 prima quality pine, cutting costs deducted (variable costs, not to be mistaken with fixed costs).

2.2. Moose management restrictions

Not all elements of biology can be adequately addressed with economic theory. In our model we have four moose management concerns included as simple restriction terms:

(i). Observed calves per cow 2+ years (moose fecundity as influenced by density) must stay ≥0.6 to secure a minimum health condition (which is reflected in the fecundity).

(ii). Moose density must stay ≥0.07 animals per km^2 not to die out (since we assume no immigration).

(iii). The cow:bull relationship in the 2+ age segment must stay ≤1.8 to limit potential delayed parturition dates (see Sæther et al., 2003) or skewed sex-ratio among born calves (see Sæther et al., 2004).

(iv). Calves shall not be orphaned due to hunting, i.e. the number of hunted cows cannot exceed the number of hunted calves divided by the observed calves per cow ratio. Another practical reason for hunting calves is the

need for short-term population adjustments (e.g. to harvest harder on a weakened cohort to mitigate potential long-term effects). When moose pass the yearling stage specific cohorts are no longer distinguishable in field. The sex-ratio tends to be skewed towards males if a cohort is harvested as yearlings vs. as calves (due to the hunter's fear of shooting the allegedly "holy cow").

The levels of (i) and (iii) was set in accordance with observed rates in the Norwegian moose population (Solberg et al., 2006). However, there exists no consensus on which levels that are optimal in view of relevant goals and so the matter is open for discussion. Surely it is not impossible to include all these restrictions as input functions (see e.g. Sæther et al., 2001 for fecundity effects of a skewed sex ratio), but arguably the complexity they add would not benefit the aim of this particular model.

2.3. Model parameter calibration

Forest transition matrix parameters were set in accordance with Braastad (1975, 1977) and Brantseg (1969), so they produced forests that, left alone, had a steady state corresponding to their anticipated climax forest (tree density and volume). Timber volumes (m^3 per tree under bark including top and bolt) were obtained from Vestjordet (1967) and Brantseg (1967), and initial tree densities (number of trees per ha in the youngest stage) from Tomter (1999).

Empirical validation data for the forest transition matrix was obtained from Stangeskovene AS (Eidskog, Norway). Their inventory data (1981, 1990 and 2004) covered approximately 10.500 ha productive forest of which 60% on poor soil productivity, 28% intermediate and 12% high. Spruce and pine comprised 60% and 40% respectively of the standing biomass. Of the initial standing biomass (1981) approximately 40% was young forest (stage class III or lower), and 20% was mature (stage class X). Basically their forest and moose management were separated in the period. The moose has still influenced the actual forest growth, though, and we chose not to exclude it from the validation runs.

The actual timber harvest has been somewhat higher than predicted by the model, resulting in less standing biomass (Fig. 1a) and more forest within moose browsing height (Fig. 1b). Unfortunately only grouped harvest out-take was available (not specified for species or soil productivity), so we could not examine it further. Though we believe the observed discrepancy is no more than the inherent noise expected with such complex data. Hence, we did not a posteriori adjust our forest growth parameters.

Moose transition matrix parameters were set based on work on Norwegian moose. Fecundity and weight data were obtained from Solberg et al., (2006). We set the annual natural mortality rates for moose (all causes apart from hunting and predation) at 10% for calves and 3% for other stages (based on Stubsjøen et al., 2000; Solberg et al., 2005). As there is little empirical data available, it is difficult to quantify moose carrying capacity, not to say its density effects on moose weights and fecundity. Our effort here is based on comparing harvest statistics, population levels and forest productivity in
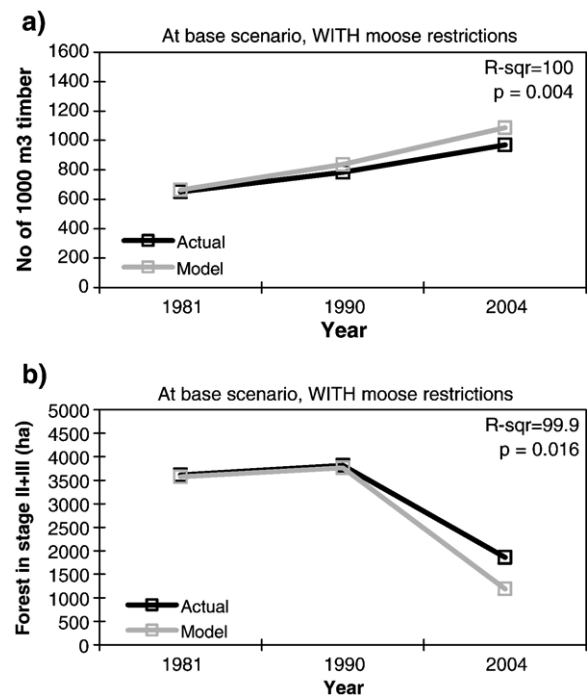
Fig. 1 – a) Standing timber biomass at Stangeskovene AS (Norway) as measured through forest inventories and as predicted by an optimization model for moose and timber harvest in Scandinavia. The latter with the objective to maximize net value of *total forest profit* over 50 years given certain moose management restrictions[1]. b) As in 1a, but showing forest within browsing height for moose (stage class II + III).

Norway with a few studies from North America that have shed some light on carrying capacity for moose (Crête, 1989; Schwartz and Franzmann, 1989; McLaren and Peterson, 1994).

Moose: forest interaction parameters was set using the work of Edenius (1992), Härkönen (1998), Persson (2003) and Kalén (2004), which are all studies geographically within Scandinavia. We have further used the work of Bergström and Danell (1987), Randveer and Heikkila (1996), Danell et al. (1985, 1997), Bergström and Bergqvist (1999) and Jalkanen (2001) to adjust the browsing parameters between the different browse species. Despite the many studies done on moose: forest interactions, we still do not have enough knowledge about this complex issue to adequately quantify the relationship. The level of browsing impact will in any way be site-specific, and thus need to be adjusted if the model is implemented in a real planning scenario.

2.4. Model sensitivity

The model was ran as a non-linear numerical optimization problem in GAMS (distribution 20.7-Windows NT) using CONOPT2® as the solver (Brooke et al., 1998). As an illustration property we chose a 67.000 ha forest (43.000 ha productive soil) in south-central Norway, with Scots pine *Pinus silvestris*,

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[1] (i). Observed calves/cow must stay ≥ 0.6, (ii). the no of moose ≥ 0.07 per km2, (iii). the cow:bull Relationship ≤ 1.8 and (iv). the no of cows shot $\leq$ the no of calves shot/observed calves per cow.
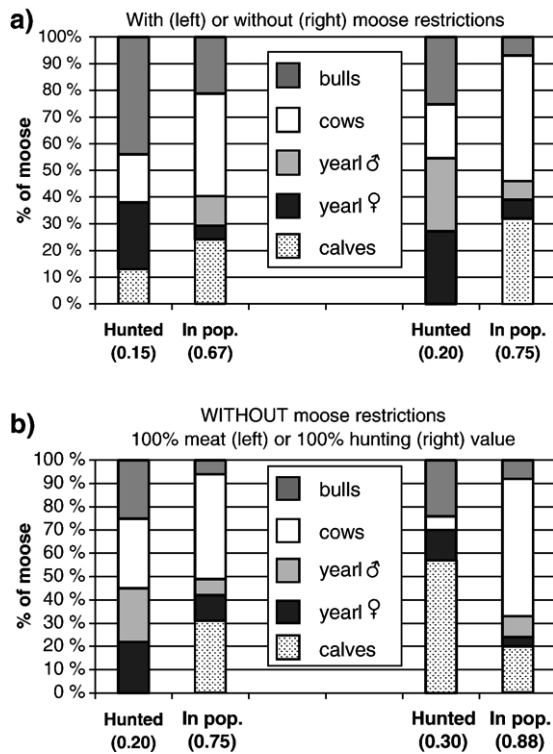
Fig. 2 – a) Effects of moose management restrictions (i–iv)[1] on optimal sex- and age composition of hunted and living moose at steady state of an optimization model for moose and timber harvest in Scandinavia. With the objective to maximize net value of *total forest profit* (base scenario). The numbers along the *x*-axis are moose/km². b) Effects of varying the relationship between moose meat and hunt value (without varying total moose value) in the model ran without restrictions. For comparison; in the base scenario (Fig. 2.a) meat contributed 89% to total moose value.

respectively. The proportion of the initial standing stock was set to: 19% each of stages I and II, 21% stage III, 15% stage IV, 8% each of stages V and VI, 4% each of stages VII and VIII), and 1% each of stages IX and X (making it a relatively young forest).

As most outputs of interest were qualitative, we found traditional statistical sensitivity analyses not to be the right tool for investigating parameter sensitivity. Instead we chose an adjusted scenario-analysis approach focusing on one parameter at a time. We started from a base scenario where parameters (to our best knowledge) resemble the most typically encountered in Scandinavia. From the base scenario we re-scaled parameter values up- and downwards to see the effects on model output such as profit, moose population structure, browsing damage and harvest outtake in terms of timber and moose.

Originally our objective function was to maximize net property value throughout a planning period of 50 years, irrespective of whether the income came from moose or timber. However, with this objective moose typically made up less than 10% of the income. Hence, in order to check the sensitivity of moose parameters, we also ran some scenarios to maximize the model for moose profit (not total profit) which equals a situation where moose is the major source of income.

In the Results section we use the term "steady state". Note that our steady state does not mathematically correspond to the term as used when reporting from a simulation model. Rather we use the term ad-hoc for years showing stable output levels, and the purpose is simply to ease the reporting of our results.

3. Results

3.1. Effects of moose management restrictions

Economic effects of having moose management restrictions (Section 2.2) were negligible. When maximizing for total forest profit, net property value was 59 PTU/ha with vs. 60 PTU/ha without restrictions (in 2006 one PTU was approximately €40 in the Norwegian market). Even when maximizing for moose profit, the effects were small: net property value was 57 PTU/ha with vs. 54 PTU/ha without restrictions (of which only 11% and 15% stemmed from moose, the remaining from timber). We therefore report economic results with moose management restrictions within the model.

Norway spruce *Picea abies* and birch *Betula pubescens* as potential timber trees. For simplicity we ran the model with only three classes of soil productivity: poor, intermediate and high (yielding 300, 338 and 450 m³ pine per ha in stage X). For those familiar with the H40 classification system used in Norway (Tveite, 1977) this represents H40≤11, 14–17 and ≥20,

Table 1 – Varying parameter values in an optimization model for moose and timber harvest in Scandinavia using a property of 67′ ha land (43′ ha productive) as an illustration example						
Base scenario			Re-scaled scenarios			
Moose parameter	Value		Value	PTU/ha (M%)	Value	PTU/ha (M%)
Primary carrying capacity (Kb) (moose per km²)	1.5		0.5	55.3 (9.7)	5.0	59.3 (20.0)
Added carrying capacity (ε_s) (pine, birch)[a]	20, 7		10, 3	55.3 (9.6)	40, 14	58.0 (15.9)
Primary fecundity (calves per cow)[b]	1.0		0.7	55.1 (6.0)	1.4	56.4 (17.1)
Net property value over time (PTU/ha)[c]	55.6					
% of property value from moose (M%)[d]	11.1					

With the objective to maximize net value of *moose* profit over 50 years (Given that observed calves/cow ≥0.6, moose population ≥0.07/km², cow: bull relationship ≤1.8 and no calves are orphaned due to hunting.). Only one parameter was re-scaled in each scenario.

[a] One ε=0.2 moose/km² added per ha forest in stage II to the carrying capacity for moose. Spruce contribution is negligible and not shown.
[b] In the model the primary fecundity is further influenced by moose density in relation to carrying capacity. Cows are 2+ years of age.
[c] One PTU = the price of 1 m³ prima quality pine (cutting costs deducted), i.e. approximately €40 in the Norwegian market (2006).
[d] The remaining stemming from timber production.

Biologically, however, the effects of moose management restrictions were more evident, in particular on the sex- and age composition of hunted and living animals (Fig. 2a). Restriction iii (cow:bull relationship) limited the hunting of bulls, so that there were approximately 2.5× as many bulls in the population as when run without moose restrictions. Restriction iv (no orphaning of calves) introduced hunting on calves compared to 0% calf hunting when run without restrictions. Without any restrictions moose density was kept higher (thereby reducing cow fecundity), but more cows were kept in the population creating an overall higher calf production. Consequently the proportion of the population that was hunted increased from 22% to 27% (stabile moose population).

The restrictions also influenced whether we saw effects of varying the relative contribution of meat vs. hunt to total moose value (without altering the total value relative to timber). As meat values depended on weights (and moose density) as opposed to hunt values, we expected the relationship to affect the structure of both hunted and living moose. With moose restrictions, however, we found no effects for the whole range from 0 up to 100% meat contribution. In contrast, without restrictions percentage meat contribution had substantial effects on the sex- and age composition (particularly of hunted animals, Fig. 2b). Most noticeable was the increase from no calves among hunted moose with 100% meat contribution to 57% calves among hunted with no meat contribution (total moose value was made up of 100% hunt value).

Restriction i (calves per cow) and ii (minimum population) affected the moose density in conjunction with other model parameters, and is therefore treated in Sections 3.2 and 3.3.

3.2. Varying moose parameters

Varying the carrying capacity for moose had only minor effect on economic output (Table 1, moose profit maximized as when maximizing total profit we found no effects of varying either moose parameters listed in Table 1). Still, it had noticeable effects on the optimal moose density. When increasing the carrying capacity (moose profit maximized), either through the primary or the added capacity, the moose density was kept higher (Fig. 3a–b, shown for primary capacity). A 10-fold capacity increase led to a 5-fold density increase, both with and without moose restrictions in the model.

At the base scenario, the actual carrying capacity for moose was made up 1:1 by primary and added capacity, with pine being the major contributor to added capacity (Fig. 3c). Doubling the value of ε (i.e. doubling the number of moose/km[2] added to the capacity per ha forest in stage II or III), changed the relationship to 1:2. Over time and due to the varying timber harvest, moose carrying capacity ranged from 2.9 to 5.6 moose/km[2] (Fig. 3d).

Varying moose primary fecundity showed stronger effects on moose density when the model was run with vs. without moose restrictions (moose profit maximized, Fig. 4a–b). With restrictions, a doubling of the fecundity led to a 4-fold increase
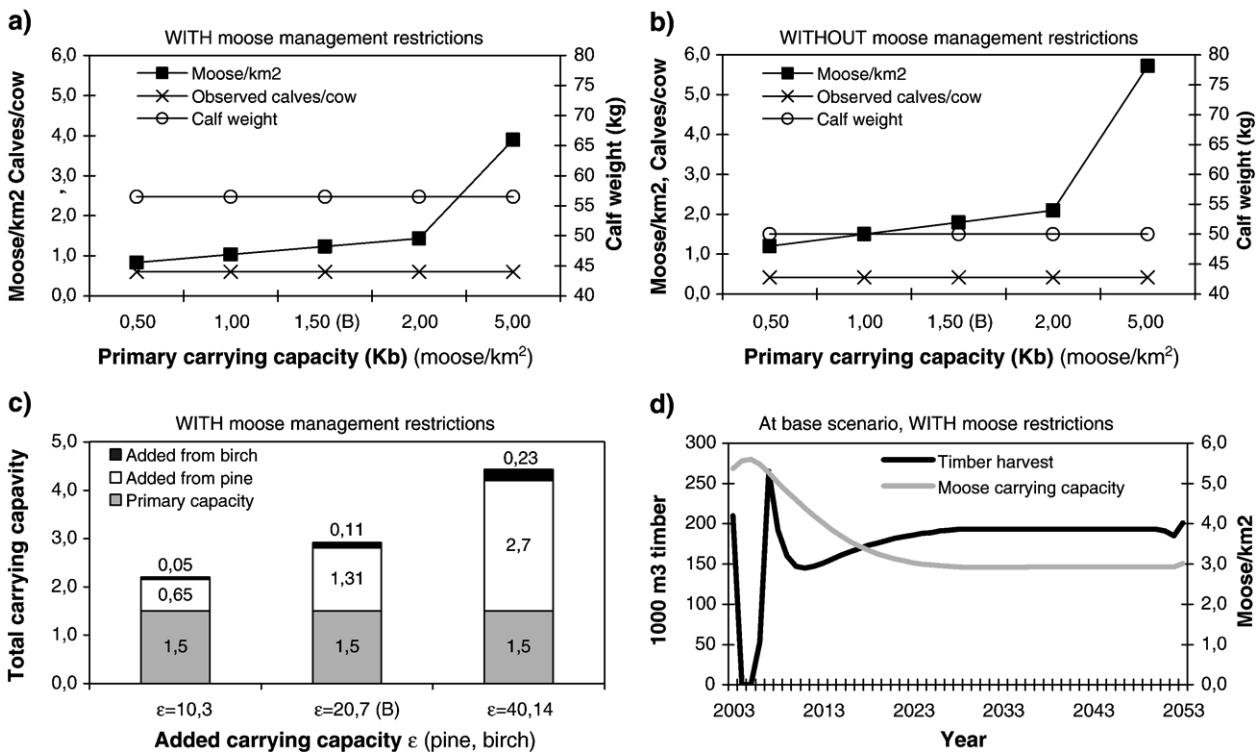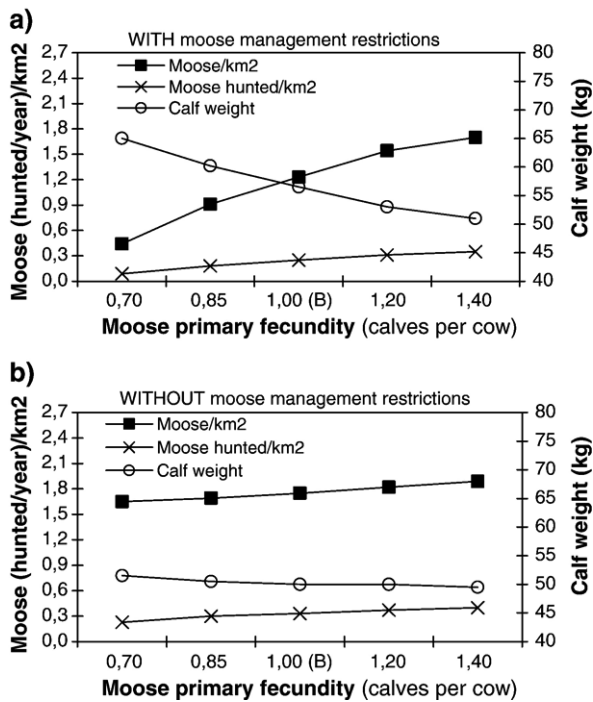

Fig. 3 – Varying primary carrying capacity (Kb) and its effect on optimal moose density, calf weights and observed calves/cow at steady state of an optimization model for moose and timber harvest in Scandinavia. B = base scenario value. With the objective to maximize net value of *moose profit* a) given or b) not given certain moose management restrictions[1]. c) Primary carrying capacity for moose and capacity added by trees within moose browsing height (pine and birch, one ε equals 0.2 moose/km[2] added per ha of forest in stage II or III). d) Total carrying capacity for moose vs. timber harvest (pine and birch) over time.

Fig. 4 – Varying moose primary fecundity and its effect on optimal moose density, moose harvest, and calf weights at steady state of an optimization model for moose and timber harvest in Scandinavia. *B* = base scenario value. With the objective to maximize net value of *moose profit* a) given or b) not given certain moose management restrictions[1].

in density. Following, calf weights dropped from 65 kg to 51 kg. Irrespective of the value set on primary fecundity, 20% of the moose population was hunted when ran with restrictions as

the observed fecundity (as influenced by density) remained constant (at 0.6 calves per cow). When ran without restrictions, however, doubling the primary fecundity from 0.7 to 1.4 calves born per cow increased the proportion that was hunted from 14% to 19% (Fig. 4b). The observed calves per cow ratio then increased from 0.33 to 0.54.

3.3. Varying moose:timber interaction parameters

Also moose:timber interaction parameters had minor economic effects (Table 2, total forest profit maximized). When varying browsing intensity, the moose density was adjusted to keep browsing damage level at 0.5% (Fig. 5a). Consequently the timber harvest remained the same (Fig. 5b). A total of 201 m³/ha was harvested throughout the planning period of 50 years, of which pine, spruce and birch contributed 88%, 8% and 4% respectively. Whether moose management restrictions were included had only minor and no directional effects on browsing damage and timber harvest.

To better illustrate the relationship between browsed and damaged trees, we also optimized the model for maximum moose profit (Fig. 5c–d). At the base scenario, the timber harvest was then reduced to approximately 100 m³/ha. Due to the linearity of the involved functions, the number of damaged trees increased proportionally to the value set on browsing intensity. At the most 38% of all pine and birch in stages II and III were damaged (maximized for moose profit, no management restrictions and the most extreme value of tb, number of trees browsed by moose per year.)

