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ARTICLE
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Food for fitness? Insights from 24 Norwegian moose populations for proactive monitoring and preventing overabundance

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Abstract

Cervid (Cervidae) populations that are overabundant with respect to their food resources are expected to show declining physiological and reproductive fitness. A proactive solution to such declines is to integrate the monitoring of food resources with animal harvesting strategies, but there are few studies available to guide managers regarding which food resources to monitor and how to do so. In this study, we used a large, rare data set that included detailed absolute measures of available food quantities and browsing intensity from field inventories, to test their relationship with fitness indices of moose *Alces alces* in 24 management units in four regions across Norway. We found that calf body mass and calves seen per cow during the autumn hunt were strongly and positively related to the availability of tree forage, especially the species most selected for by the study moose (e.g., rowan [*Sorbus aucuparia*] and sallow [*Salix caprea*]). The strength of the correlations varied between regions, apparently being stronger where the moose were closer to being overabundant or had a legacy of past overabundance. As expected, the intensity of browsing on the three most common tree species, that is, birch (*Betula* spp.), rowan, and pine (*Pinus sylvestris*), was also negatively and strongly related to the fitness. We discuss how our approach to food monitoring can facilitate a management that proactively adjusts densities of moose, and possibly other cervids, to trends in food availability and browsing intensity, thereby avoiding detrimental effects of overabundance.

KEYWORDS

carrying capacity, cervid, condition, fecundity, large herbivore, management, reproduction, ungulate, wildlife

INTRODUCTION

When cervid (Cervidae) density becomes so high relative to their food resources that negative effects are observable on the population's health status, the population traditionally is defined as overabundant (Côté et al., 2004). Overabundant cervids can quickly lead to a myriad of cascading effects on the ecosystem, especially through

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vegetation changes caused by the animals' browsing (e.g., Moe et al., 2018; Ramirez et al., 2018). The food plants can carry telltale signs of too intensive browsing before the adverse health effects of overabundance may be detected in the cervid population. Therefore, an apparent solution to counter overabundance is to integrate the monitoring of the cervids' food with the management's harvesting strategies.

Ideally, such monitoring would result in proactive management, whereby the amount of forage or the animal density is adjusted before the animals suffer adverse physiological effects. In practice, many cervid populations are instead managed in hindsight, that is, their density is not adjusted until serious problems of overabundance manifest (Kirkland et al., 2021; Vercauteren et al., 2011). Some of these situations may arise due to complex systems; for example, the presence of multispecies resource partitioning or predator–prey relations, where food monitoring may be viewed as of secondary importance, being too expensive or impractical. However, a general lack of targeted research may also have contributed. The majority of studies on food and cervid fitness focus on the quality of food rather than the quantity, for example, diversity, nitrogen, or niche widths (e.g., Jesmer et al., 2020; Long et al., 2014; Monteith et al., 2015; Oates et al., 2021; Parikh et al., 2017; Simard et al., 2008). While these studies can sometimes guide managers about overabundance (e.g., Boertje et al., 2007; Piasecke & Bender, 2009), the information provided is typically retrospective and rather aimed at understanding the basic underpinnings of the cervid's nutritional ecology.

More importantly, the studies that do focus on food quantity and cervid fitness have seldom found strong associations. This is likely due in part to an understandable reliance on cost-efficient indirect and coarse measures of food quantities, such as airborne laser scanning of vegetation structure (e.g., LiDAR), spectral reflections of vegetation greenness (e.g., NDVI) or the percentage of habitat area consisting of a certain vegetation type (Brown, 2011; Herfindal et al., 2014; Herfindal, Saether, et al., 2006; Herfindal, Solberg, et al., 2006; Simard et al., 2010; Terada et al., 2012; Wam et al., 2016; Zini et al., 2019) (but see also stronger associations in Felton et al., 2020; Lukacs et al., 2018; Simard et al., 2014a, 2014b). These studies are often also very broad in scope, with the food index being only one of a dozen explanatory parameters in a multivariate frame of study. As expected, more targeted studies using detailed ground-based measures, such as the biomass of various food types per unit area, generally show higher associations between food and fitness (Boucher et al., 2004; Giroux et al., 2014; Hjeljord & Histol, 1999; Lopez et al., 2025; Merems et al., 2020; Pettorelli et al., 2003; Proffitt et al., 2016; Saether & Heim, 1993; Sand et al., 1995; Seaton et al., 2011; Wam et al., 2010) (but see also Bender et al., 2007; Miyashita et al., 2007).

The use of indirect and coarse measures of food quantity has likely resulted in weaker correlations with cervid fitness for two key reasons. First, the selective feeding of most cervid species: If a food type comprises, for example, 70% of the "greenness" of an area, but only 10% of the cervid diet, NDVI will not reflect the actual food availability. Second, there are many spatial differences in the value of food to cervids: Edible biomass per food item and its nutritional contents vary strongly among plant species, and among sites for a given plant species (Monteith et al., 2014; Wam et al., 2018; Wam, Solberg, et al., 2021). A plant species' acceptability as food to cervids can also depend on past browsing history (Pastor, 2016; Petersson et al., 2019; Royo et al., 2010; Russell et al., 2017; Speed et al., 2013; Stolter, 2008). Although ground-based efforts that obtain absolute and detailed measures of the food of sufficient resolution are very resource demanding, more such studies are needed to parameterize the other cost-efficient indirect monitoring schemes (Melin et al., 2016).

Browsing intensity can also be used proactively to monitor cervid overabundance. For example, Seaton et al. (2011) found a strong negative correlation between twinning rates and the biomass removal by browsing on focal tree species across moose management units in Alaska. However, this is a field of research that is scarcely explored. Most studies with data on browsing intensity are not set in the context of animal fitness, but rather forest damage or vegetational changes (e.g., De Jager & Pastor, 2009; Wallgren et al., 2013; White, 2012). The relationship between browsing intensity and fitness is also expected to be highly site-dependent, due to the dynamic food selectivity of cervids (Wam et al., 2010). Consequently, what an increasing browsing intensity means in terms of reduced dietary intake varies with both plant compositions and other environmental factors (De Jager et al., 2009; Giroux et al., 2016; Hodgman & Bowyer, 1986). There is thus also a need for more studies to explore the extent to which browsing intensity is useful for proactive monitoring.

In this study, we used detailed and targeted absolute measures of available food quantities and browsing intensity from high-resolution ground-based field inventories to test their relationship with calf body mass and calves observed per cow during the autumn hunt in 24 management units of moose (*Alces alces*) in four regions across southern Norway. Calf body mass and calf production (hereafter collectively termed "fitness") have been clearly demonstrated to indicate physiological and reproductive

fitness in cervid populations (Gaillard et al., 2000). Moose in Norway is a particularly well-suited model species for this study purpose. Its year-round diet and food selectivity have been documented in detail throughout extensive areas (e.g., Wam et al., 2010; Wam & Hjeljord, 2010a), which is a crucial aspect for monitoring food resources at a meaningful taxonomic resolution. There are also long-term moose hunting statistics available across the species' complete habitat range, consistently collected and already much studied due to its relevance as an indicator of moose population performance (Solberg & Saether, 1999; Tiilikainen et al., 2012; Ueno et al., 2014).

Based on the references above, we hypothesized that (1) moose fitness is positively related to the total quantity of per capita food availability; (2) the availability of some food types is more related to fitness than others due to moose food selectivity; (3) the fitness importance of these food types selected for by moose varies between study areas, because the food varies in abundance or nutritional content between landscapes; (4) moose fitness is negatively related to browsing intensity on focal tree forage, because more intense browsing indicates higher levels of food depletion; and (5) more intense browsing on a plant species less selected for indicates a more severe food depletion than it does for a plant species more selected for.

METHODS

Study areas

The 24 study areas are situated in the south-eastern and middle parts of Norway (Figure 1). The size of the study areas varied from 47 to 1217 km^2 (median 198 km^2) of moose habitat (defined below). Each study area held a distinct moose management unit (MMU) subject to the same historic harvesting regime, and with no major movement barriers within the area. Moose in Norway are generally managed within municipality borders, with some neighboring municipalities collaborating on a larger scale. However, due to the valley-mountain topography of much of Norway, moose populations often are spatially delimited by landscape barriers such as highways and large water bodies along the valleys. One municipality can therefore have two or more moose populations quite isolated from each other. The spatial delineation of each study area was done in close collaboration with the local moose managers (mainly municipality staff). We divided the 24 study areas into four regions based on inherent differences in the habitat conditions they provide due to topography, latitude, and distance to sea (Figure 1, Table 1). We included region as a factor in the analyses to account for this environmental variation that is not controlled by moose management.

All study areas had their main moose habitat below the treeline, in forests that belong to the boreal and boreonemoral vegetation zones (Moen, 1998). Here, the forest is dominated by Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and birch (*Betula* spp.) with other broadleaf species interspersed at varying densities (Table 1). The southern fringes of two study areas (Grenland and Kjose) were in the nemoral forest zone. Two other study areas (Murudalen and Gausdal) included areas along the treeline (transition zone from boreal to alpine forest, 900–1100 m above sea level). As moose habitat, we included all forested areas and bogs within forests, while we omitted waterbodies, areas above the treeline, and heavily modified land such as agricultural fields and settlements.

Practically all forests in the study areas have been managed for production forestry. Since the 1960s and 1970s, this has generally involved clearcutting, which contributes significantly to the amount of available moose food (Wam et al., 2010). The clear-cuts are moderate in size: median 2.1 ha for spruce and 4.0 ha for pine (Granhus & Eriksen, 2017). The spruce clear-cuts have normally been replanted with seedlings 1–2 years after harvest, while pine clear-cuts have been regenerated by seed trees, both with subsequent monoculture management. The extent to which broadleaves are removed during cleaning and thinning operations in the regenerating stands, is highly variable between property owners. Almost all production forests are owned by private individuals (84%) (Statistics Norway, 2023).

Until recently, the only other cervid species in the study areas was roe deer *Capreolus capreolus* L. (and sporadic reindeer *Rangifer tarandus* L. passing through in Meråker, Stjørdal and Murudalen). Over the last two decades, red deer *Cervus elaphus* L. has been expanding its range into the moose study areas. The diet overlap between moose and other deer is fairly large in summer, but lower during winter in their traditional habitats (Spitzer et al., 2020). Due to the prevalence of hilly terrain and often deep snow in the study areas, roe deer are seldom present in the moose habitat in winter. No reliable hunting statistics for roe deer were available to estimate their density. Red deer in our study areas seem to be more inclined to stay in the moose habitat during winter. It may therefore have a larger diet overlap with moose and thus be a confounding factor for the moose per capita availability of food. The hunting bag statistics that we used to estimate the density of red deer (Table 1) are considered rather rough approximations expected to improve in precision as the red deer increase in population size (Solberg et al., 2022).