3.4. Varying miscellaneous parameters

As opposed to lack of economic effects of aforementioned parameters, there were four miscellaneous parameters that expectedly and strongly influenced the monetary output in the

Table 2 – Varying parameter values in an optimization model for moose and timber harvest in Scandinavia using a property of 67′ ha land (43′ ha productive) as an illustration example

Base scenario		Re-scaled scenarios			
	Value	Value	PTU/ha (M%)	Value	PTU/ha (M%)
Moose–timber interaction parameter					
No of trees browsed/moose/annum (tb)	300	100	60.1 (9.9)	2000	57.2 (7.0)
Browsing damage constant (α)[a]	0.021	0.007	59.9 (9.8)	0.035	58.9 (8.8)
Miscellaneous parameter					
Species % (spruce, pine, birch)[b]	10,70,20	70,10,20	50.5 (8.0)	10,20,70	35.8 (12.6)
Stage distribution (% in I, II, III, X)[c]	19,19,21,1	30,31,32,1	47.7 (7.2)	1,1,1,91	322.0 (1.9)
Soil productivity (% low, medium, high)[d]	20,70,10	90,10,0	16.7 (31.1)	0,10,90	110.9 (4.8)
Interest rate (%)	3	1	110.0 (5.9)	5	38.1 (12.0)
Moose meat price (PTU per kg)	0.3	0.1	56.0 (3.1)	1	70.1 (23.8)
Moose hunt price (PTU bull, other)	4,12	1,3	58.3 (7.5)	50,150	66.6 (19.7)
Net property value over time (PTU/ha)[e]	58.7				
% of property value from moose (M%)[f]	8.8				

With the objective to maximize *net value of total forest profit* over 50 years (Given that observed calves/cow ≥0.6, moose population ≥0.07/km², cow: bull relationship ≤1.8 and no calves are orphaned due to hunting.). Only one parameter was re-scaled in each scenario.
[a] Determines the % of browsed trees that will loose all monetary value (but still be available for moose browsing in their relevant age span).
[b] Percentage composition of productive forest area.
[c] Percentage of forest in the different growing stages (intermediate growth stages IV–IX is 1% each) at the initial phase of the planning period.
[d] Soil productivity in terms of the soil's inherent potential to produce timber.
[e] One PTU = the price of 1 m³ prima quality pine (cutting costs deducted), i.e. approximately €40 in the Norwegian market (2006).
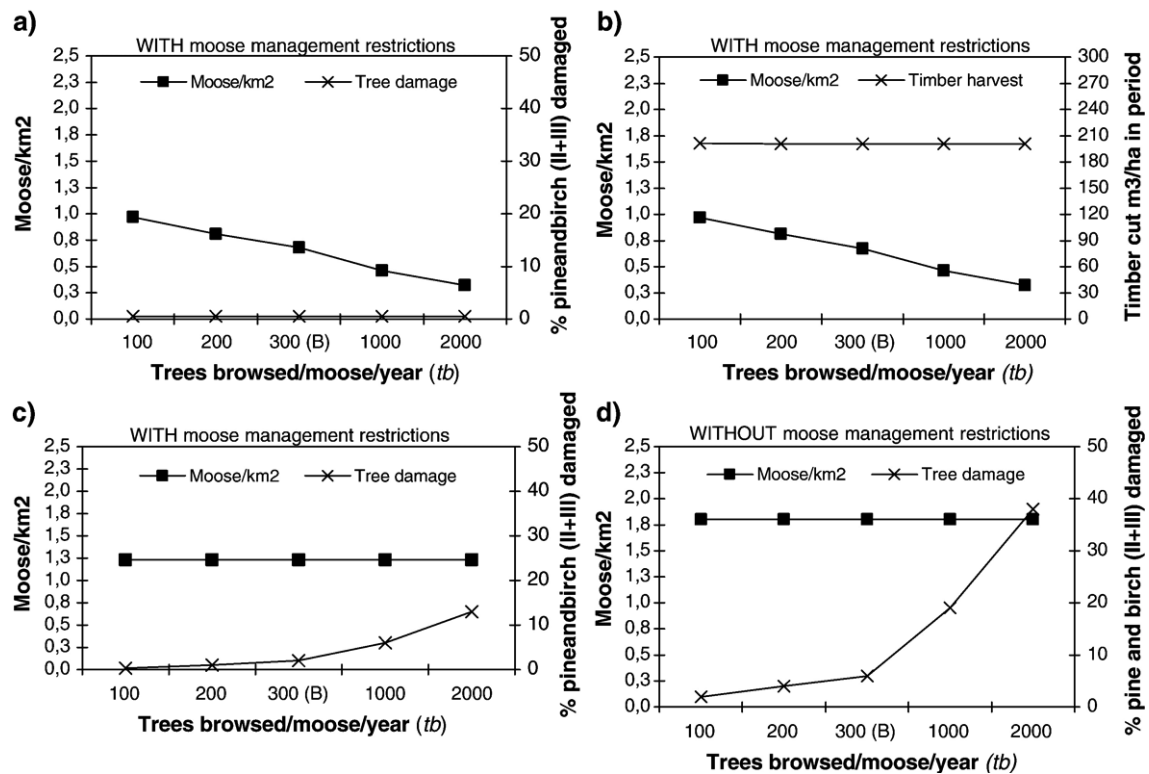[f] The remaining stemming from timber production.

Fig. 5 – a–b). Varying number of trees (stages II and III) browsed per moose per annum (tb) and its effect on optimal moose density and % of browsed trees that is economically damaged at steady state of an optimization model for moose and timber harvest in Scandinavia. *B* = base scenario value. With the objective to maximize net value of *total forest profit* given certain moose management restrictions[1]. In 5b timber harvest is shown instead of tree damage. c–d). As for 5a–b, but with the objective to maximize net value of *moose profit* and given or not given the moose management restrictions.

model (Table 2, total profit maximized): tree species composition, tree stage distribution at start of period, soil productivity and interest rate. All four parameters also affected the percentage of income stemming from moose. A lower proportion of the forest being pine, more trees in the lower growth stages at start, a lower average soil productivity or a higher interest rate all led to more of the income generated by moose hunting (albeit marginally only for some of the parameters). For the first two factors, however, the relationship was not straightforward: percentage income stemming from moose was highest for some intermediate value.

Our last miscellaneous parameters, the price set on moose, had only minor effect on the level of total economic output, although it more evidently affected the moose' relative contribution to it (up to 24% of the income stemming from moose at the most extreme meat value).

4.   Discussion

4.1.   Model framework

Considering fellow researchers' rising interest in the influence of randomness on biological systems (Lande et al., 2003), for many the most obvious shortage of our model framework will be its lack of stochasticity. With due right; moose:forest interactions do have stochastic elements. One possible exam-

ple is lasting cohort effects stemming from a stochastic influence on moose carrying capacity (Solberg et al., 2004). Another example is the temporary effects of occasional wind storms on moose browsing availability. Still, we believe that for our particular model purpose stochastic elements would add unnecessary complexity. Our model is developed to aid in long-term planning. We believe that normally stochastic effects are balanced within our planning period. In practice, the actual outtake of a forest system like ours may in any way be adjusted if and when serious stochastic events occur (like an unusual severe winter or a large wild fire).

Moose fecundity depends not only on moose density (as in our model), but is also age-specific with birth-rates being lower for very young and very old moose (Ericsson et al., 2001). When young moose constitute only a small proportion of hunted animals in the population, the mean age of the reproductive segment is reduced by two correlated mechanisms: more adult moose are shot and more young-stock is recruited. Although this dynamic was not included here, it can easily be incorporated. Mathematically we can achieve this by adding the following ratio to the moose density function $D(M_t)$ (Eq. (6)):

$$D(M_t) = (1 - M_t/K_m) \cdot (h_{y,t-1}/h_{y,max})^\mu, \; h_{y,t-1} \in \lfloor 0, h_{y,max} \rfloor$$

where $h_{y,t-1}$ is the percentage of yearling females that were hunted one year ago, and $h_{y,max}$ is the maximum percentage of these one can allow to be hunted and still balance subsequent

recruitment to the older stage. The constant μ adjusts the actual level of reduction in calf recruitment.

Summer- vs. winter browse for moose contributes differently to moose condition (Sæther and Heim, 1993; Renecker and Schwartz, 1998; Schwartz and Renecker, 1998; Hjeljord and Histøl, 1999). Thus a substantial improvement of our model would be to make this distinction. However, to do this we need more empirical research. The relationship is not straightforward: Although it is generally understood that summer browse is the most important, the effects of limited (high-quality) summer browse may to some extent be compensated by winter browse in surplus and vice versa. The degree of compensation will vary with climate and geomorphology. Furthermore, mechanisms may operate not only directly on the individual, but also through maternal pathways (ovulation, gestation and lactation).

If we could differentiate the browse in our model to summer vs. winter we could also include another element of carrying capacity currently left out: the short-term access to logging waste. When timber is logged, the extra forage made accessible to moose may be considerable, particularly from pine (Hjeljord et al., 1987). However, this forage will only be of any value for moose during winter (that stemming from conifer trees, some deciduous logging waste may benefit moose also during summer), and hence, should not be incorporated as an increased all-year carrying capacity.

Our way of including timber browsing damage is very simplified. Ideally we want browsing impact to be handled *within* the forest projection matrix. Browsed trees should enter one of several (additional) stages depending on damage level (determined by moose density in relation to carrying capacity). This, however, requires us to make a moose browsing preference vector as a function of availability. With 100 moose in the area we might know they would browse 30 000 trees over the winter, but how many would be pine vs. birch? With a static vector the scarcest species (e.g. birch) could limit moose to less than optimal levels even if pine was abundant. Moose browsing preferences in view of total species composition of available forage is maybe the most complicated issues of moose research. Although several Scandinavian studies looked into this in the 1990's (e.g. Danell et al., 1991a,b; Heikkilä and Mikkonen, 1992; Andren and Angelstam, 1993; Heikkilä and Härkönen, 1993; Histøl and Hjeljord, 1993; Shipley et al., 1998), our knowledge is not conclusive enough for us to include such a vector at this stage.

4.2. Model sensitivity

4.2.1. Economic output
Clearly, timber had a much higher potential as a source of income in the model than moose (69% or more stemming from timber). This is in accordance with what we have previously found using a far less complex bio-economic model based on logistic growth functions (Wam et al., 2005). Even when maximizing moose profit, the majority of the income came from timber cutting. Nonetheless, in all scenarios it was the combined moose and timber harvest that gave the highest net property value over time. Hence, parameter values must be at extreme ends for it to be optimal not to have any moose in the forest. A combination of several factors increasing the relative

value of moose must apply simultaneously for moose to be a major source of income; for example low soil productivity and prices favouring moose.

4.2.2. Biological output
The average moose density in Norway has been calculated by Solberg et al. (2006) to be approximately 1/km² in winter (after harvest, before reproduction), ranging from 0.1 to 3.6. In our base scenario the moose population was kept at 0.7 animals per km² when run with moose management restrictions and 1.8 without restrictions, that is well within the calculated range.

Most parameters contributed to set the actual harvest levels of moose, but more or less so. The three most important ones were: the relative value of moose to timber, soil productivity and primary carrying capacity for moose. By large it was the relative value of moose to timber that regulated the moose vs. timber production. Intuitively it is easy to think that the higher price of moose, the more it would be beneficial to have. However, with increasingly higher value of moose, more timber was cut and actually less moose were kept in the forest *until* the threshold was reached where the income of having one more moose superseded the associated timber loss. Soil productivity puts an upper limit on potential timber harvest. Consequently there is also a limit on how much added carrying capacity that can be produced through timber cutting. Hence, while low soil productivity favoured the moose vs. timber relatively more than high productivity, it also reduced the moose' overall potential carrying capacity.

Some might find our base-scenario value for primary carrying capacity at 1.5 moose per km² to be conservative. In our model, however, cutting timber strongly added to carrying capacity for moose and hence, the moose production both in terms number of animals and quantity of meat. At the most the carrying capacity was 5.5 moose/km² when run in the base scenario. In comparison, Skonhoft (2005) used 5.8 moose/km², while Nilsen et al. (2005) used 4, 6 and 8 moose/km² for their moose: wolf predation models for Scandinavia. We would like to emphasize, however, that no-one yet possesses "the genuine truth" when it comes to quantifying moose carrying capacity.

The percentage of calves in the hunt is an important and much-quoted indicator of population productivity in view of the existing hunting regime. In Norway, the observed calf percentage in the population (observed throughout the hunt) is typically between 25 and 35 (Solberg et al., 2006). Our base scenario results fell within this range, though in the lower end. The harvest structure found optimal in Sæther et al. (2001, where the objective is to maximize number of animals harvested) has been the prevailing applied practice in Scandinavia from the 1980's up to recently; a relatively high outtake of calves and large bulls with the productive cows being spared. In our model it was the moose management restrictions that channelled the hunting towards the traditional sex- and age structure.

5. Conclusions

In Scandinavia an either-or view on moose vs. timber production has prevailed for a long time. Our results support neither sides of this debate. The take-home message to applied managers from this study is that most properties will benefit from having some

moose, and on a very few moose income may supersede that of timber. In view of the present optimism around commercializing moose hunting, our findings clearly say that most landowners shall target their effort towards increased quality (e.g. guiding, accommodation) and not quantity.

Our model is not suited to determine the detailed management of timber trees. Other far more precise models are available for that purpose (Hoen and Eid, 1990; Eid and Hobbelstad, 2000). Our model should serve foremost as a decision tool for choosing the optimal levels of moose to have in the forest (in population with no across-border migration). One should follow up with running a traditional forest model in which more or less of the timber harvest findings in our model are included (depending on the relative value of moose). Likewise it would be beneficial to supplement our model with a more detailed moose harvest model (e.g. Sæther et al., 2001; Nilsen et al., 2005 if predators are present) in order to more thoroughly determine the sex- and age composition of animals to be harvested. The optimal moose levels as determined by our model could then be included as a constraint.

Our study highlights the following need for further studies: I. Quantifying the relationship between moose browse availability (forest state and moose density) and moose condition (weights and fecundity). II. Quantifying the relationship between moose browse availability (forest state and moose density) and timber browsing damage.

Acknowledgements

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Paper III

Moose Summer Diet From Feces and Field Surveys: A Comparative Study

Hilde Karine Wam[1] *and Olav Hjeljord*[2]

Authors are [1]*PhD student and* [2]*Associate Professor, Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Box 5003, 1432 Ås, Norway.*

Abstract

Microhistological analysis of feces is the most applied noninvasive method for assessing diets of wild ungulates. However, the method is complicated by differential digestibility of forage species. To evaluate the efficacy of this method in quantifying browse components in summer diets of moose (*Alces alces* L.) on Norwegian rangelands, we compared it to parallel field surveys of browsed vegetation on the same range. Although the same principal diet components were identified in the feces and in the field, there were consistent discrepancies between the two methods in estimated proportional diet contents. Birch (*Betula* spp.) showed the highest field:fecal ratio: 3.3 ± 0.50 compared to 0.9 ± 0.16 for *Salix* spp., 0.8 ± 0.16 for aspen (*Populus tremula* L.), and 0.6 ± 0.12 for rowan (*Sorbus aucuparia* L.). Until in vivo fecal correction factors for differential forage digestibility are available, we caution against broad application of fecal analyses for estimating proportions of browse in moose diet. Although we could not determine the exact amount of discrepancy implicit in each method, previous studies of moose summer diet in the area clearly indicate that fecal analyses gave a less accurate representation of actual moose browse diet than did the field survey. Fecal analyses are nevertheless needed to identify moose diet components other than browse, which are not easily obtained from field surveys.

Resumen

El análisis microhistológico de heces es el método no-invasivo de evaluación de dietas de herbívoros silvestres más utilizado. Sin embargo, la digestibilidad diferencial de las especies forrajeras complica el uso de esta técnica. A fin de evaluar la eficacia de esta técnica en cuantificar componentes de ramoneo en dietas de verano de alces (*Alces alces* L.) en pastizales naturales de Noruega, comparamos el análisis microhistológico con evaluaciones de campo de vegetación ramoneada realizadas en forma paralela en el mismo sitio. Si bien los mismos componentes dietarios principales fueron identificados en heces y en el campo, se verificaron discrepancias consistentes entre ambos métodos en las proporciones de componentes dietarios estimados. *Betula* spp. exhibió la relación campo:fecas mas elevado: $3,3 \pm 0,50$ comparado con $0,93 \pm 0,16$ para *Salix* spp., $0,8 \pm 0,16$ para *Populus tremula* L., y $0,6 \pm 0,12$ para *Sorbus aucuparia* L. Hasta tanto estén disponibles factores de corrección fecales in vivo que tomen en cuenta la digestibilidad diferencial de los forrajes, aconsejamos precaución en la aplicación amplia de análisis de fecas para estimar proporciones de forraje ramoneable en la dieta de alces. Si bien no pudimos determinar la magnitud exacta de discrepancia implícita en cada método, estudios anteriores de dietas estivales de alces en este sitio claramente indican que el análisis de fecas produjo una representación menos precisa de la dieta de ramoneo real de alces comparado con el relevamiento de campo. Los análisis de fecas son necesarios, sin embargo, para identificar componentes no ramoneables de la dieta de alces, que no pueden ser obtenidos fácilmente mediante relevamientos de campo.

INTRODUCTION

Identifying species composition of animal diets is fundamental to many aspects of wildlife research and rangeland management. The most applied noninvasive methods for analyzing diets of wild, large herbivores can be summarized as follows (Ortmann et al. 2006): 1) microhistological analyses of feces; 2) direct observation of foraging animals, often termed bite counts (Hubbard 1952); and 3) surveying bite marks on vegetation in the field. Additional lesser-used methods with restricted applications are n-alkane analysis of feces (Dove and Mayes 1991) and near infrared spectroscopy of feces (e.g., Walker et

al. 1998). The use of DNA analyses of fecal material is promising, but still unexplored for large herbivore diets (Ortmann et al. 2006).

Albeit frequently used for domestic livestock, direct observations of foraging animals are seldom applied to wild ungulates because of their elusive nature. The method might be more suitable for the less elusive megaherbivores such as the giraffe (*Giraffa camelopardalis* L.; Parker and Bernard 2006). An alternative to directly observing the foraging animal is to follow its tracks and count bite marks on browsed vegetation along the path (e.g., Vivås and Sæther 1987; Sæther et al. 1989; Shipley et al. 1998). However, this method only is suitable to situations with adequate snow cover, and hence, only can be used to estimate winter diets (although it has been used on bare ground as well; Knowlton 1960). For noninvasive estimation of summer diets of wild ungulates, only fecal analyses and field surveys of browsed vegetation are feasible. Available literature indicates that fecal analyses have been used most frequently

(Dearden et al. 1975; Cuartas and Garcia-Gonzalez 1996; Mayes and Dove 2000).

Fecal analyses necessitate correction factors to adjust for differential digestibility of plants (Pulliam 1978). Such correction factors only might be accurately determined using fistulae on tamed animals, or by feeding known diets to animals in controlled settings. Unfortunately, even these approaches cannot adequately mimic the more diverse diets of free-roaming animals, particularly because digestibility of one species might be influenced by other species in the digestive tract (Gill 1972; Westoby 1978; Hjeljord et al. 1982; Gill et al. 1983; Bernays et al. 1994). Time and funding needed for such experiments is beyond the reach of most research programs. Consequently, a comprehensive set of digestibility correction factors is available for only a few wild herbivores.

To evaluate the efficacy of fecal analyses for quantifying browse in summer diets of moose on Norwegian rangelands, we compared this method to parallel field surveys of browsed vegetation on the same range. We limited our study to shrubs and trees (hereafter termed browse), because there are no uniform quantitative browsing indices applicable to both browse and other moose forage. In order to have a large gradient in diet diversity, we allocated our sampling in space (i.e., over several ranges) rather than in time. We hypothesized that 1) due to, for example, differential digestibility of species, there would be discrepancies between the two methods in their estimation of proportional diet contents on a given range; 2) these discrepancies would be consistent across ranges; or 3) alternatively, that the discrepancies would vary with diet compositions (i.e., vary between ranges). If the latter applies, fecal analyses are further complicated because it might be necessary to develop site-specific correction factors for digestibility in moose.

METHODS

Data Collection
The study was conducted in July and August from 2005 to 2008. These are the months with the highest species diversity in moose diet (Hjeljord et al. 1990). Our study area comprised 11 moose ranges of approximately 10 000 ha each in south-central Norway (lat 58°45′N–60°52′N, long 08°51′E–12°13′E). The ranges were selected to represent separate ecological entities, i.e., with no extensive movement of moose between ranges. Each range only was surveyed in 1 yr, and all but four ranges were sampled for feces in the same year as the field surveys. Due to time constraints, the four remaining ranges were sampled for feces in 2005, and surveyed in the field the next year. We included these ranges in the data set because there were no differences in plant growth conditions (precipitation and mean day temperature) between May–August of 2005 and 2006 (generalized linear model interactions "range × year × category," where category is whether temperature or precipitation $F_{3,57} = 0.1$, $P = 0.720$; "year × category:" $F_{1,57} = 0.2$, $P = 0.638$).