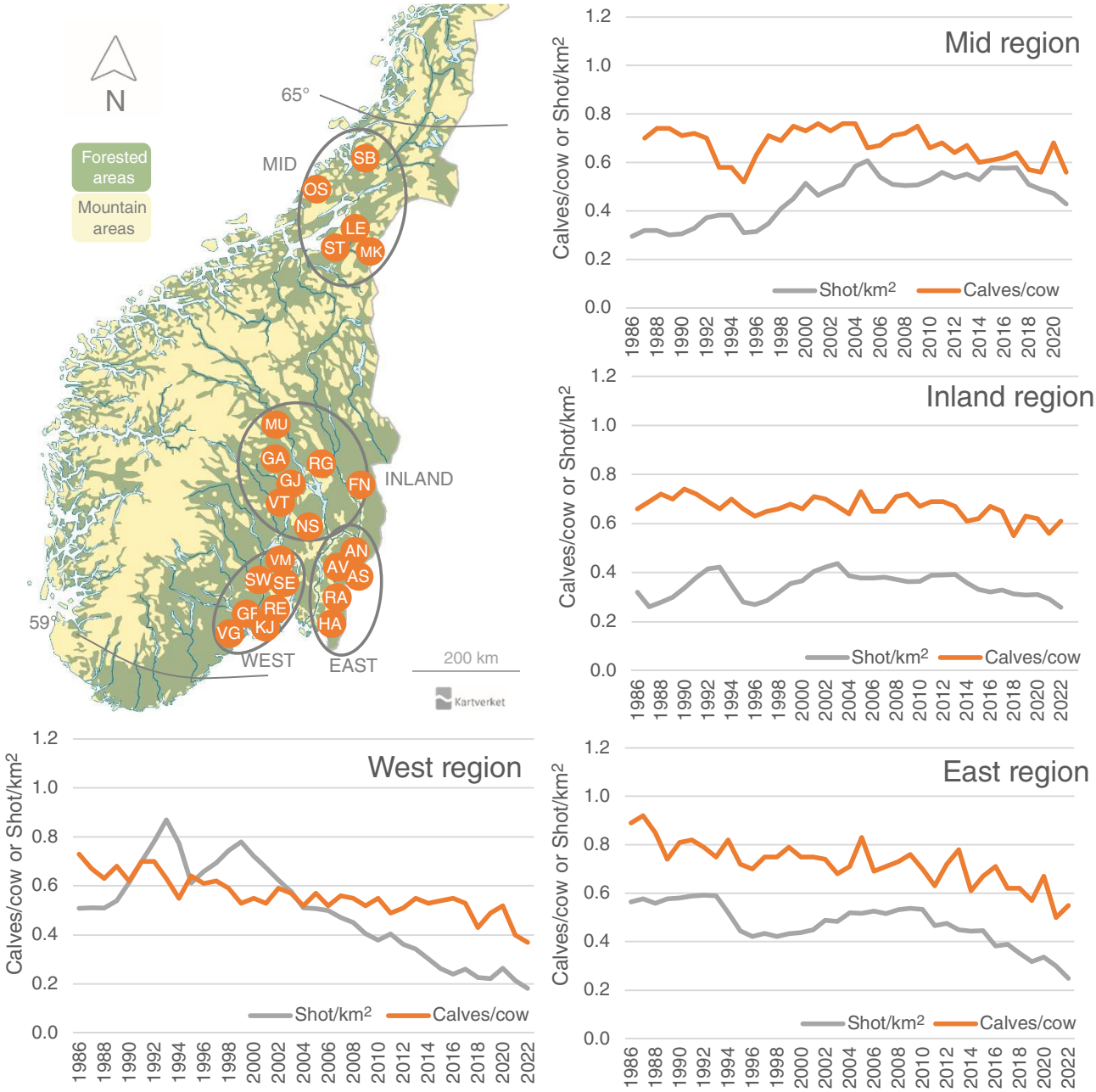

FIGURE 1 Time series of moose harvests (shot animals per square kilometer of moose habitat) and calves observed per cow during the autumn hunt in four moose regions of southern Norway. Regions are marked in the map by gray open circles. Each regions included several study areas each holding a distinct moose management unit, marked in circles with the study area name abbreviated within the circle. Abbreviations correspond to study areas in Table 1.

Large predators were a negligible factor in our study. Wolves (*Canis lupus*) and brown bears (*Ursus arctos*) are the only predators on moose in Norway. Bears were present only during the occasional migration through a few study areas: Aurskog, Finnskogen, Stjørdal, and Meråker (Bischof & Swenson, 2012; Brøseth et al., 2023). Only one region (the East) had wolf territories. At the time of the food inventories in this region (2005–2006), there were 1–2 wolves each in two wolf territories but no documented breeding (Wabakken et al., 2006). Two years prior, with breeding wolves in the territories, there was an observable effect of wolf predation on moose calves only in the very close vicinity to the wolf den (Wam & Hjeljord, 2003). The East region had one of the strongest correlations between food and moose fitness, which supports the presumption that predation was not a confounding factor in the study.

TABLE 1 Habitat type and climate in the 24 study areas, each hosting a distinct moose management unit, in four regions of southern Norway used to study food and fitness relationships.

Region and study area	Moose area (km^2)	Moose sample size[a]		Altitude (m asl)[c]	Vegetation cover type (%)			Soil fertility	Growing degrees (°C)	Snow depth (cm)	Large predators[b]	Red deer shot[a]
		Obs	Shot		Pine	Spruce	Bog					
West	**305**	**593**	**79**	**227 ± 106**	**19**	**65**	**6**	**15**	**1339 ± 134.7**	**26 ± 11.4**	**No**	**18 ± 44.2**
Vestmarka (VM)	98	126	18	318 (230–405)	0	100	0	19	1209	16	No	0
Vestskauen (SW)	63	307	37	300 (30–515)	15	69	10	14	1311	43	No	0
Østskauen (SE)	127	163	31	185 (55–290)	54	46	0	14	1222	30	No	0
Revetal (RE)	138	336	48	136 (40–360)	0	86	14	17	1554	14	No	0
Kjose (KJ)	204	640	130	110 (25–170)	3	79	13	18	1282	11	No	2
Grenland (GR)	1168	1457	161	246 (1–680)	34	63	2	14	1259	34	No	127
Vegårshei (VG)	334	1125	130	243 (150–335)	29	49	0	12	1538	35	No	0
East	**272**	**1026**	**139**	**208 ± 62**	**58**	**36**	**6**	**13**	**1428 ± 135.4**	**11 ± 5.7**	**Yes**	**0 ± 0**
AurskogN (AN)	133	718	92	262 (160–350)	37	53	10	13	1356	16	W, B	0
AurskogV (AV)	146	722	81	237 (150–330)	50	41	9	12	1356	16	W, B	0
AurskogS (AS)	191	620	92	251 (175–325)	71	29	0	13	1356	16	W, B	0
Rakkestad (RK)	266	1013	159	174 (120–260)	72	19	9	12	1372	5	W	0
Halden (HA)	623	2057	272	115 (5–190)	61	39	0	13	1699	4	W	0
Inland	**702**	**1734**	**248**	**556 ± 192**	**32**	**55**	**12**	**12**	**1154 ± 278.1**	**31 ± 11.6**	**Yes**	**25 ± 48**
Murudalen (MU)	1034	1680	286	871 (650–1080)	80	17	0	9	593	50	No	141
Gausdal (GA)	1217	1814	222	813 (330–1075)	26	71	0	10	911	44	No	22
Finnskogen (FN)	860	3236	498	346 (225–545)	32	52	16	13	1363	17	W, B	0
Ringsaker (RG)	851	2985	407	512 (125–785)	31	43	24	14	1319	21	No	3
Gjøvik (GJ)	512	1317	202	521 (215–735)	11	72	16	14	1148	35	No	5
VestreToten (VT)	153	656	66	508 (390–670)	25	63	13	14	1347	25	No	2
Nannestad (NS)	290	448	59	386 (150–620)	17	66	14	14	1399	22	No	0
Mid	**376**	**1521**	**169**	**218 ± 94**	**40**	**39**	**19**	**11**	**1243 ± 63.4**	**16 ± 10.7**	**Yes**	**26 ± 26.7**
Salsbruket (SB)	47	128	17	150 (30–230)	61	30	9	9	1204	26	No	0

(Continues)

TABLE 1 (Continued)

Region and study area	Moose area (km^2)	Moose sample size[a]		Altitude (m asl)[c]	Vegetation cover type (%)			Soil fertility	Growing degrees (°C)	Snow depth (cm)	Large predators[b]	Red deer shot[a]
		Obs	Shot		Pine	Spruce	Bog					
Osen (OS)	174	1087	70	114 (1–293)	29	52	16	10	1316	1	No	15
Stjørdal (ST)	688	3337	438	325 (90–530)	27	47	25	11	1252	15	B	69
Meråker (MK)	537	644	92	465 (150–650)	47	29	24	11	1144	30	B	2
Levanger (LE)	435	2409	226	299 (30–490)	37	38	23	12	1300	9	No	43

Note: Moose habitat primarily consists of and is defined by forest and bogs around or below the tree line. Agricultural land is also occasionally used by moose but is not included here. Values in boldface represent the mean per region and the variation (±SD) among areas within the region. Habitat data are from National Forest Inventory 2010–2022 (plot grid 3 × 3 km, see Wam, Solberg, et al., 2021). Remaining vegetation types (not listed) are impediment or forest dominated by broadleaves. Climatic data are 5-year averages of 2011–2015, from the meteorological station(s) closest to the mean altitude of each study area. Soil fertility index from 8 (min) to 26 (max) (Tveite, 1977). Growing degrees is the sum degrees on all days with mean temperature ≥5°C. Snow depth values are the mean of Dec–Apr.

Abbreviations: asl, above sea level; B, bear; Obs, observed; W, wolf.

[a]Hunting statistics at time of food inventory (t), 3-year average: year $t - 1$ to $t + 1$ (only 2-year average for areas surveyed in 2023). Number of animals per year.

[b]Large predators present but at negligibly low densities (see *Methods*: *Study areas*).

[c]Values are given as median with range in parentheses.

Field design of food inventories

We collected data on moose food availability and browsing intensity using field inventories in the summers of various years from 2005 to 2023. Different study areas were surveyed in different years as the inventories are part of a long-term project with intermittent funding. Study areas have been selected to include as much of the variation as possible that exists in moose food availability and fitness in Norway. We have previously verified that the study design and the sample sizes obtained in these inventories are well suited to capturing the expected variation in both tree forage availability and browsing intensity of the focal tree species in the study areas (Wam, Solberg, et al., 2021).

Two study areas were surveyed more than once: Stjørdal in 2006 and 2021 and Gjøvik in 2007, 2012, and 2018. We treated each of these years as a unique survey rather than a replica in our analyses. The number of years between the repeated surveys exceeded the typical management planning period in Norway (5 years), and the food availability for moose, and their fitness, changed substantially within the time frame of the resampling (in *Results*: *Variation in moose densities and fitness indicators*). The sample size for most of the results is therefore $N = 27$ rather than $N = 24$ study areas.

Prior to the field work, we placed 4-km long line transects by stratified random sampling on maps, distributing them across the landscape without targeting any area of special interest. The density of transects varied with terrain variation, based on sample size (rarefaction) curves from previous surveys (see reference to Wam, Solberg, et al., 2021 above), with a median of 15 transects per study area (range 5–28 transects). The aim was to obtain a representative cross sample of the entire moose habitat of the study area. In the first 10 study areas that were sampled, the distribution was done by systematically laying parallel lines 250–500 m apart across the landscape. We used these intensively surveyed areas to identify sufficient sample sizes of transects, plots, and sample trees for later study areas. In later surveys, we angled the number of transects so that we inventoried the area both horizontally and vertically across landscape gradients, while assuring that the overarching inherent forest characteristics (soil fertility and dominating tree species: spruce, pine or broadleaves) were sampled in their approximate proportion of occurrence according to the national forest resource maps SR16 (NIBIO, 2023). After each field inventory, we cross-checked that we had sampled the same proportions of forest age classes and soil fertility classes as in the SR16. The agreement was very high in all study areas (e.g., Wam & Hjeljord, 2022; Wam, Lande, & Bless, 2021), apart from a few moderate deviations in forest age where the SR16 was compiled several years prior to the inventory, and there had been increasing logging activity in the area (e.g., Wam et al., 2023).

Along the transects, we placed circular plots of size 12.5 m^2 ($r = 2.0$ m) every 15 m in young forest (i.e., dominating tree height < 4 m) and every 75 m in

the remaining area (older forest and bogs). The higher frequency of plots in the young forest was necessary to adequately capture the higher levels of variation in tree measurements in young relative to older forest. We corrected for these frequencies when we calculated parameters on the level of study area, by weighing the plot level data with the area's proportions of young and older forest. There were between 150 and 1632 plots per study area, with a median plot density of 1.8 km^{-2} (2.7 $\pm$ 0.74; mean $\pm$ SD). In total, the study inventoried 16,970 plots.