We define browse as bush and tree species only, and not woody plants in the field layer (e.g., bilberry, *Vaccinum myrtillus* L.). The following species or species groups were included as browse in this study: birch (*Betula* spp.), rowan (*Sorbus aucuparia* L.), aspen (*Populus tremula* L.), *Salix* spp., oak (*Quercus* spp.), and "other deciduous" (all other deciduous species). Conifers were not included because these ordinarily are not eaten by moose during summer in Norway (Bergström and Hjeljord 1987).

We did field surveys of moose summer foraging by continuously counting all trees with browseable parts within moose reach (i.e., at a height of 30–300 cm) along 2-m-wide belt transects. Trees < 30 cm are submerged in the herbaceous layer and were omitted in our survey because they rarely are browsed by moose due to conformational constraints (Hjeljord et al. 1990, using close-range observations of radiocollared, wild moose). Trees with stems branching < 5 cm above the soil level were counted as separate individuals. For each tree counted, we noted whether it had been browsed by moose in the current summer (i.e., showed signs of bites or stripping of leaf, bark, shoots, or buds). On average we walked 7 ± 0.4 transects per range, and 7.6 ± 0.33 km per transect. We counted a total of 143 815 trees ($1\,997 \pm 135.0$ per transect), of which 23 360 had been browsed by moose (336 ± 26.2 per transect). Transects were systematically distributed on the range, neither randomized nor targeted towards particular spots. Care was taken to have transects both across and along the range's valleys and hills. Roe deer (*Capreolus capreolus* L.) are sympatric with moose on all the ranges, and on two ranges there were also sheep and/or cattle (ranges 4 and 11). However, the density of these other herbivores is very low, and we believe they caused only insignificant bias in our data (see also DISCUSSION).

To quantify biomass removed by moose per browsed tree of the various forage species, we also surveyed browse in a plot survey. Transects were laid out in the same manner as the belt transects, with 12-m² circle plots placed every 15 m (as measured by steps) in young forest (tree height < 4 m) and every 75 m in older forest (tree height > 4 m). On each plot we sampled one tree of each browse species that was present on the plot (excluding the mixed group "other deciduous"). Trees were selected with respect to both shoot biomass and browsing intensity of the species within the plot. We sampled two trees if the species had two clearly different heights or browsing intensities within the plot. For each tree we counted the number of shoots browsed in the current summer, and measured the length of a representative unbrowsed shoot (current year's growth). On average we sampled 140 ± 16.6 trees per range and species (ranging from 50 ± 11.8 per range for aspen to 258 ± 33.7 per range for birch).

We quantified leaf production on the range with the least browsing pressure (range 3). Using a 50-g spring scale (0.5-g precision; Pesola AG, Baar, Switzerland), we measured shoot lengths and weighed shoots and leaves on trees with negligible apparent browsing ($n = 30$ trees per species). We limited the sampling to sites of intermediate soil fertility. Trees were subjectively selected in order to evenly represent the 30–300 cm height range. We measured three shoots per tree: one at one-third and one at two-thirds of crown height, as well as the long shoot (the uppermost shoot). *Salix* spp. were sampled equally in young and old forests (because of different growth forms); all other species were sampled in young forest only. The survey was done over 2 yr (15 July–15 August in 2006 and 2007). To avoid effects of date and year, sampling of each species was

evenly spread within the study period by measuring an equal number of trees per species on any given survey day.

We collected 19 ± 1.9 fecal samples from moose per range (one sample taken from each group of pellets). Sampling of feces was evenly distributed on the range, either systematically by searching with hunting dogs (Norwegian grey elkhound), or opportunistically when doing the field surveys. Based on activity patterns of radiocollared Norwegian moose (Sæther et al. 1992), we set 2 km between fecal deposits as a minimum distance threshold in order to obtain samples from different moose.

We analyzed plant epidermal fragments microscopically using the procedures of Garcia-Gonzalez (1984). After thawing, about five pellets from each fecal deposit were lightly ground in a mortar. We transferred approximately 1 mL of the sample to a test tube containing 4 mL of concentrated nitric acid. The tube was placed in boiling water for 1 min, the contents then diluted with 200 mL water and boiled for another 4 min. We next passed the suspension through 1.00-mm and 0.20-mm sieves, rinsed with water, and conserved the 0.20-mm fraction in a mixture of 85% ethanol (of 70% solution), 10% formalin (of 40% solution), and 5% glacial acetic acid. The fragments were dispersed on microscope slides in a 50% aqueous solution of glycerine, fixed with 20×40 mm cover slips, and sealed with nail varnish. Two slides were made from each sample. All fragments (not just browse) partly or in whole dissecting 40×1-mm-long transects were counted, and if possible, identified to species or genus, with a minimum of 200 fragments in total per slide (running out the last started transect). On average we identified 446 ± 1.7 epidermal fragments per fecal sample ($n = 206$). When we report percent diet content of browse as found in the feces, this value is the species proportions calculated among identified browse fragments only.

Data Analyses

We analysed data with SAS statistical software (release 9.2, SAS Institute Inc. 2008). All measures are given as mean $\pm$ SE if not otherwise stated. For most species, the number of browsed shoots per tree was highly skewed towards the low numbers (i.e., a right-sided tail), and for these we used the median.

We checked for sufficiency of fecal and tree count sample sizes by randomly and independently drawing 3, 6, 9, ..., n_{max} of our samples and plotting the standard error of their species diet content against sample size. For all species and all ranges, the standard errors of percent diet content were visually stabilized at $<10\%$ for n_{max} ($3.7 \pm 0.55\%$, $n = 66$ for fecal, and $4.9 \pm 0.73\%$, $n = 66$ for tree-count). For the fecal samples, this corresponds well to data by Anthony and Smith (1974), who found that 15 fecal samples were a minimum to cover the individual variance in diets of deer populations.

We calculated biomass removed by moose per browsed tree as follows: from the detailed measurements taken on range 3 we fitted linear regression equations of leaf biomass (g) in relation to shoot length (cm). For *Salix* spp., which had been sampled in both young and old forest, we used the mean of the measures taken in the two age classes. We applied the equations to range-specific data to obtain a range's species-specific average of biomass removed per browsed tree. The species-specific biomass removed per browsed tree all were normally

distributed across ranges with the exception of *Salix* spp., for which approximately all trees on range 11 were sallow (*Salix caprea* L.), whereas on the other ranges the group was more evenly composed of several species. We used a balanced two-way analysis of variance to test whether the biomass removed per browsed tree differed between species and ranges, choosing not to omit the outlier (range 11) for this particular purpose. For simplicity of discussion, we report biomass removed per browsed tree pooled for all ranges, but all related tests were run with range-specific data. Biomass removed per browsed tree was multiplied by the tree counts in order to find biomass browsed per species on each range. When we present percentage diet content as found in the field surveys, this represents the proportion of total browsed biomass of browse species.

In order to quantify the overlap between fecal and field-survey diets we calculated the Schoener's index (Schoener 1968):

$$R_0 = 1 - 0.5 \cdot \sum |p_{ij} - p_{ik}|,$$

where p_{ij} and p_{ik} are the proportions of species i in the diet as found by method j and k, respectively. Although a significance decision level to determine similar diets has been suggested for this index (Scrimgeour and Winterbourn 1987), we believe it is not suitable for correlated data (it was originally suggested for comparing diets among animals or populations, not survey methods). Instead, we used generalized mixed models (GLIM-MIX in SAS), which accounts for interspecific dependency in the data. Oak was grouped with "other deciduous'" to avoid too many cells with a zero value (oak is endemic to the western parts of our study area). We initially fitted a model with diet contents treated as "pseudo-binomial" variables because the underlying tree-counts had a binomial outcome, and the epidermal fragment counts were a Poisson approximation. However, we concluded (based on the scaled Pearson statistic χ^2/degrees of freedom as well as residual displays) that this was not appropriate. We therefore used and found appropriate the variance function $var_{prop} = \mu^2(1 - \mu)^2$ (McCullagh and Nelder 1989), in which the distribution of data is treated as unknown, and consequently GLIMMIX uses a quasi-likelihood estimation technique. Because we were interested in the three-way interaction effect "method $\times$ species $\times$ range" (hypotheses 2 and 3) as well as the two-way interaction "method $\times$ species" (hypothesis 1), we fitted a saturated model (the three main effects and all possible interaction effects) with the intention of performing backward elimination (e.g., Agresti 1996). We report type-III tests of fixed effects and exact P values for two-sided alternatives.

We used paired Student's t tests to check whether one method consistently gave higher or lower values than the other method (testing per species across ranges, results are given as one-sided alternatives). We thereafter quantified the species-specific methodological discrepancy as a ratio:

$$div_{i,j} = \frac{(p_{ij,field} + 1)}{(p_{ij,fecal} + 1)},$$

where $p_{ij,field}$ and $p_{ij,fecal}$ are the percent diet content of species i on range j as found by the field surveys and the fecal analyses, respectively. We added an increment of 1 to the percentages to

Table 1. Linear regression analyses of leaf biomass (g) in relation to shoot length (cm) for current year's growth of unbrowsed deciduous trees in south-central Norway (lat 59°22′N, long 10°17′E). Three shoots measured at various crown heights per tree ($n = 30$ trees per species) on intermediate soil fertility in July–August 2006 and 2007 (an equal number of trees were measured per species per survey day to avoid effect of date).

Species	Regression equation	SE of regression coefficients[1]	Statistics
Birch	$y = 0.6 + 0.17\ x$	2.04, 0.041	$t_{29} = 4.1$, $R^2 = 0.378$, $P < 0.001$
Rowan	$y = 0.2 + 0.25\ x$	0.68, 0.042	$t_{29} = 5.8$, $R^2 = 0.546$, $P < 0.001$
Salix spp.	$y = 0.1 + 0.10\ x$	0.21, 0.012	$t_{29} = 9.1$, $R^2 = 0.746$, $P < 0.001$
Aspen	$y = 1.6 + 0.12\ x$	0.43, 0.012	$t_{29} = 10.0$, $R^2 = 0.782$, $P < 0.001$
Oak	$y = -1.4 + 0.46\ x$	1.02, 0.048	$t_{29} = 9.7$, $R^2 = 0.771$, $P < 0.001$

[1]y-intercept and slope, respectively.

avoid zero values. Because there was much variation in discrepancy ratios between ranges, we present overall species-specific ratios obtained in two ways: 1) by first calculating ratios per range, and then taking the average; and 2) by first taking the average of diet contents across ranges, and then calculating the ratios. Range 11 had an extreme ratio for *Salix* spp., and was omitted from the average ratio calculations. Because we found that the discrepancies might have been affected by diet composition, we used multiple regression analysis to examine which diet components were most associated with the discrepancy on a given range, regarding the ratios as statistically independent of the percentages.

RESULTS

The estimated biomass removed by moose per browsed tree in the field surveys varied both between species ($F_{5,65} = 5.3$, $P = 0.001$; Tables 1 and 2), and between ranges ($F_{10,65} = 3.1$, $P = 0.004$). For the three most important browse species (birch, rowan, and *Salix* spp.), the number of shoots browsed per plant contributed the most to this variance, because the biomass available per shoot were approximately the same.

In the microhistological analyses of the feces, browse species together made up $50 \pm 1.8\%$ of all identified fragments per sample ($n = 206$), ranging from 27% to 80%. The remaining contents were dominated by bilberry ($19 \pm 1.0\%$), grasses and grass-like plants (species of Poaceae and Cyperaceae; $10 \pm 1.2\%$), and raspberry (*Rubus idaeus* L.; $9 \pm 0.9\%$). There was no linear relationship between percent browse in feces and diet overlap between the two methods (Schoener's index of fecal vs. field) across ranges ($t_{10} = 0.21$, $R^2 = 0.005$,

$P = 0.835$). Thus, the agreement between the two methods did not vary with fragment sample size within our data range.

We identified the same principal diet components with the fecal analyses and the field surveys (Fig. 1); birch, rowan, *Salix* spp., and aspen together made up 90% or more of the browse with both methods on all but the two southernmost ranges, where oak was also important in the diet. In the field surveys, birch and then rowan were the two most frequently browsed species, whereas in the fecal analyses, rowan and then *Salix* spp. were both found to be more frequent in the diet than birch.

The two methods did not give the same proportional content, neither across ranges nor within each range. In the generalized linear model, both the three-way interaction effect "method $\times$ species $\times$ range" ($F_{38,1\,248} = 7.5$, $P < 0.001$) and the two-way interaction "method $\times$ species" ($F_{4,1\,248} = 91.3$, $P < 0.001$) were highly significant. Thus, the discrepancies between the two methods varied not only with species per se, but the species-specific discrepancy also varied between ranges (and hence, possibly the diet compositions). The effects were not artifacts of our estimations of biomass removed per browsed tree, because the same model that ran with the tree count frequencies directly was also highly significant ($P < 0.001$).

The species-specific discrepancies were consistent for three of the four main species: the contribution of rowan ($t_{11} = 2.9$, $P = 0.009$, pair-wise testing across ranges) and aspen ($t_{11} = 2.1$, $P = 0.032$) to the moose diet was overestimated in the fecal analyses compared to in the field surveys, whereas the relationship was opposite for birch ($t_{11} = -6.3$, $P < 0.001$). For *Salix* spp. there was variation both ways, and so the overall discrepancy was not significant ($t_{11} = 1.2$, $P = 0.125$). However, omitting the outlier range 11 gave significant test results also for *Salix* spp. ($t_{10} = 2.0$, $P = 0.037$).

Table 2. Leaf biomass (g) available and removed by moose per browsed tree (*Alces alces* L.) in south-central Norway (2005–2008). Mean ± SE or median (quartiles) among 11 ranges (lat 58°45′N, long 8°51′E–lat 60°42′N, long 12°13′E).

Species	Average shoot length (cm)	Available leaf (g) per shoot[1] (x)	No. of shoots browsed per tree (y)	Leaf removed per browsed tree (g) ($z = x \cdot y$)
Birch	12.3 ± 0.16 ($n = 3\,260$)	2.8 ± 0.14	4 (2, 8)[2]	11.2
Rowan	9.3 ± 0.22 ($n = 2\,339$)	2.5 ± 0.36	2.2 (2.00, 2.69)	5.9
Salix spp.	16.8 ± 0.53 ($n = 706$)	2.1 ± 0.21	5.1 (3.11, 6.20)	9.9
Aspen	13.6 ± 0.53 ($n = 577$)	3.0 ± 0.18	2.5 (2.00, 2.80)	7.4
Oak	7.0 ± 0.28 ($n = 405$)	1.8 ± 0.09	4 (2, 6)[2]	8.6
"Other deciduous"[3]	11.8 ± 1.70	2.4 ± 0.14	3.5 (3.32, 4.08)	8.2

[1]Available leaf per average shoot length. Regression equations of leaf weight (g) in relation to shoot length (cm) obtained by measuring negligibly browsed trees ($n = 30$ per species, equally distributed within 30–300-cm tree height) on intermediate soil productivity on a range with low browsing pressure.
[2]Birch ($n = 248$ trees) and oak ($n = 50$ trees) measured on one and two ranges, respectively. The remaining species measured on all ranges.
[3]Mean (or median) of the above five browse species were used to represent values for this mixed species group.
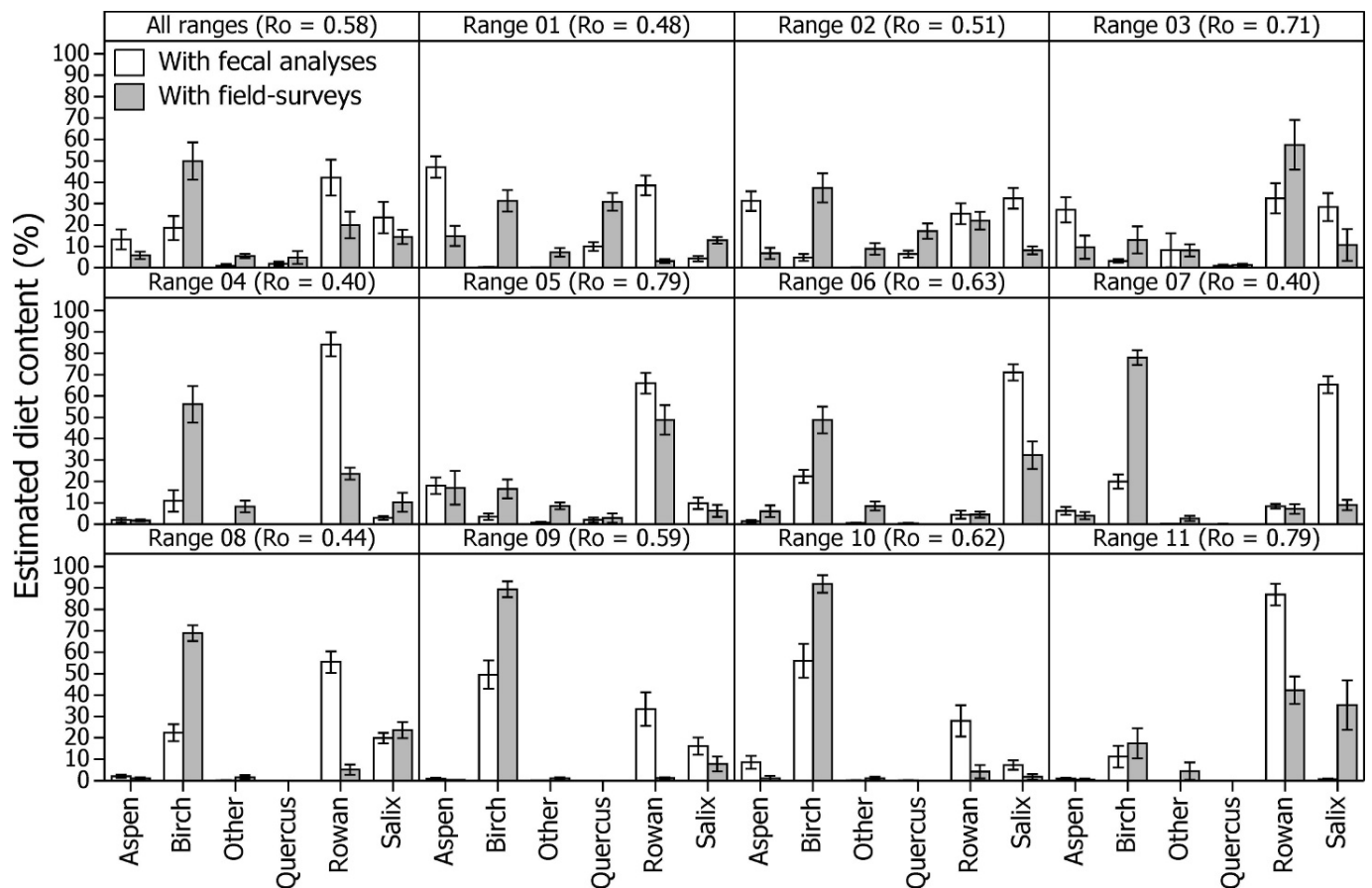
Figure 1. Percentage species contribution among browse in moose (*Alces alces* L.) summer diet on 11 ranges in south-central Norway (2005–2008), as found by fecal analyses ($n = 206$ fecal deposits) and field surveys of browsed vegetation ($n = 23\,360$ trees). Bars are mean $\pm$ SE. R_0 = Schoener's index of diet overlap between the two methods.

The consistency of the discrepancies is best illustrated by a scatter plot (Fig. 2), where the observations should lie consequently on one side of the straight line $y = x$. For birch and aspen the methods seemed to diverge more with higher diet contents. If we remove two outliers from the data (range 3 and range 11), even rowan and *Salix* spp. seem to follow the pattern of increased discrepancy with higher diet proportions. The plot also supports the assumption that very low densities of sheep and cattle on ranges 4 and 11 did not constitute bias in our data (the ranges are not distinct outliers to the right-side lower corner of the figure).

Birch had the highest field:fecal ratio: 3.3 ± 0.50 compared to 0.9 ± 0.16 for *Salix* spp., 0.8 ± 0.16 for aspen, and 0.6 ± 0.12 for rowan (Fig. 3). In accordance with the significant "method × species × range" (i.e., species-specific discrepancies varied between ranges), taking the average of ratios calculated per range gave a different value than calculating the ratios from diet proportions that had been averaged across ranges (the latter ratios were 5.6 for birch, 0.7 for *Salix* spp., 0.5 for aspen, and 0.5 for rowan). We found no obvious patterns in diet composition and species-specific discrepancies, and the explanatory variables for the significant three-way interaction effect "method × species × range" remain unsolved.

DISCUSSION

Our study shows that the much-applied method of fecal analysis should be used with caution for estimating proportions of browse in the diets of moose (and hence, possibly other herbivore browsers with similar diets). We found support for hypothesis 1 (there were discrepancies between fecal and field-survey estimations of diet proportions on a given range) as well as for hypothesis 3 (the discrepancies varied between ranges, and thus were possibly influenced by diet composition). There were consistent patterns in the discrepancies, which show that they were not simply coincidental results caused by inadequate sampling procedures. Previous knowledge of moose summer diet in the study area suggests that fecal results diverged more from the actual moose diet than did field-survey results. There is no doubt that birch is a far more important summer browse than shown by our fecal analyses on many of these ranges (see review by Hjeljord and Histøl 1999).

We will discuss four possible explanations for the discrepancies between our fecal analyses and field surveys in estimated proportional diet contents (not arranged in order of importance): 1) different time span of foraging; 2) differences in biomass removed per browsed tree of various forage species; 3) differential digestibility of various forage species; and 4)
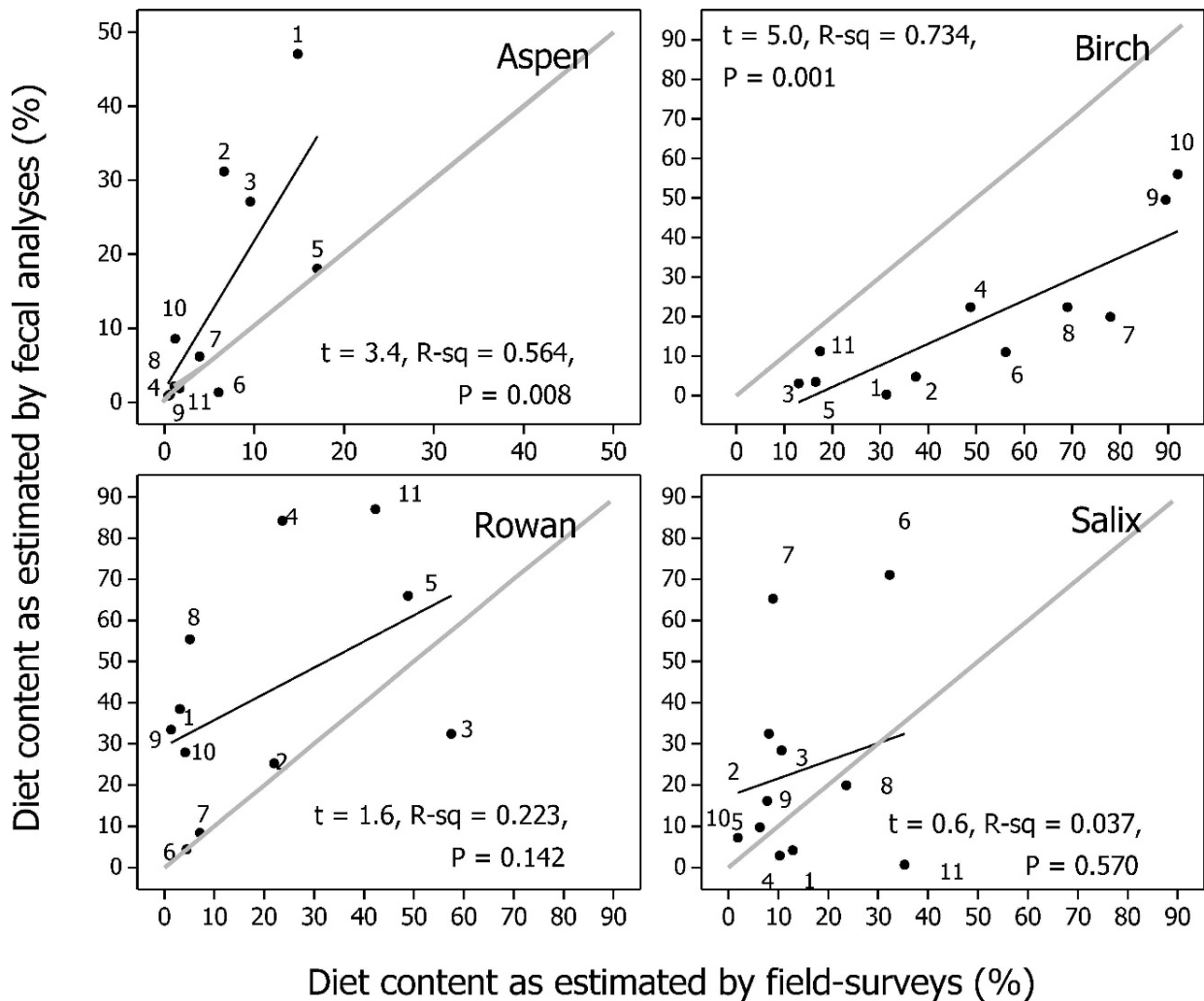
Figure 2. Percentage species contribution among browse in moose (*Alces alces* L.) summer diet in south-central Norway (2005–2008) as found by fecal analyses (*n* = 206 fecal deposits) compared to as found by field surveys of browsed vegetation (*n* = 23 360 trees). Observations above or under the grey line *y* = *x* indicate over- and underestimation, respectively, by fecal analyses compared to by field surveys. The black line is the linear regression fit.

consistent bias in epidermal fragmentation between forage species.

Different Time Span of Foraging

One simple explanation for the fecal vs. field-survey discrepancy could be that the two methods do not completely overlap in time. The field surveys reflect moose diet accumulated over the summer (3.5 mo at the most, but see later comment on birch regrowth). Each fecal deposit reflects moose diet within the last 1–4 d only (Hjeljord et al. 1982). The feces in our study were collected over 33.9 ± 2.64 d per range with a mean collection day on 29 July (range 2 July–26 August). Hjeljord et al. (1984) found that from early (7 June–16 July) to late (20 August–15 September) summer, the ratio of browsed birch trees to browsed rowan trees decreased from 0.66 to 0.59 (on a range where the availabilities of birch and rowan were approximately equal). Likewise, the ratio found in a bite-count study of radiocollared moose on the same range decreased from 0.80 in early (May–June) to 0.71 in late (July–August) summer

(Hjeljord et al. 1990). In this study we found no relationship between collection date and birch diet content as expressed in the feces (however, we did not collect feces until the beginning of July).

The relative changes in birch consumption as indicated by Hjeljord et al. (1984, 1990) are noteworthy, but too small to explain a substantial amount of the discrepancy in our study. The possible bias stemming from early summer browsing on birch also is likely to have been partially counteracted by birch refoliation (Bergstrøm and Danell 1995).

Differences in Biomass Removed Per Browsed Tree

Moose are likely to browse fewer shoots per tree if a species is less preferred or more abundant (Vivås and Sæther 1987; this study). We therefore invested much effort to obtain data to sufficiently estimate the species-specific numbers of shoots browsed per tree as well as the available shoot lengths. The measures of foliage weight in relation to shoot length were taken on one range only, and might not adequately reflect the
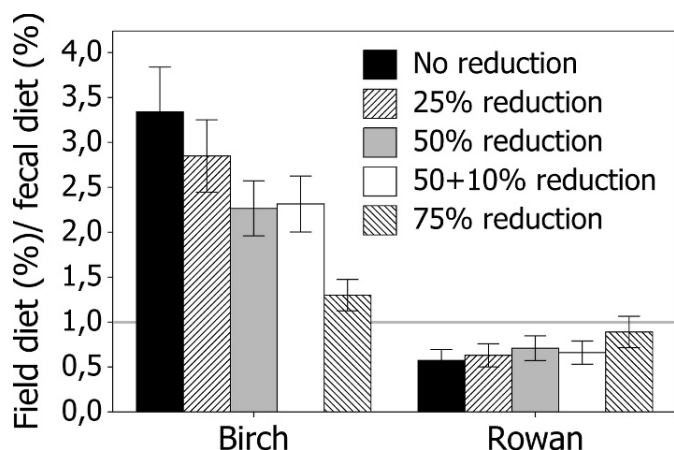
Figure 3. Ratios of estimated content of birch (*Betula* spp.) and rowan (*Sorbus aucuparia* L.) among browse in moose (*Alces alces* L.) summer diet in south-central Norway (2005–2008) as found by fecal analyses ($n = 206$ fecal deposits) and field surveys of browsed vegetation ($n = 23\,360$ trees). Ratios are calculated for various assumed degrees of leaf removal per browsed birch shoot in the field survey ($50 + 10\%$ ratio includes a simultaneous 10% reduction in leaf removal of rowan shoots). Bars are mean $\pm$ SE among 11 ranges.

variation that probably exists between ranges. Although the regression lines were highly significant, there was much variation and the sample size of 30 trees per species is rather small. On the other hand, leaf weights (g) per shoot length (cm) observed in our study compare well to the few other Scandinavian studies that have measured moose summer browse (Bergström and Danell 1995 on birch; Guillet and Bergström 2006 on *Salix* spp.). Furthermore, it is not likely that the negligibly browsed trees on range 3 should consistently have less birch foliage per shoot, and simultaneously have more foliage of the other main forage species (however, the seeming increase in discrepancies with higher diet proportions might be due in general to higher browsing intensity, and thus less biomass available per shoot-centimeter than estimated from the measures taken on range 3).

There is one important variable in biomass removed per browsed tree that was not accounted for in our study: when moose browse on birch, they typically strip leaves from the shoot for less than 100% of the shoot length. If we correct the field-survey data accordingly, we find that a 25% reduction in biomass removed per browsed birch leads to a $15 \pm 2.4\%$ ($n = 11$) decrease in the originally calculated diet proportions (and a comparable increase distributed among the other species). Even a 50% reduction only leads to a birch diet decrease of $32 \pm 4.4\%$. With the reduced diet proportions, the field:fecal ratio for birch falls from 3.3 to 2.8 and 2.2, respectively (see Fig. 3). In the figure we also have illustrated a 50% reduction in birch with and without simultaneously reducing biomass of rowan 25% (which might, for example, occur if rowan is intensively browsed). The countereffect of this simultaneous reduction seems negligible. In order to balance the fecal and field estimates, a $>75\%$ reduction in biomass removed per browsed tree is necessary. This would mean that moose should remove less than half as much foliage per browsed tree of birch compared to rowan (see Table 2), which does not seem very realistic.

Differential Digestibility

Fecal analyses in general overestimate the less digestible portions of an animal's diet (Cuartas and Garcia-Gonzalez 1996). Few studies have looked at bias within the ligneous species group (but see Dearden et al. 1975; Leslie et al. 1983), and there are no correction factors available to adjust for differential digestibility of browse species in the diet of moose. Although differential digestibility must have influenced our results to some degree, birch foliage would have to be several times more digestible than rowan foliage in order to explain a substantial portion of the discrepancies between our fecal and field-survey diet estimates. Such a magnitude does not seem likely. The winter twigs of birch are less digestible than the winter twigs of rowan (in vivo and in vitro, Hjeljord et al. 1982; in vitro, Shipley et al. 1998). Only one study has yet looked at summer digestibility: Hjeljord et al. (1990) found that the in vitro digestibility (using rumen liquor from sheep) of foliage was 49% for silver birch (*Betula pendula* Roth) and 64% for rowan. Using in vitro analysis with rumen liquor from cattle, we found less difference in summer foliage digestibility, but rowan was still the most digestible (88% vs. silver birch 82%; H. K. Wam and O. Hjeljord, unpublished data, 2008, foliage collected from six different trees per species at Ås, Norway). Although the in vitro technique using donor rumen liquor does not completely mimic moose digestion, the bias in its relative interspecific digestibility differences is unlikely to be manifold.

Epidermal Bias

There is general consensus that highly trained personnel are necessary to adequately detect and identify epidermal fragments (Ward 1970; Westoby et al. 1976; Holechek and Gross 1982; Holechek et al. 1982; Alipayo et al. 1992). We have not tested specifically for observer effects in our study. However, the results show that if there was observational bias, the majority of it was consistent (Fig. 2). One observational bias might be caused by ligneous parts having a lower proportion of identifiable epidermal fragments than leaves and buds (Holechek and Valdez 1985; Alipayo et al. 1992). The rowan plant parts browsed by moose on our study ranges were practically only leaves (rowan consisted almost entirely of trees whose current year's growth was severely stunted by moose browsing), whereas more ligneous material might have been consumed when the moose browsed on birch (the outer part of the shoot). This might have led to a consistent, albeit small, underestimation of birch compared to rowan in our fecal analyses.

Another and possibly more important source of bias is fragment size. In our experience, leaves of birch have more strength, and consequently disarticulate in larger fragments than rowan. This could create bias when counting the number of fragments. Although our samples were ground to a maximum of 0.2 mm, there still was some variation in the fragment sizes. Unfortunately, we are unable to quantify this bias as long as we do not know the volume of what was originally ingested.

In summary, it seems likely that more than one of these four possible explanations have caused some bias in our fecal and/or field estimates of browse content in moose summer diet.

Apparently, none of them can separately account for all the observed discrepancy. The first two (different time span and differences in removed biomass) might be quantified in future studies, but the latter two (differential digestibility and epidermal fragmentation) unfortunately are less likely to be solved (see introduction).

IMPLICATIONS

Although quantification of underlying factors for the observed fecal discrepancies is sought from a scientific point of view, what matters most to applied management is to be able to monitor shifts in major diet components within a moose population. These shifts can indicate declining or improving conditions. Based on our findings in this study, we believe that field surveys currently are a better option to monitor moose ranges than fecal analyses. Fecal analysis also demands more expertise and facilities than field surveys. On the other hand, field surveys of browsed vegetation cannot be used to assess the complete summer diet of moose, where herbaceous forage might contribute a substantial part. Fecal analyses are the only practical way to obtain data on moose foraging in the herbaceous layer.

ACKNOWLEDGMENTS

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Paper IV

ORIGINAL PAPER

Moose summer and winter diets along a large scale gradient of forage availability in southern Norway

Hilde K. Wam · Olav Hjeljord

Abstract Studies on dietary functional responses in large herbivores are traditionally conducted by following individual animals. The method is very time-consuming, and hence, typically provides only a narrow array of forage species compositions. Here we use a range level approach to look at moose (*Alces alces*) selectivity for and utilization of forage species in relation to availability in both summer and winter. We compare 12 Norwegian ranges representing a large scale gradient in plant communities. The most important forage species in the diet were birches (*Betula* spp., comprising 43% of all trees browsed in summer and 27% in winter), rowan (*Sorbus aucuparia*, 25% of trees browsed in summer, 37% in winter), and bilberry (*Vaccinum myrtillus*, 42% of herbaceous epidermal fragments in summer feces). Selectivity for birches was positively related to its availability and negatively related to availability of rowan, *Salix* spp., and aspen (*Populus tremula*) together (all more selected for than birches). Multiple regression models including availability of several forage species were thus superior to single-species models in explaining the diet content of main forage plants. Selectivity for birches was also stronger in summer than in winter, while the opposite pattern was found for rowan. The finding is relevant for our evaluation of the quality of summer and winter ranges, and hence, their relative influence on population productivity. Our study underlines the need to incorporate species composition of available forage when quantifying dietary functional responses in selective herbivores such as moose. Furthermore, care should be taken when extrapolating data on moose diet across ranges or seasons.

Keywords Carrying capacity · Fitness · Herbivory · Management · Optimal foraging

Introduction

How animals utilize food sources in relation to their availability (the "functional response," Solomon 1949) is one of the most studied topics in ecology. The nature of the relationship, particularly whether there is density dependency (e.g., type I–III, Holling 1959), is of great importance for our understanding and prediction of ecosystem interactions (see, e.g., Noy-Meir 1975; Kondoh 2003; Murdoch et al. 2003; Beckerman 2005 on herbivore-plant systems). For concentrate selectors (*sensu* Hofmann 1985), the functional response is likely to involve complex density dependant relationships, as the selectivity magnifies the heterogeneity of the foraging landscape (Belovsky et al. 1988). Extensive collection of field data is therefore required to reveal the basic nature of these animals: forage interactions.

For large herbivores, the available literature on functional responses is dominated by studies at the level of individual decisions, i.e., intake or encounter ("should I stay or should I go" see review by Searle et al. 2005) and bite or chew (see review by Shipley 2007). This mechanistic approach may shed light on herbivore selectivity at many different levels of foraging "patches" (e.g., from the plant level to the terrain level). However, because the field work is so time-consuming, studies at this level typically provide only a narrow array of data on the influence of available forage species composition. We maintain that the most efficient way to obtain large gradients in these data is

H. K. Wam (✉) · O. Hjeljord
Department of Ecology and Natural Resource Management,
Norwegian University of Life Sciences,
P.O. Box 5003, 1432 Ås, Norway
e-mail: hilde.wam@umb.no

to study the selectivity at the level of ranges (i.e., populations).

Another aspect of herbivore diet that can give valuable insights on ecological interactions is whether there are differences between seasons. For northern ungulates, seasonal cycles of energy metabolism and nutritional needs, and hence, possibly their forage selectivity, appear linked to fluctuations in forage quality. Numerous studies have found habitat quality on the summer range to be a major factor governing body growth and fecundity (see, e.g., Klein 1970; Gaillard et al. 2000; Cook et al. 2004). The quality of winter ranges is also important for body growth, but less so, as for most ungulates there is a decrease in metabolism in winter (though see Mautz et al. 1992; Mauget et al. 1997). Growth of body tissue is then mainly that of the cow's fetus towards the end of the season. Since returns of energy and nutrients are ultimate causes for forage selectivity in herbivores, there is a need for studies that look into how selectivity varies with season. Even if a selective feeding provides only a small change in quantity or quality of food intake, it may cause a substantial multiplier effect on animal performance (White 1983).

Moose (*Alces alces*) is an herbivore that shows strong forage selectivity (Peek 1974; Bergström and Hjeljord 1987). It is the largest browsing animal in the boreal forests and a "keystone" species in its ecosystem (Molvar et al. 1993; Persson et al. 2000; Suominen et al. 2008; Bump et al. 2009; den Herder et al. 2009). Studies of moose forage consumption and selectivity have been conducted on various scales. On the smallest scale, Shipley (2007), e.g., used moose as an example to demonstrate the importance of bite size on daily foraging time. On a larger scale, Shipley et al. (1998) used moose trails to investigate diet choices of moose in northern Sweden. Several studies at the range level have shown empirically that moose selectivity for and utilization of certain forage may be influenced by the species composition of available plants (Heikilä and Härkönen 1996; Jia 1996; Ericsson et al. 2001; Hörnberg 2001, but see also Danell et al. 1991 as well as Edenius 1991 and Härkönen 1998). However, most of these studies have focused on the commercial timber species Scots pine (*Pinus sylvestris*), and none have looked into how moose selectivity may vary between summer and winter within the same range.

We here present a study that examines moose summer and winter diets in relation to forage availability on 12 Norwegian ranges representing a large scale gradient in plant communities. The study included all plant species in both the tree/shrub layer and the herbaceous layer. We use data at the range level to test the hypothesis that (1) moose selectivity for and the diet content of one forage species depends on not only availability of the species in question, but also on the availability of other species. We also test the

hypothesis that (2) moose forage selectivity varies between summer and winter.

Materials and methods

Study area

Our study comprised 12 moose ranges of approximately 10,000 ha each throughout southern Norway: Veg (58° 45'N, 8°51'E), Kjo (59°6'N, 9°55'E), Rev (59°22'N, 10° 17'E), SaW (59°42'N, 10°7'E), SaE (59°40'N, 10°17'E), Hal (59°11'N, 11°20'E), Rak (59°30'N, 11°22'E), AuS (59°49'N, 11°43'E), AuN (59°55'N, 11°27'E), Fin (60° 42'N, 12°13'E), Gjø (60°52'N, 10°37'E), and Stj (63° 32'N, 11°15'E). With the exception of Veg and Kjo, the selected ranges are within the boreal forest zone (Moen 1999), dominated by Scots pine and Norway spruce (*Picea abies*) mixed with deciduous trees like birches (*Betula* spp.), rowan (*Sorbus aucuparia*), and aspen (*Populus tremula*). Veg and Kjo are located along the south-western coast and are best described as an ecotone between the boreal and nemoral zones, with oak (*Quercus* spp.) being an additional common tree species.

The ranges represented a large scale gradient in plant growth conditions: proportion of intermediate to high soil fertility varied from 27% to 96%, start of growing season from day 110 (20 April) to day 130 (10 May), while proportion of young forest (timber tree height <4 m) of all forest area varied from 5% to 13%. The ranges were selected to represent separate local populations, i.e., with no extensive movement of moose between ranges.

Field work

In July and August 2005–2007, we made comprehensive plot surveys on all 12 study ranges in order to obtain data on moose forage availability, as well as use of browse during winter. In this study, we use the term "browse" for bush and tree species only, not woody plants in the herbaceous layer such as bilberry (*Vaccinium myrtillus*). The remaining species are termed "herbaceous forage." All plant species were recorded, regardless of their importance as moose forage. Some species of negligible importance (like low-growing forbs and *Ericaceae* spp. other than bilberry), and those very time-consuming to identify (grasses and sedges), were grouped to family. For simplicity, in the following we use the term "species" also for these family groups.