To minimize observer bias, a limited number of trained personnel were involved in all the inventories (five persons 2005–2006, and four persons 2007–2023, all trained by the same team leader). In each inventory, the whole team surveyed the first transect together to calibrate their standards. Transects in different vegetation types and topography were distributed similarly between personnel. After each season, we computed observer biases and adjusted for these during the next field calibration. The detected biases were generally small, with personnel obtaining similar averages and variances of tree parameters for most parameters of interest of all focal plant species (see examples in Appendix S1: Figure S1).

Food data collected in the field inventories

Along the transects, we recorded all vascular plants to the level of species or genus (mosses and lichens were not recorded). For this study, all taxonomic levels were later grouped into four categories: "all tree forage," "selected tree forage," "all field-layer forage," and "selected field-layer forage." A separation between tree forage and field-layer forage (i.e., all other food than tree forage, e.g., ferns, forbs, Ericaeous shrubs, grass) was made to distinguish food that is available year-round from food that is only available when the ground is not covered by normal snow depths.

"All tree forage" included all tree species comprising >5% of any of the moose seasonal diets in the study regions (Wam & Hjeljord, 2010a). Tree forage included all *Salix* spp. irrespectively of whether the species can grow into a proper tree (most only grow to shrub heights). "Selected tree forage" included all tree species at least partially selected for by moose in the study areas according to previous research: rowan (*Sorbus aucuparia*), aspen (*Populus tremula*), sallow (*Salix caprea*), and oak (*Quercus* spp.) (Wam & Hjeljord, 2010a). A species was "selected" in this previous study if it was of higher frequency in the diet than available in the field.

"All field-layer forage" comprised all other food than tree forage. "Selected field-layer forage" included raspberry (*Rubus idaeus*), bilberry (*Vaccinium myrtillus*), and a merged group of "selected herbs" (based on Hjeljord et al., 1990). We merged these herbs because of their low availability in the field. They included meadowsweet (*Filipendula ulmaria*), alpine sow-thistle (*Cicerbita alpina*), bog asphodel (*Narthecium ossifragum*), fireweed (*Epilopium angustifolium*), and goldenrod (*Solidago virgaurea*). We recorded the field-layer as their horizontal coverage of the plot (percentage of area). Coverage was not corrected for varying plant heights because no interspecific comparisons were made between the plants.

For the tree forage, we recorded the species-specific tree densities within moose browsing height (30–300 cm, assuming plants <30 cm are covered by snow or the field-layer). We counted all trees that had their base within the plot and at least parts of their crowns within the designated height interval. Detailed tree parameters were measured on one sample tree per species per plot. We selected this tree from anywhere on the plot, based on the criteria that it was the most representative for the species on the plot, as determined by visual inspection of its age, growth vigor and browsing intensity.

From the sample trees, we recorded the tree height for the species to the nearest 5 cm, the number of shoots browsed at various points in time (summer, recent winter, previous winters), the number of unbrowsed shoots with current annual growth (CAG), and the CAG length measured to the nearest cm per unbrowsed shoot. For this study, browsing from the most recent and previous winters was summed into accumulated browsing. For the CAG length, the leader shoot was not used for measurements unless it was the only one available. If shoots varied a lot in length, more than one was measured and the average taken.

Calculated availability of food quantities and browsing intensity

From the inventory data, we computed species-specific availability of food quantities and browsing intensity for each study area in its field inventory year. Our indices of food quantity represented both current summer and upcoming winter food availability (it also represented the non-eaten portion of food available in the preceding winter). Tree forage (unbrowsed CAG) is a measure of all the food available when snow covers the ground (all winter food), but also a partial index of summer food, when moose eat the leaves and minor fractions of woody parts along the CAG. The amount (mass) of leaves should be proportional to the length of unbrowsed CAG, according to a pilot study we conducted in one of the study areas (Wam & Hjeljord, 2010b).

The inventories were mainly done during the peak growing season (late June to mid-July) and reflect peak food availability for the year. CAG lengths are affected by sampling date, primarily until the peak of the growing season. Four study areas were partly surveyed at the end of the growing season to verify and quantify this relationship: two areas in the most productive region (West) and two areas in the least productive region (Mid). We calculated species-specific regression coefficients of CAG lengths versus date, which we then used to extrapolate CAG lengths to peak season (maximum) values for any plots in our inventories that had been sampled before peak season. These comprised only 7% of the plots in total.

Field-layer forage indicates the rest of the available summer food. On average, moose in the study areas eat about a 50:50 ratio of tree forage to field-layer forage in the summer, but this varies greatly between study areas (Wam & Hjeljord, 2010a). In the analyses, we used the field-layer forage as it was recorded in the field inventories: percent of area covered.

We calculated the available tree forage quantity of each species on each plot, by multiplying the shoot length (in centimeters) with the number of unbrowsed shoots per tree, and then multiplying this shoot length per tree by the tree density (number of trees on the plot) to obtain the available shoot length per plot. This measure was later summed for species according to the grouping of food types ("all tree forage" or "selected tree forage" etc.; see *Food data collected in the field inventories*, above).

We calculated browsing intensity on each plot of each tree species as the percentage browsed of all shoots, where all = browsed + unbrowsed. For this study, we only used the browsing intensity on the three most focal species, defined as the three most common in all regions: birch, rowan, and pine (willows are more common than rowan, but comprise a varied multi-species group). We calculated per capita availability (per moose) of tree forage by dividing the absolute availability (in centimeters per plot) by the moose density (number of moose per square kilometer).