Along a priori set straight transects, we systematically distributed 12.5-m² circular plots ($r = 2.0$ m) every 15 m (paced off by steps) in young forest (height class I+II, see Table 1) and every 75 m in the remaining forest. The different sampling frequencies were based on the higher

Table 1 Parameters registered in a field survey (circular plots of 12.5 m^2) of forage for moose on 12 Norwegian ranges (58°45'N, 8°51'E–63° 32'N, 11°15'E) surveyed in summer 2005–2008

Parameter	Scale/description
Forest characteristics (*based on the dominating timber tree at 0.1 ha surrounding the plot*)	
Height class	0 (logged last year); I (<0.5 m); II (0.5–4 m); III (4–10 m); IV (>10 m), bog
Plot characteristics (*counted separately for all plant species*)	
No. of trees	Trees with browsable parts 30–300 cm in height.
	Stems branching <5 cm above ground were counted as separate trees.
No of browsed trees	Trees with signs of moose bites on twigs or stripping of leaves or bark.
Herbaceous coverage	∑ area coverage (%) of remaining plant species (not tree species).
Sample trees (*birches, rowan, aspen, Salix spp., oak, and pine if present on the plot*)	
No. of twigs	Total number of twigs (>2 mm at base) within 30–300 cm above the ground.
	A twig=shoots of current year's growth or dead stumps from earlier browsing.
No. of browsed twigs	Differentiating between accumulated browsing (i.e., twigs bitten off or bark stripping) and current summer browsing (i.e., leaf stripping).
Shoot length	Length of current year's growth on an unbrowsed shoot.
For birch, which may have hundreds of shoots, we visually estimated the proportion of shoots that were browsed on all ranges, but counted the exact shoot number only on one range.	

forage availability in younger forests, and hence, a need for larger sample size. A systematic rather than a random approach was selected as the most efficient method to obtain a sufficient cross-section of the terrain within a reasonable number of survey plots. Transects were evenly distributed, but with care taken to cover the range both along and across valleys and hills. Each day we started surveying from opposite ends of the range in order to avoid bias in transect selection. Four field workers surveyed 11 of the 12 ranges, all working on every range and each taking every fourth transect. The northernmost range (Stj) was surveyed by a separate field worker. On average, we walked 18±1.3 transects of 2,182±63 m each and surveyed 706±67 plots (8,780 m^2) per range. We counted a total of 4,645±386 trees per range, of which 2,230±177 had been browsed by moose.

On each plot we registered nine parameters (Table 1). For important tree species we subjectively chose a representative sample tree (with respect to shoot biomass and accumulated browsing pressure of the species within the plot) for detailed measurements. Two sample trees were measured if the species constituted two clearly different height strata or browsing intensities within the plot. On average 146±16.5 sample trees were measured per species per range.

The plot survey method provided too few sample trees for estimating browse selection in summer. We therefore made additional surveys of summer browse in July and August 2006–2008 by continuously counting all trees along 2-m wide belt transects (using the same counting criteria as in the plot survey). For each tree we recorded species and whether or not the plant showed sign of moose summer browsing (bites or stripping of leaf, bark, or shoots). We did

not include trees <30 cm in height, which are submerged in the field-layer and very rarely browsed by moose (Hjeljord et al. 1990, using close-range observation of radio-collared moose). A priori set transects were evenly distributed on the range, with care to cover the range both across and along hills and valleys. We walked 7±0.4 transects per range (7.6±0.33 km per transect, *n*=72) and counted 13,074±1,371 trees per range, of which 2,396±265 had been browsed by moose in the summer. The summer belt survey was not done on the northernmost range (Stj).

In order to obtain data on selectivity for herbaceous forage, we collected fresh summer feces from moose in July–August 2005–2008. Each range was sampled for feces in the same year as the summer belt survey, except in Kjo, Rev, Hal, and Rak, which were sampled the subsequent year. We set 2 km as a minimum distance between fecal pellets groups to increase the probability of obtaining samples from different animals. Sampling was evenly distributed on the range, either systematically by searching with hunting dogs (Norwegian gray elkhound) or opportunistically when walking the survey transects. On average we collected fecal samples from 18±1.5 moose pellets groups per range, from which we identified 446±1.8 epidermal fragments per sample. We microscopically analyzed plant epidermal fragments in the feces using procedures after Garcia-Gonzales (1984; for technical details, see Wam and Hjeljord 2010). Diet content of the different species was calculated as their proportion of the total identified epidermal fragments.

The roe deer (*Capreolus capreolus*) is sympatric with moose on all the ranges in our study, and on two ranges (SaW and Gjø), sheep or cattle were also present in

summer. However, as their density is very low, we believe they were not a source of significant bias in our data (Wam and Hjeljord 2010).

Data analyses

We quantified browse availability (B) as shoot-cm/m^2:

$$B_{i,j} = \sum_{h=1}^{H} \left(t_{h,i,j} \cdot s_{h,i,j} \cdot l_{h,i,j} \cdot \text{cP}_{h,j} \right), \, h = \{\text{young, other}\}$$

where $t_{h,i,j}$ is the number of trees of species i counted per plot in forest height class h (young=I+II, other=remaining classes) on range j, s is the average number of shoots/tree, l is the species' average shoot length (cm), and cP is proportion of height class corrected for different sampling frequency (plots taken five times as frequent in young as in the remaining forest). For plots where we had measured two sample trees per species, measurements were averaged before calculating the shoot-centimeters per square meter. For species within "other deciduous" for which we had not taken detailed measurements (these trees constituted 6% of all trees), we used the mean number of shoots and shoot length of oak, rowan, aspen, and *Salix* spp. When we present total shoot availability, this includes all browse species except spruce (not used by moose, only 0.8% of all spruce trees in the plot survey had been browsed).

Availability of herbaceous forage (F) was calculated as:

$$F_{i,j} = \frac{\sum_{h=1}^{H} \left(12.5 \cdot c_{h,i,j} \cdot \text{cP}_{h,j} \right)}{12.5 \cdot n_j},$$

where $c_{h,i,j}$ is the area coverage (%) of species i summed over all plots in forest height class h on range j, and n is the total number of plots surveyed on the range. cP is the height class frequency correction.

We compared species frequency of available versus utilized forage (i.e., moose forage selectivity) using generalized linear mixed models (GLIMMIX), which accounts for interspecific correlations in proportional data. The model was fitted using the variance function $\text{var}_{\text{prop}} = \mu^2(1-\mu)^2$ for data with unknown distributions (McCullagh and Nelder 1989), whereby GLIMMIX uses a quasi-likelihood estimation technique. We entered data at the level of transects in order to have replicates per species and range, thereby being able to test interaction terms. We present results for the simplest models, i.e., stripped of non-significant terms. Spruce was not included. We based winter browse selection on trees counted in the plot survey, which we regard as an index of moose winter browsing only (summer-browsed trees with no sign of winter browsing made up <5% of all counted trees). We based summer browse selection on trees counted in the belt

transects and selection for herbaceous forage on area coverage and epidermal fragments in feces. We report type-III tests of fixed effects and exact P values for two-sided alternatives. Significant GLIMMIX findings were followed (and illustrated) by paired t tests (of diet≠availability) for easier interpretation of results.

We calculated year-round mean density of moose (Dj) in the study period based on a simple model adapted from Hatter and Bergerud (1991):

$$D_j = H_j \cdot \left(\frac{(R_j - M)}{(1 - R_j)} - \beta_j \right)^{-1} + H_j \cdot S,$$

where H is the annual number of animals shot per square kilometer of moose habitat on range j, R is proportion of calves among all hunter-observed moose (i.e., recruitment rate), M is the natural mortality rate (set at 0.05, Solberg et al. 2005), β is the discrete population growth rate, and S is the proportion of the year the range is utilized by moose shot (4 months). Growth rates were calculated with the equation $\beta = e^r - 1$, where r is the linear regression coefficient of log moose seen per hunter day on year.

We quantified the moose' relative selectivity for a given species (rS) as:

$$\text{rS}_{i,j} = \frac{d_{i,j} - a_{i,j}}{a_{i,j}},$$

where $d_{i,j}$ is the proportion of species i in the diet of moose on range j, and $a_{i,j}$ is its proportion among available forage. We used regression analyses to compare relative selectivity to availability (total and *per capita*) and general linear models (GLM) to compare relative selectivity between seasons. The GLM was first run as a full model including all interaction terms (input data at the transect level), and then significant results were followed by paired t tests for each species separately (input data at the range level). We report type-III tests of fixed effects and exact P values for two-sided alternatives.

We used regression analyses to determine intraspecific relationships between forage availability (shoot-cm/m^2 or % area coverage) and diet (as indicated by frequency counts of trees or fecal fragments). We finally tested for effects of available forage species composition on the diet using best subset regression analyses, where we evaluated models by their Akaike information criteria (Akaike 1974) as well as the divergence between R^2 and R_{adj}^2. In the subset analysis, data were first entered at the level of transects in order to have replicates per range. As there were no significant interaction terms, the analysis was rerun and is presented with data at the range level.

SAS statistical software (release 9.2, SAS Institute Inc. 2008) was used for GLIMMIX and GLM procedures as well as regression analyses. MINITAB statistical software

(release 15.1.1.0, MINITAB Inc. 2007) was used for *t* tests and descriptive statistics. In the reported t_n statistics, n is degrees of freedom for two-sample tests, and sample size for paired tests. In the reported $F_{m,n}$ statistics, m is the number of terms and n is observational degrees of freedom. All measures are given as mean±SE.

Results

Forage availability

The most common forage species available (defined as being the most frequently found in the plot survey) to moose on our study ranges were bilberry, grasses (*Poaceae* spp., *Cyperaceae* spp.), and *Ericaceae* spp. among herbaceous forage and birches, rowan, and pine among browse (Table 2). Although not considered moose forage in this study, spruce was the most common tree species in the forest (found on $52 \pm 4.4\%$ of the plots). The available shoot-cm of birches, the most common browse on all ranges, far surpassed that of rowan, the second most common browse. While less common, both pine and *Salix* spp. had overall higher shoot availability than rowan.

Forage selectivity

Moose selected for certain browse species, particularly in winter (GLIMMIX interaction "species · category" $F_{7,3021} = 31.6$, $P \leq 0.001$ where category is whether

Table 2 Abundance (shoot-cm/m^2 for browse, % area coverage for herbaceous forage) and frequency of occurrence of available forage plants on 12 Norwegian moose ranges (58°45'N–63°32'N) surveyed in summer 2005–2008

Species	Abundance	Percentage of plots
Browse		
Birches	69±9.3	40±3.2
Rowan	10±2.6	38±5.2
Pine	16±3.1	26±4.0
Salix spp.	12±3.9	9±1.6
Oak	1±0.6	6±3.4
Aspen	3±0.6	7±1.5
Other deciduous	7±2.6	11±3.0
Herbaceous forage		
Bilberry	21±2.1	69±3.6
Grasses	11±1.3	56±5.6
Ericaceae spp.	14±2.2	51±5.9
Forbs	5±1.0	46±6.4
Ferns	4±0.8	30±5.9
Raspberry	1±0.3	8±1.8

available or browsed versus in summer $F_{7,1075} = 1.9$, $P=0.083$). Overall, rowan was most strongly selected for (Fig. 1a, b), thereafter, *Salix* spp. and aspen. However, the relative selectivity differed between seasons (GLM interaction "species · season" $F_{7,5003}=4.6$, $P \leq 0.001$). Most importantly, birches were more strongly selected for (albeit still not positively selected for overall) in summer than in winter ($t_{11} = 5.5$, $P \leq 0.000$), while rowan ($t_{11} = -2.2$, $P=0.050$) was less selected for in summer.

Not all species were uniformly selected for across the ranges in winter (GLIMMIX interaction "range · species · category" $F_{7,3021} = 2.9$, $P \leq 0.001$). Specifically, birches were not selected for by moose at low availabilities (shoot-cm/m^2), but increasingly selected for at higher availabilities ($t_{11} = 5.5$, $R^2 = 0.749$, $P \leq 0.001$). Simultaneously, selectivity for birches ($t_{11} = -3.8$, $R^2 = 0.590$, $P=0.004$) and also pine ($t_{11} = -3.3$, $R^2 = 0.540$, $P=0.010$) were negatively related to availability of rowan, aspen, and *Salix* spp. together (Fig. 2). The positive relationship between selectivity for and availability of birches was evident in the summer diet as well, albeit less pronounced ($t_{10} = 2.5$, $R^2 = 0.413$, $P=0.033$). Also the negative relationship between selectivity for birches and availability of rowan, aspen, and *Salix* spp. was less strong in summer ($t_{10} = 1.9$, $R^2 = 0.282$, $P=0.093$).

Moose also selected for certain species in the herbaceous layer (GLIMMIX interaction term "species · category" $F_{7,2589}=709.1$, $P \leq 0.001$). Bilberry and raspberry (*Rubus idaeus*) were overall most selected for and *Ericaceae* spp. was the least selected for (Fig. 1c), but selectivity was not uniform for all species across ranges ("range · species · category" $F_{7,2589} = 12.2$, $P \leq 0.001$). Specifically, selectivity for bilberry ($t_{10}=-3.6$, $R^2 = 0.566$, $P=0.005$) and grasses ($t_{10}=-3.8$, $R^2 = 0.596$, $P=0.003$) decreased with availability.

We found no relationships between the relative selectivity for the main species and the *per capita* availability of total browse (e.g., for birch in summer $t_{10} = 1.0$, $R^2 = 0.104$, $P=0.364$ and in winter $t_{11} = 1.3$, $R^2 = 0.166$, $P=0.243$).

Forage utilization

A few species dominated the moose diet both in summer and in winter (Figs. 3 and 4); birches and rowan among browse and bilberry among herbaceous forage. In the summer fecal samples (the time of the most diverse forage availability), we identified 13.1 ± 0.47 species in total per range, and overall only 15 different browse species, including two family groups, and 31 different herbaceous species, including 13 grasses grouped to family, were identified.

As expected, diet proportions of the main forage species were positively related to availability (shoot-cm/m^2 for browse, and % area coverage for herbaceous forage), except for grasses (Fig. 5). Although the linear regression models
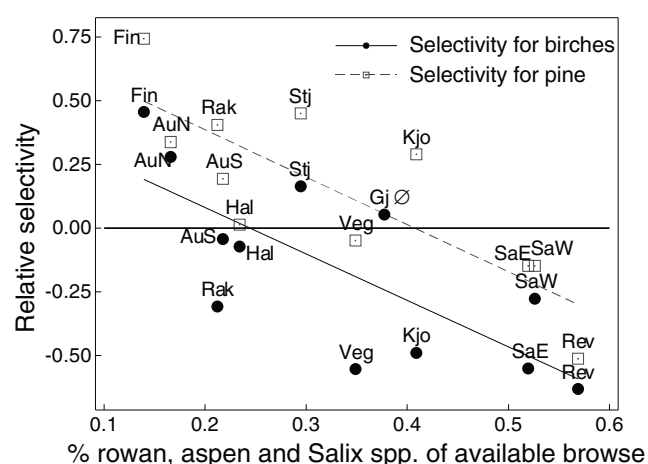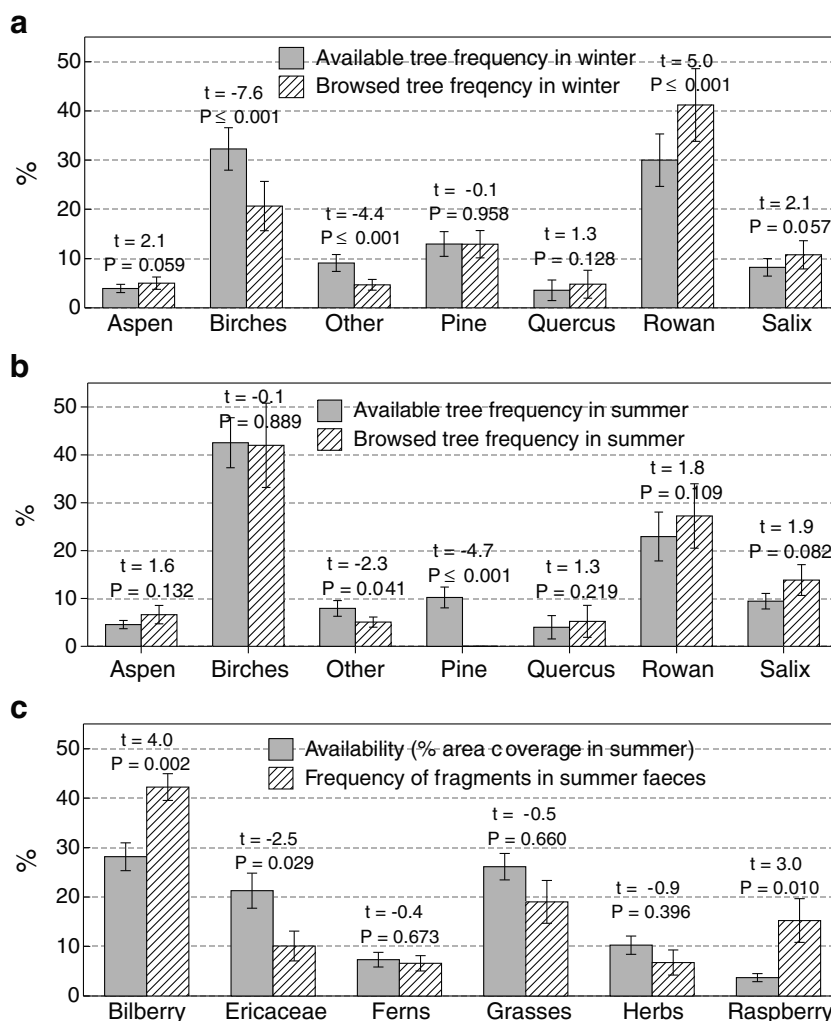
Fig. 2 Moose relative selectivity for birches and pine compared to proportion of rowan, aspen, and *Salix* spp. of available browse on 12 Norwegian winter ranges (58°45'N–63°32'N). Relative selectivity quantified as (proportion in browse diet − proportion of available browse)/proportion of available browse

were significant for all main forage species (in both seasons), they typically explained only 50–70% of the variance in the intraspecific relationships. Accordingly, multiple models including availability of several forage species were superior to single-species models in explaining diet content of all main forage plants (Tables 3 and 4). Availability of bilberry was the most important variable for explaining summer diet content (included in eight of the 12 best subsets). Next most important for explaining summer diet was availability of rowan (seven subsets), and thereafter birches (six subsets). For the winter diet, rowan was the most important explanatory variable (included in seven of the eight best subsets), followed by birches and pine (each in five models).

Discussion

We found support for both our postulated hypotheses: (1) moose selectivity for and diet content of one forage species was influenced by not only the availability of the species in question, but also by availability of other species and (2)

Fig. 3 Species frequency of trees browsed by moose on 12 Norwegian ranges (58°45'N–63°32'N) 2005–2008. Summer data from 2-m wide continuous transects (50±3.6 km per range), and winter data from systematic circle plots (706±66.7 plots of 12.5-m^2 per range) (summer browsing not recorded on the northernmost range)
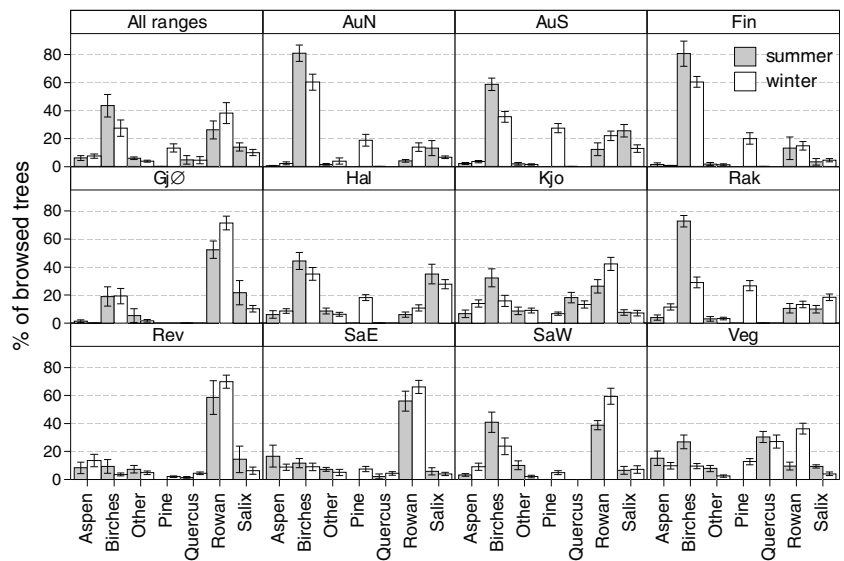

moose browse selectivity varied with season. Overall it was less pronounced in summer compared to winter, but this differed between species.

A possible source of bias in our data is that we did not account for biomass ingested per browsed tree, for which there are consistent interspecific differences (Wam and Hjeljord 2010). Likewise, less digestible plants are generally overrepresented in fecal fragments (Cuartas and Garcia-Gonzalez 1996). These two biases are likely to have caused some imprecision as to the exact level of diet contents and interspecific differences in selectivity. However, it should have negligible influence on the intraspecific comparisons between ranges or seasons. Although there may be intraspecific variations at a small scale (e.g., between plots within the range), they are likely to even out on such a broad scale as the range level that was used in our study.

While functional responses in herbivores are normally studied in relation to proportional and not *per capita* forage availability, it is important to account for moose density when comparing selectivity across ranges. Higher population densities may force moose to be less selective (Emlen 1966; MacArthur and Pianka 1966). This—rather than species composition *per se*—could hypothetically explain the differential selectivity for birches observed in our study. However, such density effects did not apply, as moose forage selectivity on our study ranges was not related to *per capita* availability of total browse.

Only a small number of species were important in the moose diet in our study. This is also generally the situation for moose in Scandinavia: typically less than five species contribute >5% of the diet both in summer and in winter (Bergström and Hjeljord 1987). Even the dominance of

Fig. 4 Species composition of herbaceous forage in moose summer diet on 12 Norwegian ranges (58°45'N–63°32'N) 2005–2008 as found by fecal analyses, proportions among herbaceous fragments only (18 ± 1.5 feces per range). *Parentheses* show percentage of herbaceous forage of all identified fragments
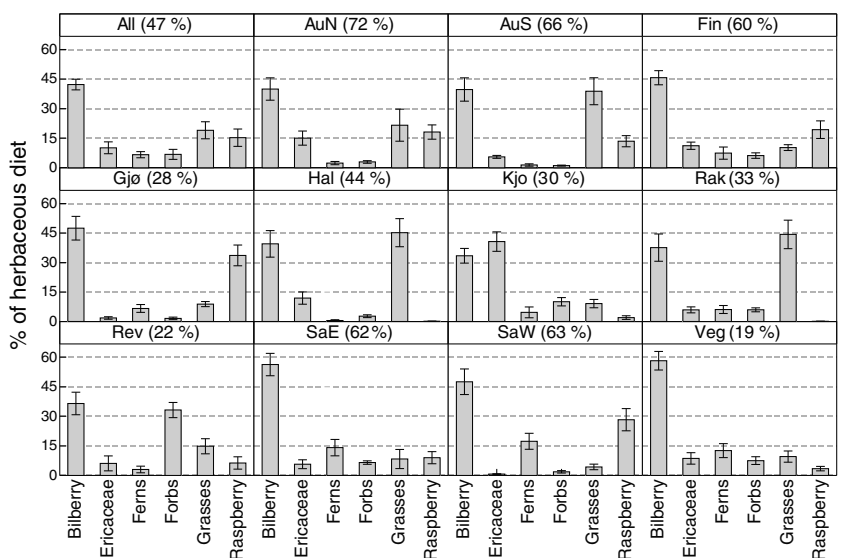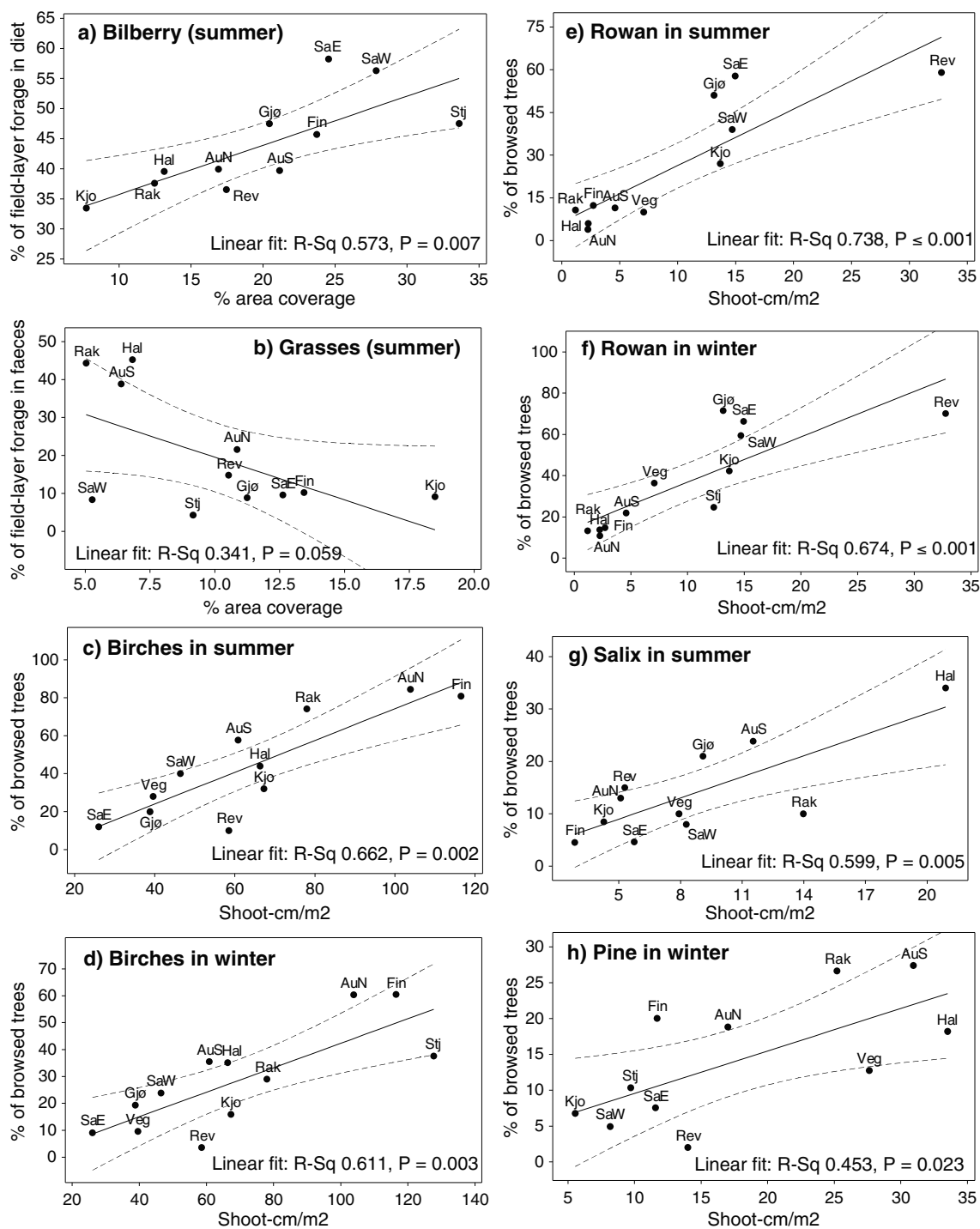
Fig. 5 a–h Moose diet content in relation to availability of the most important forage on 12 Norwegian ranges (58°45'N–63°32'N) 2005–2008. Browse diet based on frequency among all browsed trees, herbaceous diet based on fecal analysis. Summer browsing not recorded on the northernmost range. Shoot-cm is current year's growth >2 mm at base. *Dotted lines* are 95% confidence intervals

birches among available and consumed browse for moose both in summer and in winter is well-known from the other large scale Scandinavian studies published on the subject (Hagen 1983; Hjeljord and Histøl 1999 and references therein; Hörnberg 2001).

Few components are needed to create complexity in a system, though, and moose diet selectivity on these ranges clearly was a complex product of quantitative forage availability in relation to species composition. Most importantly, selectivity for birches increased with lower

Table 3 The two best subsets in multiple linear regression models explaining moose summer diet content in relation to availability of the most important browse and herbaceous forage on 11 Norwegian ranges (58°45'N–60°52'N) 2005–2008

	β_0	β_1	β_2	β_3	β_4	β_5	β_6	AIC	R^2	R_{adj}^2	F	P
Birches												
1	−2.2	1.05	−1.97	–	1.10	−1.49	–	55.4	0.936	0.893	22.0	0.001
2	−4.0	1.10	−1.35	–	1.07	−1.47	−5.76	51.6	0.955	0.909	21.0	0.002
Rowan												
1	20.8	−0.32	1.32	–	–	–	7.54	51.4	0.869	0.813	15.5	0.002
2	17.3	−0.24	2.13	–	–	–	–	54.1	0.805	0.756	16.5	0.001
Salix												
1	−4.3	–	–	0.20	–	–	2.45	55.5	0.693	0.617	9.1	0.009
2	−8.6	–	–	0.22	–	0.53	–	56.7	0.667	0.584	8.0	0.012
Bilberry												
1	37.4	−0.12	–	–	0.66	–	–	38.7	0.655	0.569	7.6	0.014
2	28.7	–	–	–	0.81	–	−1.0	40.3	0.591	0.489	5.8	0.028
Grasses												
1	78.1	–	−0.59	–	−1.37	−2.69	–	45.5	0.878	0.826	16.8	0.001
2	72.4	0.09	−0.53	–	−1.28	−2.84	–	46.7	0.888	0.814	11.9	0.005
Raspberry												
1	−9.9	–	−1.09	–	1.07	–	9.31	48.9	0.670	0.528	4.7	0.042
2	5.4	–	–	–	0.88	–	–	52.5	0.325	0.250	4.3	0.067

βs are available browse (shoot-cm/m^2) and herbaceous forage (% area coverage): β_1 birches, β_2 rowan, β_3 Salix spp., β_4 bilberry, β_5 grasses, β_6 raspberry, – denotes not selected in the subset

availability of rowan, Salix spp., and aspen together (all more selected for than birches). Although the intraspecific linear regression fit between availability and diet content was significant for all the major forage species, there was still quite some variance left unexplained by these simple models. Consequently, all the "best subsets" models included interspecific relationships as well. Dietary functional responses in moose that depend on density of available forage are generally expected for this large selective herbivore (Spalinger and Hobbs 1992; Gross et al. 1993) and have earlier been shown empirically for winter browse in Scandinavia (Andersen and Sæther 1992; Hörnberg 2001). However, as far as we know, our study is the first to show effects of the complete available species composition on moose selectivity.

The moose on our study also showed seasonal differences in their forage selectivity. In general, browse selectivity was more pronounced in winter than in summer. Specifically, selectivity decreased for birches and increased for rowan when going from winter to summer. When comparing summer and winter browsing on deciduous trees, one should bear in mind that leaves stripped in summer and twigs eaten in winter are quite different food items. During summer, new leaves emerge and grow at different rates over the season, offering a wide array of energy and nutrient returns for moose per individual tree. The intraspecific differences may to some extent override the interspecific differences and accordingly, the moose's search for nutritious plant tissue will be less linked to plant species (Hjeljord et al. 1990). Our study thus has not

Table 4 The two best subsets in multiple linear regression models explaining moose winter diet content in relation to availability of the most important browse species on 12 Norwegian ranges (58°45'N–63°32'N) 2005–2008

	β_0	β_1	β_2	β_3	β_4	AIC	R^2	R_{adj}^2	F	P
Birches										
1	14.5	0.41	−1.50	–	–	57.1	0.779	0.730	15.9	0.001
2	11.8	0.49	−1.44	−0.17	–	57.5	0.805	0.731	11.0	0.003
Rowan										
1	70.7	−0.46	2.08	–	−0.31	43.3	0.965	0.955	73.3	0.000
2	70.4	−0.41	2.10	−0.10	−0.33	44.1	0.970	0.952	56.1	0.000
Salix										
1	11.5	–	−0.39	0.16	–	48.1	0.339	0.192	2.3	0.155
2	0.99	–	–	0.19	0.10	48.1	0.339	0.192	2.3	0.156
Pine										
1	8.3	–	−0.83	–	0.16	38.8	0.792	0.745	17.1	0.001
2	3.5	0.08	−0.79	–	0.16	38.1	0.835	0.774	13.5	0.002

βs are available browse (shoot-cm/m^2): β_1 birches, β_2 rowan, β_3 Salix spp., β_4 pine, – denotes not selected in the subset

identified a lower need for nutritious forage during winter compared to summer. Irrespectively of its proximate pathway, though, the less pronounced selectivity in summer has bearings on our evaluation of the quality of summer and winter ranges, and hence, their relative influence on population productivity (Klein 1970). A dominance of birch over rowan will, e.g., have a greater effect on the quality of the winter range compared to the summer range.

Ideally, studies of selectivity should be coupled with chemical analyses (see, e.g., Verheyden-Tixier et al. 2008). Although we did not analyze the chemical composition of moose forage plants in this study, it has previously been investigated in regard to, e.g., digestibility. From these studies it is well established that winter twigs of birches are less digestible than those of rowan (*in vivo* and *in vitro*: Hjeljord et al. 1982; *in vitro*: Shipley et al. 1998). Furthermore, using rumen liquid from sheep, Hjeljord et al. (1990) found that the *in vitro* digestibility of foliage was 23% lower for birch (*Betula pubescens*) than for rowan in summer, while the digestibility of the winter twig was more than twice as high for rowan as for birch. Using *in vitro* analysis with rumen liquor from cattle, we found even less difference in foliage digestibility: birch foliage was 7% less digestible than rowan foliage (Wam and Hjeljord 2010). The lower interspecific difference in summer compared to winter supports our finding that moose forage selectivity is less linked to plant species in summer than in winter.

In conclusion, our study underlines the need to incorporate species composition of forage availability when calculating dietary functional response curves for selective mammalian herbivores such as the moose. We thus advocate more application of range level approaches, as this is the most efficient way to obtain sufficient gradients in available forage species compositions. Furthermore, moose forage selectivity varied not only with species composition, but also between summer and winter. Care should therefore be taken when extrapolating data across ranges or seasons.

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Paper V

Differential forage utilization makes carrying capacity equivocal for high density Scandinavian moose.

Hilde Karine Wam[1*], Olav Hjeljord[2] and Erling Johan Solberg[3]

[1]Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Box 5003, 1432 Ås, Norway. E-mail: hilde.wam@umb.no

[2]Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Box 5003, 1432 Ås, Norway. E-mail: olav.hjeljord@umb.no

[3]Norwegian Institute for Nature Research, N-7485 Trondheim, Norway. E-mail: erling.solberg@nina.no

[*]Corresponding author. Telephone: +47 64 96 57 72. E-mail: hilde.wam@umb.no

Abstract: Availability of preferred forage is hypothesized to be positively related to fitness for selective herbivores. Comparing ten high density moose (*Alces alces*, (L., 1758)) ranges comprising two regions with contrasting animal fitness (twinning rate, calf body mass) and plant species compositions, we show that a positive relationship may not always apply. The high fitness region (HF) had 41% more browse shoots available per moose in total, but 15% less preferred browse (i.e. rowan *Sorbus aucuparia*, aspen *Populus tremula*, and *Salix* spp.) than the low fitness region (LF). Recent logging activity was the most important determinant of forage availability. While the lightly browsed birch (*Betula* spp.) was the most abundant browse in both regions (comprising 66% and 50% of all browse available in HF and LF, respectively), it dominated the moose diet only in HF. In LF, the intensively browsed rowan was the most common browse in the diet, although it contributed only 18% of the available browse (2% in HF). Fitness estimates at the time of study were negatively related to accumulated browsing pressure, but only weakly associated with forage availability. Our study shows that indices of carrying capacity based on forage availability may not apply uniformly across ranges for selective ungulates.

Key-words: condition, density dependence, management, optimal foraging, selectivity

Introduction

I have watched… the south-facing slopes wrinkle with a maze of new deer trails. I have seen every
edible bush and seedling browsed, first to anaemic desuetude, and then to death… In the end the
starved bones of the hoped-for deer herd, dead of its own too-much…

- Aldo Leopold, 1949

The concept of carrying capacity is considered one of the pioneer efforts to bridge applied and theoretical wildlife management, largely due to the work of Aldo Leopold 60-70 years ago (Young 1998). Nevertheless, carrying capacity has remained one of the most ambiguous terms in ecology. While we may rather easily agree on a theoretical and mathematical definition (Sayre 2008), measuring carrying capacity in the field still is a daunting task. By large, the challenge lies in the concept's principle of population regulation. To empirically find support for this, we need extensive, parallel time-series on animal density and forage availability, which is rarely available (Forsyth and Caley 2006).

For large herbivores like the ungulates, one useful alternative is to define carrying capacity on the basis of animal fitness (Caughley 1977). However, a major disadvantage with such a retrospective approach is that we cannot use it to make predictions about the future. The latter is particularly important for the management of forest-dwelling herbivores, for which carrying capacity can vary extensively and rapidly through external effects such as logging (Thompson and Stewart 1998) and fires (Odum 1983).

The moose (*Alces alces*, (L., 1758)) in Scandinavia is a notable example of such a forest-dwelling herbivore: in the latter half of the 20th century it showed strong population growth and reached globally record-high densities (Cederlund and Markgren 1987; Lavsund et al. 2003). The forest industry's transition from selective cuttings to large-scale clear-cutting is considered to be a major supporting factor for this extensive population increase. In such scenarios, knowing the bottom-up part, and not just observing its ultimate effects on animal fitness, is thus likely to facilitate sustainable management. Accordingly, a practical starting point for disentangling carrying capacity for species like the moose is to establish what determines forage availability.

Typically, not all forage contributes equally to carrying capacity. For concentrate selectors of large herbivores (*sensu* Hofmann 1985) e.g., preferred forage is generally assumed to be of higher quality. It should thus contribute more to carrying capacity, as the greater the nutritional quality, the more food can be metabolized per unit of time (Schwartz and Renecker 1998). Accordingly, animals with higher availability of preferred forage are expected to have higher fitness. This has long been proposed as a hypothesis for explaining geographical variance in moose body mass (Hjeljord and Histøl 1999). Still, few if any attempts have yet been made to critically test the hypothesis with empirical data at the population level (see Sæther and Heim 1993 for a study at the level of individual moose).

The forest land on each side of the Oslofjord in southern Norway provides a unique opportunity to test the 'range quality hypothesis' for moose at a spatial scale. The two regions have distinct plant communities (Moen 1999) and thus, different proportions of plant species preferred by moose. Like for Scandinavia in general, the moose populations in both regions expanded to globally record-high densities

by the 1980s (Lavsund et al. 2003), but only the western region has shown serious declines in moose fitness (Solberg et al. 2006) (Fig. 1).

In this study we use the Oslofjord area to look at what determines moose forage availability, and how forage availability relates to moose fitness. Specifically, we investigate the effects of a) innate plant productivity (soil fertility and start of growing season), b) recent logging and c) accumulated browsing pressure on the forage availability. Furthermore, we test the hypothesis that I) moose fitness (calf body mass and twinning rate) are positively related to total availability of forage; or alternatively that II) moose fitness is only positively related to availability of preferred forage.

Materials and methods

Study area

The study was conducted on ten moose ranges (approximately 10 000 ha each) in southern Norway (Fig 1). The north-south oriented Oslofjord together with townships and infrastructure effectively separate the ranges in a western and an eastern region with little or no interregional movement of moose. Within each region, the ranges were selected to represent separate local populations, i.e. with no extensive movement of moose between ranges. The eastern region is within the typical boreal forest zone, while the western region is best described as an ecotone between the boreal and nemoral zones (Moen 1999).

The forest on all ranges is intensively influenced by commercial forestry, with practically all logging performed as clear-cutting. In global comparison, cuttings are small (0.1 ha to 1 ha) and naturally restricted by local topography. Spruce is almost exclusively regenerated by planting, while pine is regenerated by natural seed dispersal. During the survey period, herbicides were applied to a small extent on one range (Kjose). Thinning was regularly practiced up to the early 1990's, thereafter gradually abandoned with the trend reversed within the last two years due to new governmental incentives. Thinning is typically done at tree heights that have edible plant parts above the reach of moose (>300 cm).

Field surveys of moose diet and forage availability

Moose forage availability and winter diet were surveyed in July-August 2005-2007. We distributed straight transects evenly on the range, covering the terrain both along and across valleys and hills. Along the transects we systematically sampled 12.5-m^2 plots for every 15 m (paced off by steps) in young forest (height-class I and II, defined below) and every 75 m in the remaining forest. Four field workers were involved, all working on every range and each taking every 4th route. A new transect was surveyed every new day, starting from the opposite end of the range than on the previous day. In total, we walked 19 ± 1.5 transects and surveyed 706 ± 66.7 plots (8 780 m^2) per range.

On each plot we registered height-class (0 = logged within last year; I = conifer trees <0.5 m; II = 0.5–4 m; III = 4–10 m; IV >10 m; (-) = no or very sparsely tree cover) and soil fertility based on the dominating vegetation on 0.1 ha overlapping the plot. Soil fertility was visually classified after species diversity and plant growth vigour to the five classes low, intermediate, high, bog and non-productive land (i.e. rocks). We counted all trees with browseable parts within 30–300 cm height (stems branching <5 cm above

ground were counted as separate trees), and noted the number that showed signs of moose browsing (bites or stripping of leaves, twigs or bark). In total, we counted 4 822 ± 426 trees per range, of which 2 330 ± 157 had been browsed. The following browse were counted: spruce, pine, juniper (*Juniperus communis*), birch, rowan, aspen, sallow (*Salix caprea*), eared willow (*Salix aurita*), other willows (*Salix* spp.), oak and 'other' (remaining deciduous tree species). Note that we define browse as tree species only, and all other species (hitherto small-growing woody plants such as bilberry (*Vaccinum myrtillus*)) as herbaceous forage. For the latter we estimated the horizontal coverage (% of plot area). All plant species were included in the survey whether important as food plants for moose or not.