Estimation of moose densities

We used autumn hunting statistics (moose observed and moose shot) to estimate the moose density within each study area. Hunting statistics in Norway are collected from smaller units within the municipality (i.e., hunting fields, typically 5–15 per municipality), so that study areas that did not follow municipality borders could still be matched with statistics from the overlapping hunting area. We used open-source data (Miljødirektoratet, 2023b), with some missing material supplemented by local moose managers. Hunters' observations in Scandinavia are sufficiently accurate for estimating population size and fitness given that the area and number of moose seen and shot are large enough (e.g., Ericsson & Wallin, 1999; Kalén et al., 2022; Solberg & Saether, 1999), and preferably, that the population density is stable or changes only slowly over time. Strong fluctuations in population numbers over short time periods can diminish the accuracy of hunting statistics (Ueno et al., 2014). The latter aspect should be less of a concern in our data though, because only 1–3 study areas had fluctuating estimated moose densities within the 5 years closest to the time of study (Appendix S1: Figure S2, time series of both moose shot per square kilometer and observed per hunter day for each study area, of which shot per square kilometer is believed to be the most accurate one; Ueno et al., 2014).

To estimate the year-round moose density in the inventory year t, we used the mean of a given hunting statistic (shot or seen) from the 3 years closest to the inventory year: year $t-1$, year t and year $t+1$. We opted for 3 years to account for possible random bias in the hunting statistics. We used the population density model of Hatter and Bergerud (1991), which accounts for population trends. To their original model, we added the summer presence of moose shot during the autumn hunt, because these moose consume forage during summer. We refer to the calculated density as number of moose per square kilometer (D):

$$D = H \times \left(\frac{(R-M)}{(1-R)} - \beta \right)^{-1} + H \times S,$$

where H is the number of animals shot per square kilometer and R is the proportion of calves observed among all moose of known sex during the autumn hunt (i.e., the recruitment rate). All input parameters were 3-year averages as described above. We corrected R for observability bias toward bulls, which typically have a 24% higher likelihood of being observed than other moose (Solberg et al., 2014). By dividing the bulls observed by 1.24, the calf proportion increases, and the estimated moose density becomes lower compared to without the correction. M is the moose mortality rate from causes of death other than hunting. For the most recently inventoried study areas we had available area specific statistics on such mortality for all years t, $t-1$ and $t+1$ (Miljødirektoratet, 2023a) (typically 3%–8% of post-hunt population). For the remaining study areas, we set it to 5% based on Stubsjøen et al. (2011). β is the discrete growth rate, which equals

the linear regression coefficient of ln "moose observed per hunter day" versus year. S is the length of summer (set to 4 months, $S = 4/12$), so $H \times S$ is the addition of the proportion of moose shot in autumn that utilized forage in summer. Without adding these moose, the density index would indicate the density in the upcoming winter, which is substantially lower than the density that utilized the food in the summer of the study.

Our model assumes no net migration in the study area, which is a simplification. However, seasonal migrations across area borders were substantial for only four to five of the study areas (Nannestad, Murudalen, Gausdal, Meråker and to some extent Stjørdal). In late autumn and partly during the hunt, moose migrate for the most part into these areas. The calculated moose densities in these areas are therefore underestimated. We made no attempts to correct for this, due to a lack of data on migration dates and numbers.

Moose fitness indicators

We used two indices of moose population fitness from the hunting statistics (using means of the same 3 years described for the density model): (1) Calves observed per cow (all cows, with or without calves) during the autumn hunt (median 364 cows observed per year and study area), hereafter referred to as calves per cow. (2) Calf body mass (dressed carcass, median 30 calves per year and study area). We used the weighted mean of shot male and female calves, which has a mean sex ratio of 1.1 males to females across all study areas and years. Moose hunting in Norway has been tightly regulated and surveyed especially over the last 35 years, with detailed instructions on how to report moose seen, and how to dress carcasses for reporting body mass data. Also, there is limited change in the personnel within the hunting teams, with the majority being local and often participating for several decades (Hoffman & Flø, 2017). In the results, we ended up focusing on calves per cow because it showed more variation between the study areas and resulted in stronger model fits. Results for the calf body mass are given in Appendix S1.

We also indicated the historical baseline ("normal") fitness of moose for each region. We defined this as the average of the five earliest years for which all study areas within the region had data, preferably prior to the time of the first historical national peak in the population density (set to 1993, Solberg et al., 2022). We obtained calf per cow data from 1985 (1987 in the Mid region), and calf body mass data from 1991 for all regions apart from in the East, where the earliest body mass data available were from 1999. For the Inland region we opted to use 1990–1994 for calf recruitment due to low sample size in earlier years. In 1993, moose in the different regions likely were at various levels of overabundance: highly overabundant in the West, low in the East, and not yet overabundant in the Inland and Mid region (Figure 1). Therefore, the indicated "baseline" fitness of moose in the West may not equate with their historical maximum fitness but be somewhat lower.

Data analyses

We analyzed all data in the open-source software R, version 4.1.1 (R Core Team, 2025). Our aim was to estimate how well each of the food indices was associated with moose fitness, to pinpoint which indices may be best suited to proactive monitoring. We used three response variables ("calf body mass," "calves per cow," and "moose density"), exploring each in separate sets of two-way univariate or multivariate models of food availability or browsing intensity. The multivariate models were used mainly for exploratory analyses. In the *Results* section, we focus on univariate models because our purpose was the singular association of each food index to each fitness measure.

All explanatory and response data in the modeling were at the scale of the study area (MMU). During the exploratory phase, we used linear multivariate models including region as an independent explanatory variable (function "lm()" in R) and found that results were region-specific. We therefore continued with a nested model structure, using linear mixed-effects models with random intercept nesting of study areas within regions (function "lme()" in R). The final models are given for nested models unless the random intercept effect of the region was insignificant. In any non-nested models, region was also tested as an interaction term. In either case, we used Wald statistics (t tests, maximum likelihood estimations) to determine the significance of explanatory variables. We ran tests with two options of food availability: per unit area and per capita (per moose). We did not explicitly examine explanatory factors beyond food, such as snow or altitude, though these are implicitly accounted for in our geographical variable "region."