For the important browse species (birch, rowan, aspen, sallow, willows, oak and pine), we took the following measurements on a representative sample tree (selected with respect to shoot biomass and browsing pressure of this species within the plot): 1) the number of all twigs (>2 mm at base); 2) the number of twigs browsed (distinguishing between those browsed in the current summer, and those previously browsed, i.e. accumulated browsing); and 3) the average length of current year's growth on an unbrowsed shoot (hereafter termed shoot length). Note that a twig, in contrast to shoots, may include stumps from previously browsed shoots with no current annual growth. Two trees were measured if the species constituted two different height strata or browsing intensities within the plot. For birch, which may have hundreds of twigs, we estimated the proportion of browsed twigs on all ranges, but counted the exact number on only one range. In total, we measured 146 ± 16.5 sample trees per species and range.

The plot survey provided too few sample trees for estimating moose browse diet in summer. We therefore made additional surveys in July-August 2006-2008 where we continuously counted all browse trees (30-300 cm in height, branches <5 cm counted as separate trees) along 2-m wide pre-defined belt transects. Transects were evenly distributed, covering the range both across and along hills and valleys. Trees <30 cm in height (submerged in the field layer) were not counted as these are hardly ever browsed by moose (Hjeljord et al. 1990 using close-range observations of foraging moose). In total, we walked 7 ± 0.4 belt transects (7.6 ± 0.33 km per transect, *n* = 72) and counted 13 074 ± 1 371 trees per range, of which 2 396 ± 265 had been browsed by moose in the summer. Other ungulates are of low densities in the area, and not likely to have caused significant impact on our data (Wam and Hjeljord 2010a).

Data on herbaceous forage in the diet was obtained from fresh summer feces collected in July-August 2005-2008. Each range was sampled for feces in the same year as the summer browse survey, except in Kjose, Re, Halden and Rakkestad, which were sampled the subsequent year. Feces were collected minimum 2 km apart to increase the likelihood of sampling from different individuals. On average we obtained 18 ± 1.5 fecal samples per range. Epidermal fragments (446 ± 1.8 identified per feces) were analyzed microscopically in the lab using the procedures by Garcia-Gonzalez (1984, for details see Wam and Hjeljord 2010a).

Moose density and fitness data

For moose density and fitness (calf body mass and twinning rate) data at the time of study we used the average of 2004-2008. These data along with the number of moose harvested were obtained from hunters'

reports as well as the national monitoring program for cervids (Solberg et al. 2009b), with some material supplemented by the local game authorities.

We calculated year-round mean density of moose based on a simple model adapted from Hatter and Bergerud (1991). The natural mortality rate was set at 0.05 (*sensu* Solberg et al. 2005). Population growth rate was derived from hunters' observations of moose (see Solberg and Sæther 1999). Under the assumption of no net migration, the moose density (*D*) (animals/km^2) was estimated as:

$$D_j = H_j \cdot \left(\frac{(R_j - M)}{(1 - R_j)} - \beta_j \right)^{-1} + H_j \cdot S,$$

where *H* is the annual number of animals shot per km^2 of moose habitat on range *j*, *R* is proportion of calves among all hunter-observed moose (i.e. recruitment rate), *M* is the natural mortality rate, *β* is the discrete per capita growth rate and *S* is the proportion of the year the range is utilized by shot moose (four months). We calculated per capita growth rates from the equation $\beta = e^r - 1$, where *r* is the linear regression coefficient of log moose seen per hunter day on year. The hunter observations indicated a change in moose density during the study period (2004-2008) only on one range (Kjose, where there was a declining trend).

Data analyses

We quantified browse availability as shoot centimetre per area of moose habitat (shoot-cm/m^2). When we present total shoot availability, this includes all browse species except spruce. For simplicity, aspen and oak (both of low availability) are presented as part of the collective group 'other'. Availability of herbaceous forage was calculated as the total area coverage (%) on the range. For details on the forage availability calculations, see Wam and Hjeljord (2010b).

We first analysed regional differences in moose densities and fitness at the time of study using two-sample *t*-tests. We likewise analysed the regional variation in absolute (per m^2) and relative (*per capita*) forage availability.

We thereafter tested to what extent our postulated determinants (soil fertility, forest age, accumulated browsing pressure and start of growing season) explained variation in forage availability. Browsing pressure was then categorized into two classes: low (<30% of twigs browsed) and high (≥30% of twigs browsed). The relationships were analysed with general linear models (PROC GLM in SAS), including one- and two-way terms of explanatory variables: 1) for browse availability (shoot-cm/m^2), where we included the variables region, soil fertility and forest age; and 2) for shoot lengths, with the variables region, soil fertility, forest age and browsing pressure. When we present GLM effect terms these are from the simplest model, i.e. non-significant terms are excluded. We entered data at the level of ranges for shoot-cm/m^2, and at the level of sample trees for shoot lengths. Significant results from the GLM were followed by two-sample *t*-tests to differentiate the effects on single species. We likewise used *t*-tests to check if the browsing pressure varied with forage age.

We also used GLM to determine relationships between moose density and forage availability, and between moose fitness and availability of all (hypothesis I) and preferred (hypothesis II) forage. To keep our degrees of freedom, we first ran separate tests for each explanatory variable including region and the associated two-way interaction. If the interaction was not significant we ran the model with all main effects, and selected the model with only significant terms. We also give linear regression fits for the species-specific relationships. As preferred forage we defined plant species positively selected for by moose in this area, i.e. rowan, aspen and *Salix* spp. among browse and bilberry and raspberry (*Rubus idaeus*) among herbaceous forage (Wam and Hjeljord 2010b).

SAS statistical software (release 9.2, SAS Institute Inc. 2008) was used for the data analyses. All measures are given as mean ± SE. *t*-test results are given as one-sided alternatives if not stated otherwise. In the reported t_n-statistic, *n* is degrees of freedom for two-sample tests, and sample size for paired tests. For the GLM tests, we report type-III tests of fixed effects with *P*-values for two-sided alternatives.

Results

Moose density and fitness

The estimated moose density during the study period (2004-2008) was higher in the west than in the east, although not significantly so (Table 1). Calf body mass in the west was 19% less than calf body mass in the east, and also the twinning rate were noticeably lower in the west.

Forage availability and moose diet

The most abundant forage species available were birch and bilberry (Table 1). In total, the western ranges had 33% less browse shoots available than the eastern ranges. Summer browse (i.e. all deciduous species) made up 85 ± 4.2 % of all browse in the west and 81 ± 3.5 % in the east. Relatively to the moose density, the western region had 15% more preferred browse, but 41% less browse in total than the eastern region. In the herbaceous layer, there was no regional difference in coverage of preferred forage relative to moose density.

Although birch dominated the forage availability on all ranges, it constituted a major part of the moose diet only in the eastern region (Fig. 2). Herbaceous forage made up 39 ± 9.6 % (west) and 55 ± 7.1 % (east) of all identified epidermal fragments in the summer feces, the rest being browse.

Determinants of forage availability

The proportion of intermediate to high soil fertility was almost twice as high in the west compared to in the east (Table 1). Also browsing pressure showed a regional pattern, with all the main browse species being more intensively browsed in the east than in the west (Table 1, bear in mind that the availability was not the same in the two regions).

The effect of recent logging

Availability of all the main browse and herbaceous species were strongly affected by recent logging (Fig. 3 and 4). Overall, young forest had 3.9 (east) and 4.0 (west) times as much browse as the remaining

6

forest (averaged for soil fertility). Birch was most strongly affected, with 6.4 (east) and 4.4 (west) times as high shoot availability in the young forest. In the herbaceous layer, bilberry was negatively affected by recent logging, particularly in the eastern region, were there was 3.9 times less coverage of this species in the young compared to in the remaining forest (in the west 1.5 times).

The effect of recent logging varied with soil fertility for browse (GLM across regions, $F_{3, 197} = 153.0$, $P \leq 0.001$), while this interaction was less clear for herbaceous forage ($F_{3, 244} = 2.4$, $P = 0.125$). For all the main forage species but pine, the effect of logging was stronger on the richer soils.

A disproportionably high percentage of trees browsed by moose in summer were found in the young forest (young forest covered only 8.4 ± 0.84 % of the study area): for birch 69 ± 8.3 % of browsed trees versus 52 ± 7.0 % of available trees (paired-$t_{10} = 5.4$, $P \leq 0.001$); for rowan 50 ± 8.2 % versus 34 ± 6.9 % ($t_{10} = 7.5$, $P \leq 0.001$); and for *Salix* spp. 26 ± 6.3 % versus 19 ± 4.4 % ($t_{10} = 1.7$, $P = 0.058$). We could not calculate comparable data for the winter browsing from the accumulated browsing index (i.e. older trees have a greater chance of being browsed at least once by moose).

The summer browsing pattern in young versus the remaining forest was also revealed in the proportion of trees that were browsed: for rowan 28 ± 1.6 % of all available trees in the young forest was browsed in the current summer compared to 11 ± 1.0 % of the trees in the remaining forest (paired-$t_{10} = 5.6$, $P \leq 0.001$); for birch 19 ± 3.0 % versus 8 ± 0.1 % ($t_{10} = 4.3$, $P \leq 0.001$); and for *Salix* spp. 35 ± 3.0 % versus 25 ± 1.8 % ($t_{10} = 3.3$, $P = 0.004$).

Shoot lengths in relation to browsing pressure

The relationship between browsing pressure and shoot length was strongly negative for rowan, pine and *Salix* spp., while it was positive for birch (Fig. 4). Birch trees with high browsing pressure had 1.2 (east) and 1.1 (west) times longer shoots than trees with low browsing pressure. In contrast, pine trees with low browsing pressure had 1.6 (east) and 1.5 (west) times longer shoots than trees with high browsing pressure. Rowan had 2.8 (east) and 2.0 (west) times longer shoots on trees with low browsing pressure, and for *Salix* spp. the relationship was 1.3 (east) and 1.1 (west).

For pine and rowan, the relationships between shoot lengths and browsing pressure varied with soil fertility (GLM across region and forest age, $F_{3, 1311} = 16.8$, $P \leq 0.001$) and forest age (GLM across region and soil fertility, $F_{3, 1807} = 61.6$, $P \leq 0.001$), respectively. For pine, the relationship was more negative on higher soil fertility. For rowan, the relationship was more negative in young forest.

Moose fitness in relation to forage availability

The moose densities at the time of study were not related to browse availability (Fig. 5a-b), neither for all browse (GLM across region, $F_{1,9} = 0.9$, $P = 0.379$) nor for preferred browse ($F_{1,9} = 1.0$, $P = 0.357$), and this applied to both regions (interaction term 'region · shoot-cm/m^2' $F_{3,9} = 0.5$, $P = 0.520$ and $F_{3,9} = 1.5$, $P = 0.271$, respectively).

Consequently, the *per capita* browse availability was neither related to calf body mass (Fig. 5c-d) (GLM across region, all browse $F_{1,9} = 0.8$, $P = 0.393$; preferred browse $F_{1,9} = 0.0$, $P = 0.942$) nor twinning rate (Fig. 5e-f) (all browse $F_{1,9} = 1.4$, $P = 0.277$; preferred browse $F_{1,9} = 0.3$, $P = 0.579$).

Likewise, we found no associations between availability of herbaceous forage and moose fitness in any of the two regions.

In contrast to forage availability, moose fitness showed rather strong, negative associations with accumulated browsing pressure on the main browse species: calf body mass (GLM across region and species, $F_{1,9} = 4.8$, $P = 0.065$); and twinning rate ($F_{1,9} = 11.4$, $P = 0.012$), but this varied to some extent with browse species (Fig. 6a-f). There was also a tendency for the negative relationships to be more evident on the western than the eastern ranges. However, this was mainly due to one range with relatively high moose fitness in the west.

Discussion

What determines forage availability?

Of the forage determinants investigated in our study, recent logging was clearly the most influent factor affecting availability of both browse and herbaceous forage. While the effect of soil fertility was negligible for browse availability in the remaining forest, it significantly augmented the effect of recent logging. For e.g. birch, the most abundant browse species, the shoot availability was as much as eight times higher on the richer soils.

Despite a broad consensus that overstory removal is a major contributor to moose carrying capacity (Telfer 1974; Peek et al. 1976; Renecker and Schwartz 1998), few studies have explicitly quantified the effect of recent logging on browse production. Hjeljord et al. (1990) found that tree density on richer soils was ten times as high for birch and four times as high for rowan in young forests (< 4 m tree height) as in older forest (> 10 m). Månsson (2009) found that the total horizontal coverage of browse was approximately five times in forest <30 years of age as in forest >30 years of age. Both studies compare well to our findings.

The plants' nutritional quality may also be affected by logging, e.g. through plant age and light exposure. A pioneer study by Cowan et al. (1950) showed that moose browse in logged areas was nutritionally superior to browse in old-growth forests. However, numerous studies have later shown that the relationship is less clear, particularly due to higher contents of protein-reducing tannins on clear-cuts (e.g. Van Horne et al. 1988; Happe et al. 1990; Hjeljord et al. 1990). In our study, a higher proportion of browsed trees were found in young forest than expected from their availability, indicating that moose favoured to browse in the young forest. However, without nutritional analyses we cannot differentiate whether this was due to nutritionally better plants, or simply that the young forest provided more energy-efficient foraging.

Even accumulated browsing pressure was an important determinant of browse availability on our study ranges. The contrast between rowan and birch is relevant when comparing the eventual carrying capacity of the eastern and the western ranges. Because birch constitutes far more of the moose forage in the east, these ranges will be less negatively affected by a given moose density (all else being equal). Hjeljord and Histøl (1999) studying increasing moose populations in southern Norway also concluded that calves maintained their body mass better on the eastern than the western ranges. They speculated that this was due to forage in the east being more tolerant to browsing than forage in the west.

Mechanistic simulation studies in Sweden have shown that birch may increase its shoot length and leaf size if browsed in winter (Danell 1982; Danell et al. 1985; Bergström and Danell 1987; Danell and Bergström 1989, Danell et al. 1997). Moose also seems to prefer to re-browse birch (Danell et al. 1985), which may temporary reinforce a positive association between browsing and shoot lengths. Ultimately, though, the net effects of browsing are likely to be negative for both birch and moose when browsing becomes too intense (Persson et al. 2005, Persson et al. 2007).

The lack of association between growing season and forage availability in our study was most likely a result of scale, i.e. its variation between the ranges was small enough to be absorbed by the variation of other determinants. Yet, rather than through the effect on biomass production *per se*, start of growing season may have a larger influence on moose fitness through associated factors such as onset and duration of spring flush, plant growth rate and time for plants to develop herbivory defences (see e.g. Sand 1996; Hjeljord and Histøl 1999; Ericsson et al. 2002; and the contrasting studies of Herfindal et al. 2006a,b).

From forage availability to moose fitness

The lack of linear model fit between moose' fitness and forage availability can be due to the intra-regional fitness variability being too low. In effect, we only had two fitness levels (east versus west). However, it may also indicate that forage availability is not the only factor affecting moose fitness. Nevertheless, the pair-wise comparisons clearly show that moose on the high fitness ranges had less preferred forage available than the moose on the low fitness ranges (Table 1). Hence, our study shows that availability of preferred forage is at least not a pre-requisite for Scandinavian moose to obtain and maintain high fitness.

Birch, the dominant summer diet content in the east, is of only medium preference to moose (Bergstrøm and Hjeljord 1987). Therefore, moose ranges dominated by birch have generally been regarded as being of lower quality (Oldemeyer et al. 1977; Hjeljord et al. 1982; Lundberg et al. 1990). The eastern region in our study suggests that birch does not universally deserve this low status.

Although the western moose had 41% less browse per individual than the eastern moose, their current fitness seems disproportionably low. This was particularly striking given their low utilization of birch, the most abundant browse in the region (Table 1). Allegedly, a higher utilization of birch would have increased their foraging rates, and hence, possibly improved their fitness (Westoby 1974). Trading quality for quantity when the resource level is substantially reduced has been shown for several northern ungulate populations (e.g. Vivås and Sæther 1987; Sæther and Andersen 1990; Nicholson et al. 2006; Bremset Hansen et al. 2009). We see five possible explanations for the seemingly contradictive relationship between fitness and birch utilization in the west, of which two appear more likely than the others, 1) nutritionally deviating birch; and 2) cohort effects in moose fitness (see below).

The remaining three explanations cannot be ruled out although we find them less likely to apply: 3) Behavioural lags stemming from previous times when preferred forage was plentiful, and operating through maternal role model effects. The latter are generally strong for diet selection in ungulates (Launchbaugh and Howery 2005); 4) A different life history trade-off (e.g. age and size at first reproduction, or size and number of offspring), possibly with an inherent genetic link (Solberg et al.

2009a); or 5) Lower encounter frequency of birch (compared to the east). However, unless 4) applies, a negative energetic balance of eating more birch seemingly requires a very high energy expenditure of obtaining the species. Our data does not seem to support this theory: more than every 3rd plot where rowan was encountered in the west also had birch on the plot (467 out of 1 360). Also, even birch trees standing in the immediate vicinity of an intensively browsed rowan, very rarely showed signs of being browsed by moose in the western region (Wam and Hjeljord *pers. obs*).

Nutritionally deviating birch

   One simple reason for differential utilization of birch may be different proportions of the various *Betula* spp. species. Moose in Scandinavia shows a higher selectivity for *B. pendula* than for *B. pubescens*, the two main birch species (Danell et al. 1985; Danell and Ericson 1989; Månsson et al. 2007). In general, *B. pendula* occurs in drier habitats than *B. pubescens* (Arnborg 1946), and the eastern ranges in our study were drier than the western ranges. Nonetheless, according to data provided by the Norwegian National Forest Inventory, there are four times as many *B. pendula* trees/ha in the west as in the east, and they constitute no more than 12.2% and 2.3% of all birch trees, respectively. The importance of *B. pendula* in the moose diet on these ranges is therefore limited, at least on the regional level, and should in anyway benefit the western more than the eastern moose population.

   The nutritional value of birch may still differ between the two regions. Several studies have shown site-specific chemical characters for birch that is of relevance to moose (e.g. Haveraaen and Hjeljord 1981 on digestibility; Danell et al. 1997 on protein and minerals; Ohlsson and Staaland 2001 on minerals, McArt et al. 2009 on protein). Furthermore, Vihera-Aarnio and Heikkila (2006) have showed that moose utilization of birch may be affected by latitudinal seed origin, i.e. there may even be a genetic component. However, altitude, latitude and climate varied very little between the regions in our study. If birch still differed in nutritional content, it likely stemmed from soil characteristics, possibly in interaction with differences in innate herbivory defence. Herbivory *induced* reduction in nutritional content is not a likely explanation since at the regional level only 9% of all birch twigs were browsed in the west.

   The western ranges had more than twice as much land with intermediate to high soil fertility than the eastern ranges. Plants growing on richer soils have higher growth rates (Wilson 1988), and may thus be more palatable to herbivores (the 'carbon-nutrient balance hypothesis', Bryant et al. 1983). If so, however, birch should be more, and not less attractive to moose in the west. The carbon-nutrient balance has been substantially criticised for its simplicity by e.g. Hamilton et al. (2001), showing that there are more factors involved in herbivory defence than carbon: nutrient allocations. Our study should thus be complemented by future research looking into chemical and/or genetic differences between birch in the two regions.

Cohort effects

   Comparing the development in moose density and fitness (Fig. 1), the density in the west has on average been much higher than in the east, particularly in the early 1990s. Indeed, given the lower recruitment rates observed in the west, the density differences in relation to forage availability were

probably larger than the differences observed in the number of moose shot/km^2. Several cohorts of small calves can have been recruited to the population in those high density years. Like for ungulates in general (Gaillard et al. 2003), cohort effects in moose may have long-lasting consequences for the individuals' fitness (Solberg et al. 2004; Solberg et al. 2008).

Cohort effects may also be transmitted between generations if smaller mothers produce smaller calves (Albon et al. 1987; Beckerman et al. 2002). A positive relationship between body mass of calves and the body mass of their mother has been demonstrated for moose (Sæther and Heim 1993; Histøl and Hjeljord 1995). However, a large variance indicates that compensatory processes, e.g. due to life history trade-offs (such as size and number of calves) or improved nutritional conditions, reduce the transmission of body mass variation between generations. Moreover, although affecting adult body mass, the effects of conditions in year of birth fade with age in moose (Solberg and Sæther 1994; Solberg et al. 2004). Although compensatory processes may to some extent have mitigated the most severe cohort effects from the 1990s, we postulate that moose body mass in the west could still be partly influenced by such effects.

Applied conclusions

Our study illustrates the complexity involved in the important concept of carrying capacity. On our study ranges, an eventual index of carrying capacity will be substantially complicated by the moose' differential plant utilization, and possibly other factors such as e.g. demographical lags from more severe food limitation in the past. These complications make carrying capacity equivocal, and care should be taken when extrapolating data across ranges. The latter apparently applies to even the most fundamental component of carrying capacity, i.e. forage availability.

Our study also confirms the strong influence of logging activity on production of moose forage. Depending on soil fertility, logging multiplied the amount of browse shoots on the one hand, but simultaneously reduced availability of bilberry, an important forage plant for moose. Clearly, logging activity should be integrated with moose management, which is currently not the situation in Scandinavia (Wam and Hofstad 2007).