Prior to choosing model structures for testing, we explored data distributions at the plot and study area level using histograms and QQ plots. After testing our models, we also inspected model fit by again looking for patterns in the QQ plots of residuals (Zuur et al., 2007). With few exceptions the underlying plot level data were normally distributed. The availability of some of the species selected for by moose was zero-inflated, which is expected given that these tend to be more rarely

available. Consequently, the lump sum variable "selected tree forage" was also moderately skewed. The other food variables were normally distributed, as were all the response parameters. We normalized "selected tree forage" by log transformation and ran affected models with the transformed data. However, in the final models we mostly present results from the nested structure models, with region as a random intercept. Within regions, even "selected tree forage" was normally distributed.

RESULTS

Variation in moose densities and fitness indicators

The moose densities varied highly: from 0.5 to 2.8 moose per square kilometer across study areas (1.3 ± 0.52; mean ± SD; $N = 27$). This encompasses the whole range of moose densities in Norway at the start of the study period (Solberg et al., 2006). Many study areas had fitness measures well below their baseline value (i.e., the fitness average in years before the national peak in moose density in 1993) (Figure 2). Moose in the Inland region were generally closest to their baseline fitness value. The variation in moose fitness was very high: calves per cow varied from 0.41 to 0.79 across study areas (0.59 ± 0.112), and calf body mass varied from 41 to 71 kg (61 ± 7.7 kg). The two fitness measures were significantly related to each other both within region ($t_{22} = 5.4$, $p < 0.001$, regions nested), and across regions ($F_{1,25} = 39.8$, $p < 0.001$).

Variation in available food quantities

The amount of available tree forage varied highly between study areas. This particularly applied to the plant species most selected for by the study moose. The mean total tree forage available was 460 ± 169 cm per plot. The most abundant tree forage was birch (60% ± 13.3% of total across study areas), pine (11% ± 10.3%), willows (*Salix* spp. apart from sallow) (8% ± 8.3%), and rowan (7% ± 6.6%). The mean selected tree forage available varied even more, 70 ± 67 cm per plot. Only eight study areas had >25% of selected tree forage among the total tree forage available. Availability per capita and per plot were correlated (selected $P = 0.88$, $t_{25} = 9.2$, $p < 0.001$ and total $P = 0.63$, $t_{25} = 4.0$, $p < 0.001$).

There was a large total amount of field-layer available for all the moose, 77% ± 23.1% of the ground was covered across study areas. The proportion of selected field-layer among the total varied from 11% to 53%, with a mean of 38% ± 10.0% across areas. In contrast to the tree forage, 24 out of 27 areas had >25% selected field-layer among the total field-layer. The most abundant field-layer was bilberry (33% ± 9.0% of total across areas) and grass (23% ± 6.8%).

Associations between available food quantities and moose fitness

Almost all associations between food and fitness were region-specific. Overall, calves per cow ($t_{22} = 2.8$, $p = 0.010$) (Figure 2A) and calf body mass ($t_{22} = 2.2$, $p = 0.043$) (Appendix S1: Figure S3A) were positively related to the total tree forage available per unit area, apart from in the Inland region. We found stronger associations for selected tree forage than for total tree forage, for both calves per cow ($t_{22} = 4.1$, $p < 0.001$) (Figure 2B) and calf body mass ($t_{22} = 3.7$, $p = 0.001$) (Appendix S1: Figure S3B). This pattern was not completely consistent across regions: the Mid region showed stronger associations for total tree forage than for selected tree forage.

We found largely the same patterns using per capita availability of food (for calves per cow: $t_{22} = 2.1$, $p = 0.051$, and for calf body mass: $t_{22} = 2.2$, $p = 0.035$). However, this was less consistent across regions (Appendix S1: Figures S4 and S5), and for total tree forage it depended partly upon two outliers with much higher per capita food availability than the other study areas in their region (Appendix S1: Figures S4A and S5A). For one of these outliers (MK-23), we know that the moose density was underestimated due to migration (see *Methods*: *Estimation of moose densities*). The other (RE-05) had unusual high soil fertility combined with unusual low browsing intensity for its region (Table 1; Appendix S1: Figure S7). For selected tree forage per capita, the outliers were less prominent, and the associations with moose fitness were very strong (calves per cow: $t_{22} = 2.9$, $p = 0.009$, and calf body mass: $t_{22} = 3.5$, $p = 0.002$).

The availability of total field-layer forage was negatively related to calves per cow ($t_{21} = -2.5$, $p = 0.021$), except for in the Inland region (Figure 3), and to calf body mass ($t_{21} = -2.9$, $p = 0.008$; Appendix S1: Figure S6). Moose fitness was not related to the availability of any of the selected field-layer species or their total. The total field-layer tended to covary negatively with the total availability of tree forage per unit area ($t_{21} = -1.8$, $p = 0.094$, log-transformed data because of different units).

Variation in browsing intensity

The browsing intensities varied more between plant species than between study areas (see spread along the *x*-axes in Figure 4). Browsing intensity was consistently