A practice that is applied in Scandinavia, is to focus on the highly preferred rowan, aspen and sallow when monitoring moose browsing pressure. The eastern region in our study shows that when scarce, these species may be intensively browsed even though the moose population does not yet show a serious decline in fitness. On such ranges, changes in browsing pressure may be earlier reflected in the staple food, which should thus be included in the monitoring program.

Acknowledgements

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Table 1. Ecological parameters in two regions with contrasting moose fitness, southern Norway 2005-2008 (east = high fitness 59°11'N - 60°42'N and west = low fitness 58°45'N - 59°42'N). Mean ± SE among five ranges per region, and two-sample t-tests east versus west.

	East	West	t_9-value	P-value
Moose year-round density (per km²)	1.5 ± 0.11	2.0 ± 0.18	-1.1	0.147
Calf body mass (kg, dressed carcass)	71 ± 1.2	57 ± 2.9	4.4	0.003
Twinning (calves per cow with calf)	1.26 ± 0.021	1.13 ± 0.044	2.5	0.023
Browse (shoot-cm available per m²)	96 ± 10.0	128 ± 5.4	-3.2	0.008
Birch	85 ± 10.8	48 ± 7.2	3.2	0.010
Pine	24 ± 4.1	13 ± 3.8	2.2	0.029
Rowan	3 ± 0.6	17 ± 4.3	-3.8	0.007
Salix spp.	11 ± 3.2	6 ± 0.8	1.2	0.142
Other[a]	5 ± 3.5	12 ± 2.9	-1.1	0.152
Herbaceous forage (% area coverage)				
Bilberry	33 ± 2.0	38 ± 6.2	-1.0	0.165
Grasses	22 ± 3.2	30 ± 9.5	-1.1	0.143
Ericaceae spp.	37 ± 4.2	15 ± 2.4	4.0	0.003
Forbs	7 ± 2.7	9 ± 1.2	-1.0	0.161
Ferns	2 ± 0.2	11 ± 1.0	-7.2	≤0.001
Raspberry	1 ± 0.3	2.2 ± 1.3	-1.5	0.097
Per capita forage availability[b]				
All browse	96 ± 19.3	56 ± 13.6	1.7	0.068
Preferred browse	11 ± 4.1	13 ± 2.1	-0.4	0.353
Preferred herbaceous forage	0.21 ± 0.033	0.24 ± 0.033	-0.6	0.271
Browsing pressure[c]				
Birch	20 ± 4.2	9 ± 1.5	2.4	0.039
Pine	27 ± 7.2	17 ± 3.1	1.3	0.121
Rowan	60 ± 2.3	51 ± 3.1	2.3	0.026
Intermediate to high soil fertility (%)	39 ± 4.4	66 ± 4.5	-4.3	≤0.001
Start of growing season[d]	118 ± 1.9	114 ± 1.9	0.6	0.724
Proportion of young forest[e]	8 ± 1.2	8 ± 1.4	-0.2	0.406

[a] Includes all remaining browse species except for Norway spruce (*Picea abies*)

[b] Browse shoot-cm/m² per moose, herbaceous forage coverage (km²) per moose. Preferred species are rowan, aspen and *Salix* spp. (browse), bilberry and raspberry (herbaceous).

[c] Proportion of twigs browsed (accumulated, not only last year's browsing)

[d] First day of the year with mean temperature >5°C

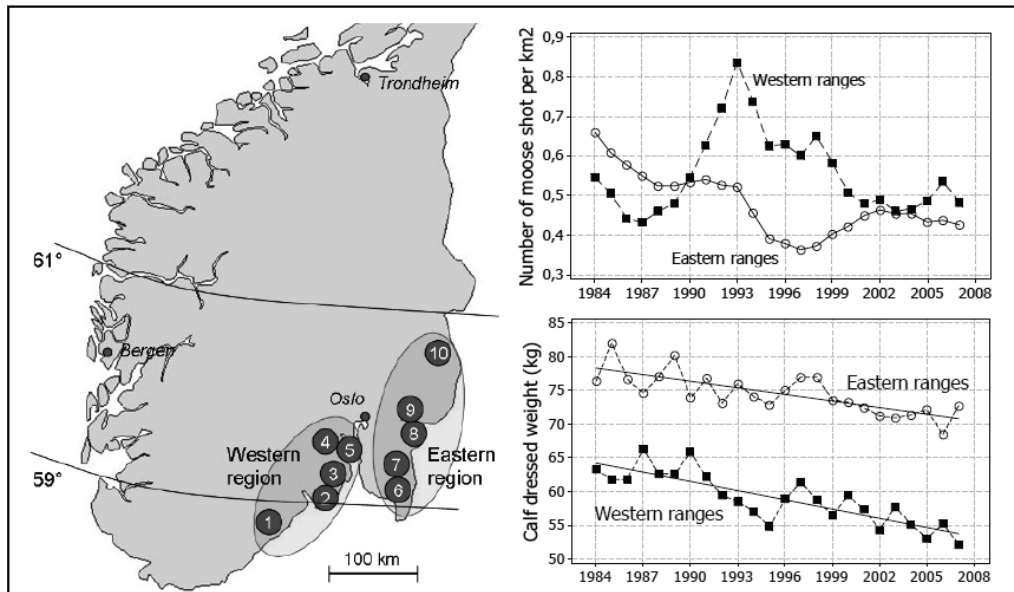[e] Dominant conifer tree height <4 m

Fig. 1. Total number of moose shot per km^2 and calf body mass (dressed carcass, $N = 66 \pm 23.6$ shot per year and range) in two regions of southern Norway with contrasting moose fitness and plant composition. Encircled numbers on map are study ranges: 1 = Vegårshei, 2 = Kjose, 3 = Re, 4 = Sande W, 5 = Sande E, 6 = Halden, 7 = Rakkestad, 8 = Aurskog S, 9 = Aurskog N and 10 = Finnskogen.
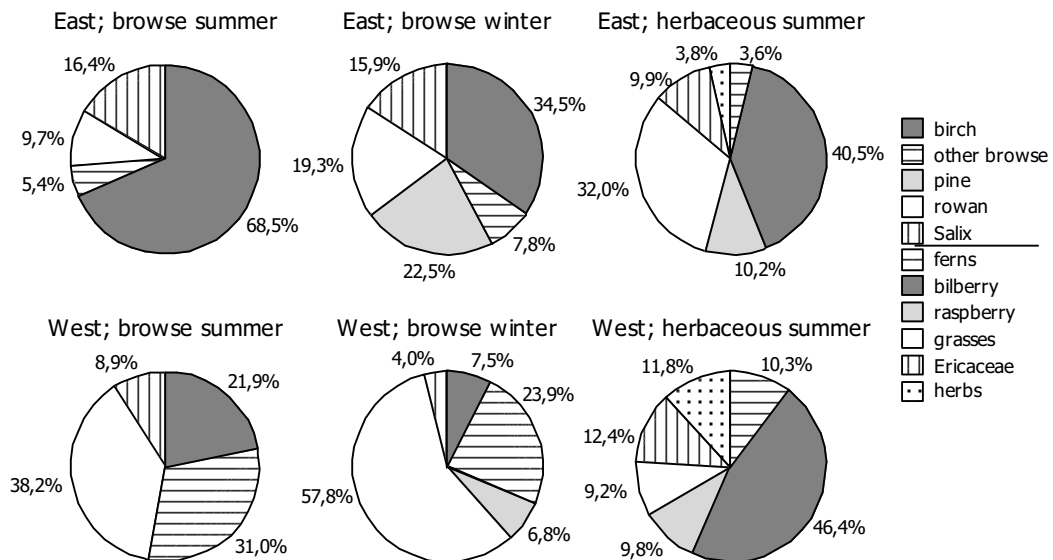

Fig. 2. Moose summer- and winter diet in two ecologically contrasting moose regions in southern Norway 2005-2008 (west 58°45'N - 59°42'N and east 59°11'N - 60°42'N of the Oslofjord). Browse diet based on proportion of browsed trees ($N = 2\ 330 \pm 157$ per range in winter, $2\ 396 \pm 265$ in summer). Herbaceous forage based on fecal analyses ($N = 18 \pm 1.5$ per range), in which these species constituted 39 ± 9.6 % (west) and 55 ± 7.1 % (east) of all epidermal fragments (not corrected for effects of digestion).
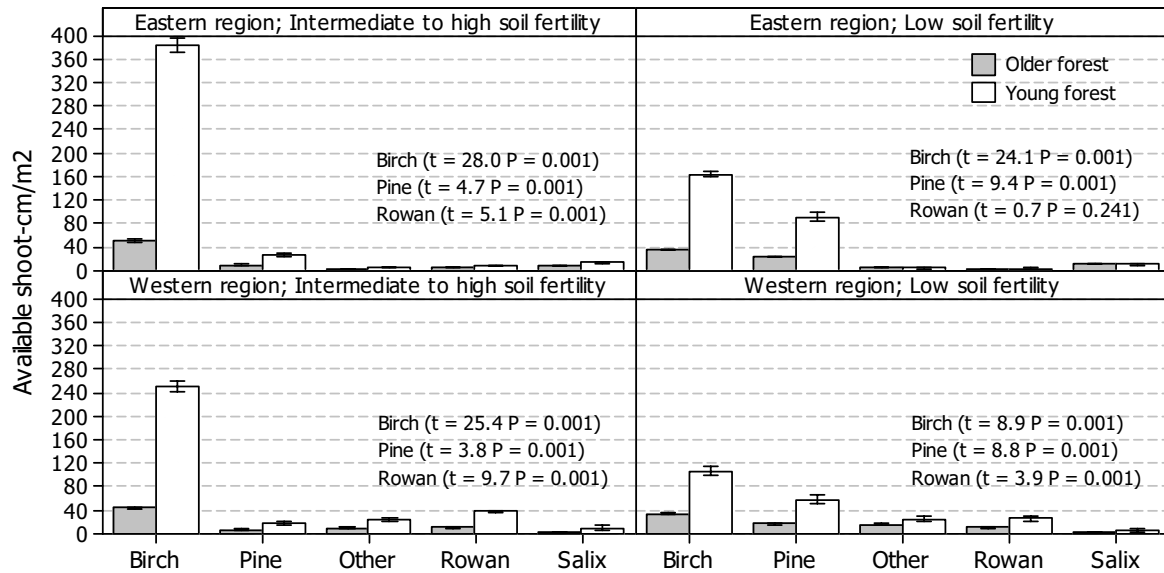
Fig. 3. Availability of browse in relation to forest age in two ecologically contrasting moose regions in southern Norway 2005-2008 (west 58°45'N - 59°42'N and east 59°11'N - 60°42'N of the Oslofjord). Young forest = dominating coniferous tree <4 m in height.
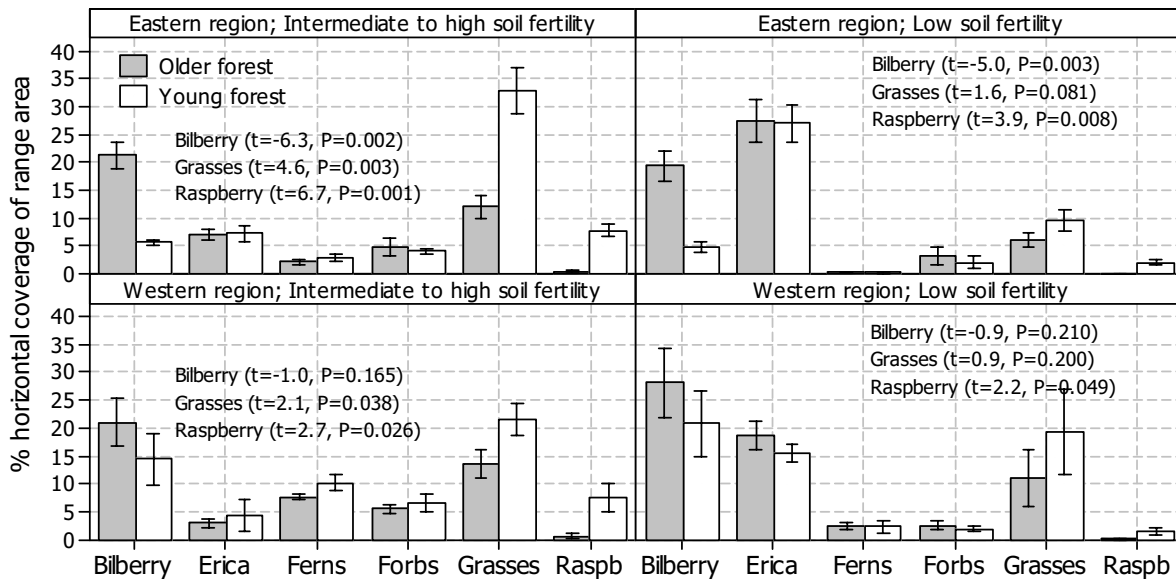

Fig. 4. Percentage area coverage of herbaceous forage in relation to forage age in two ecologically contrasting moose regions in southern Norway 2005-2008 (west 58°45'N - 59°42'N and east 59°11'N - 60°42'N of the Oslofjord). Young forest = dominating coniferous tree <4 m in height.
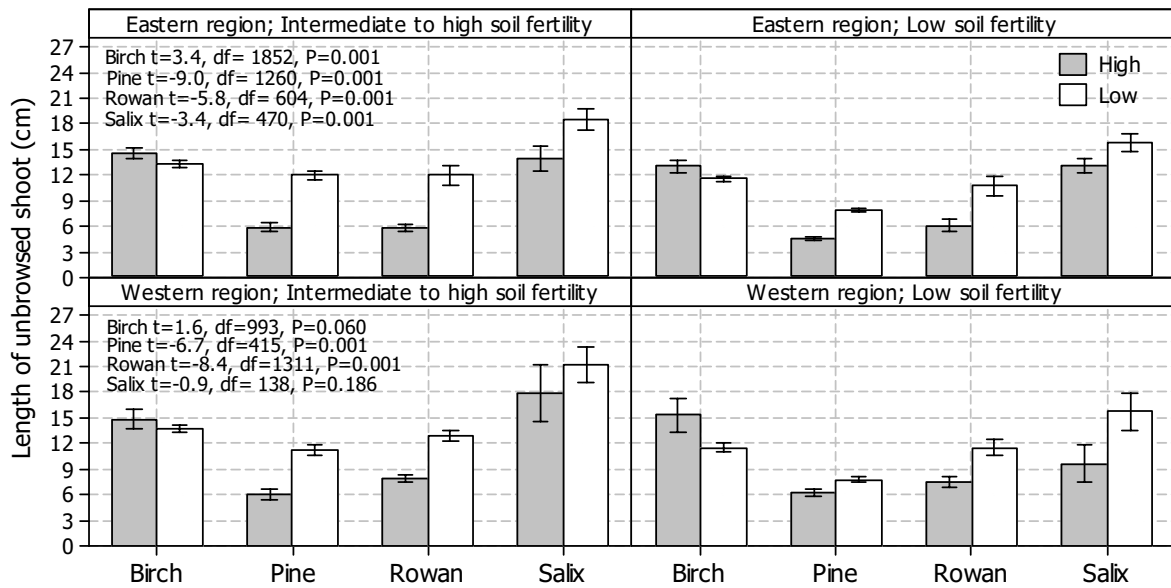
Fig. 5. Length of an average unbrowsed shoot in relation to browsing pressure and soil fertility in two ecologically contrasting moose regions in southern Norway 2005-2008 (east 59°11'N - 60°42'N and west 58°45'N - 59°42'N of the Oslofjord). High browsing pressure ≥1/3 of shoots browsed at least once, low <1/3. *t*-tests are high versus low, tested across soil fertility.
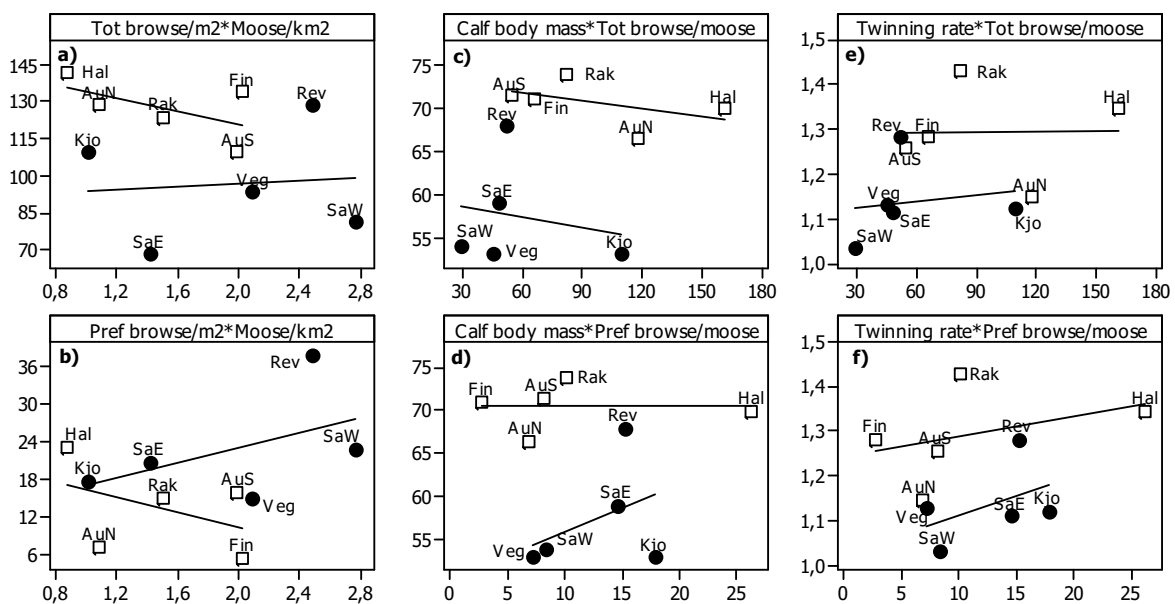

Fig. 6. Available shoot-cm/m^2 of **a)** all and **b)** preferred (i.e. rowan, aspen and *Salix* spp.) browse in relation to moose density on ten ranges in southern Norway 2005-2008 (east 59°11'N - 60°42'N and west 58°45'N - 59°42'N of the Oslofjord); as well as **c-d)** calf body mass (dressed carcass, mean 2004-2008, *N* = 61 ± 24.8 per range) and **e-f)** twinning rate (calves per cow with calf) in relation to the *per capita* browse availability.
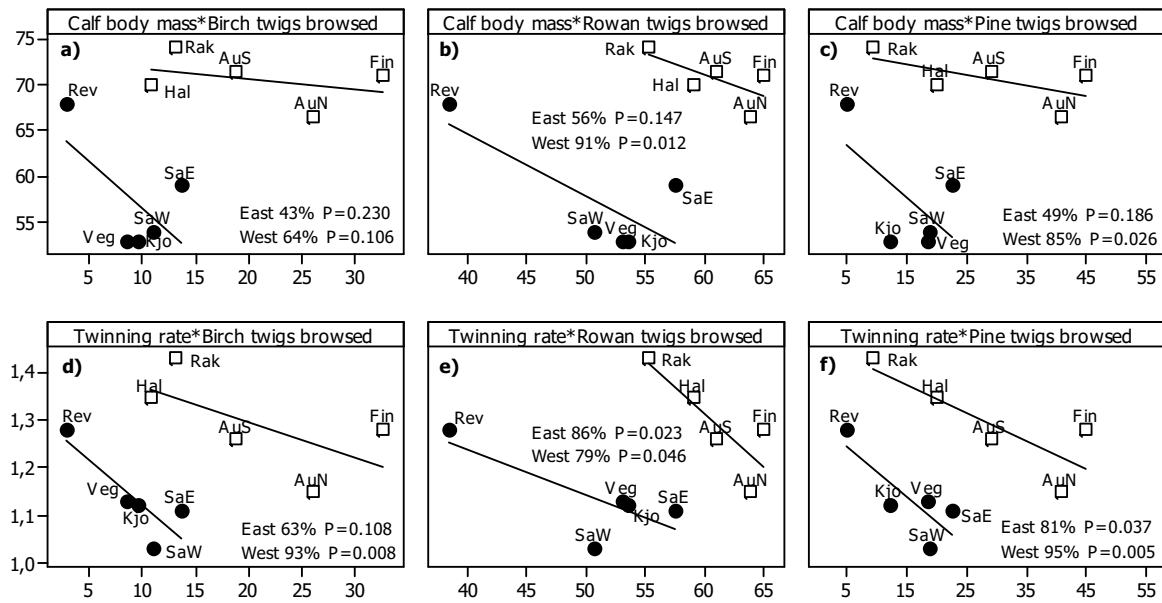
Fig. 7. **a)** Moose calf body mass (dressed carcass, mean 2004-2008, $N = 61 \pm 24.8$ per range) and **b)** twinning rate (calves per cow with calf) in relation to accumulated browsing pressure (% of twigs browsed) on ten ranges in southern Norway 2005-2008 (east 59°11'N - 60°42'N and west 58°45'N - 59°42'N of the Oslofjord). % is R^2 in intra-regional linear regression analyses. Panel titles are *y*-axis label, *x*-axis label.