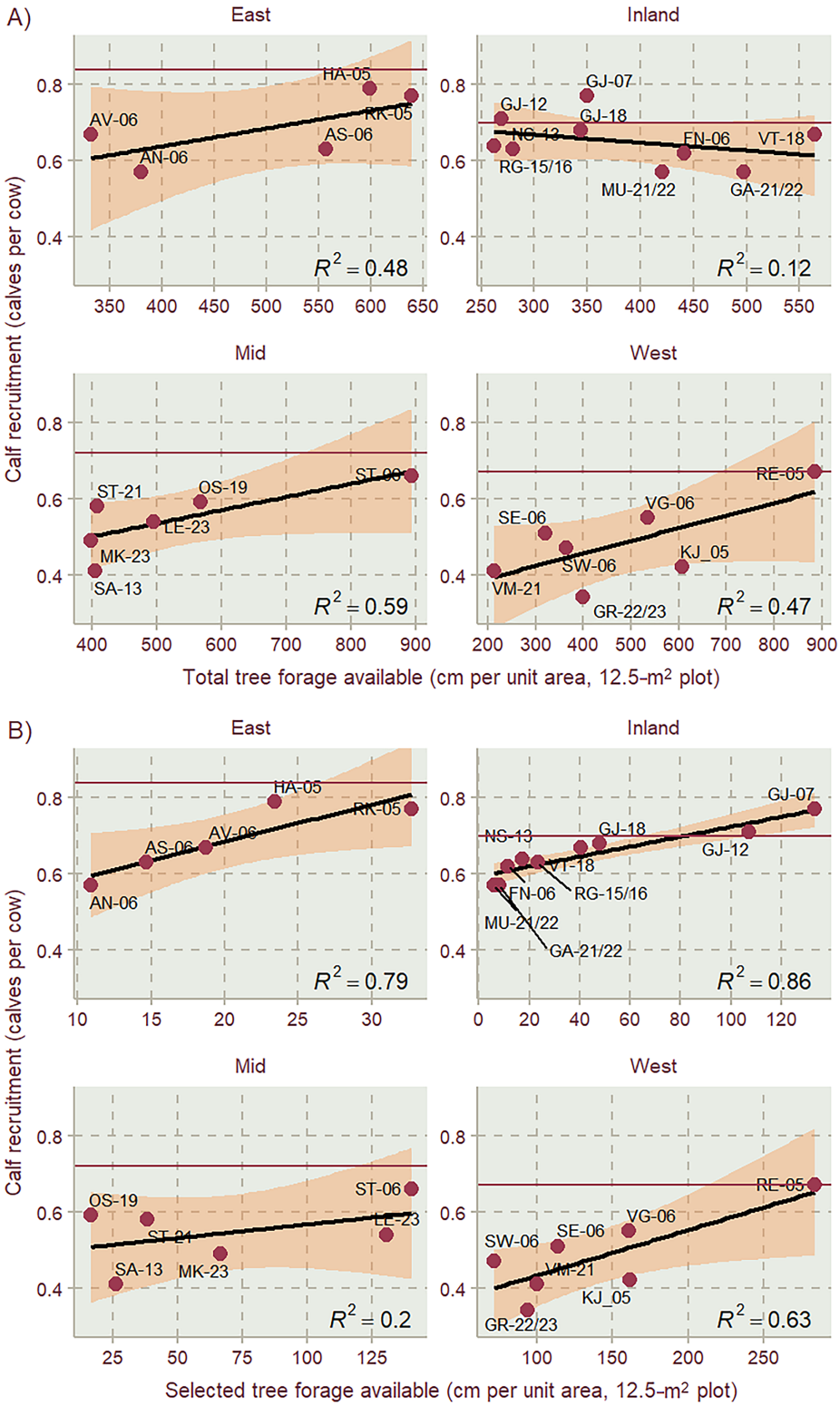

FIGURE 2 Region-wise associations between moose calf recruitment in 24 study areas in Norway (calves observed per cow during the autumn hunt) and the availability of (A) total tree forage per unit area (centimeter of unbrowsed annual growth on shoots 30–300 cm above ground, as measured in 12.5-m^2 plots), including birch, oak, rowan, aspen, *Salix* spp., and pine. (B) Same index but only including tree species selected for by moose (rowan, aspen, sallow, oak). Abbreviations are study areas (see Table 1) and food inventory year (t). Calf recruitment is the average of year t, $t - 1$ and $t + 1$. R^2 and the solid black line represent the linear fit for region. The shaded area represents the 95% CI. The red line indicates the average baseline calf recruitment within the region, that is, the average of 1986–1990 (1990–1994 in the Inland), which is prior to the general historic peak in moose abundance in Norway. Note the different range of values on the x-axes.

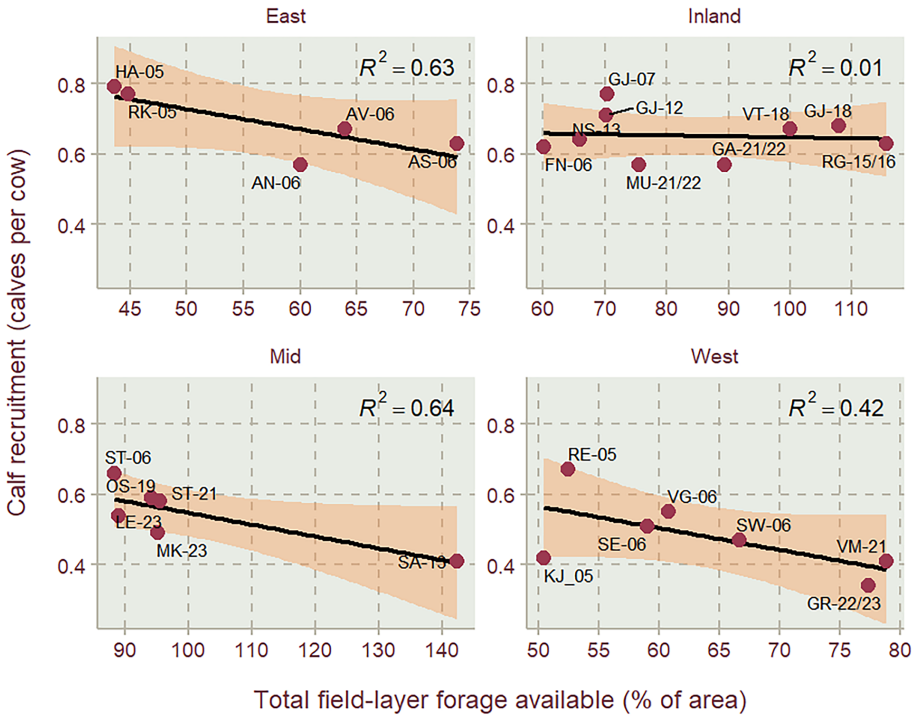

FIGURE 3 Region-wise associations between moose calf recruitment in 24 study areas in Norway (calves observed per cow during the autumn hunt) and availability of field-layer forage (percentage of horizontal cover of area, as measured in 12.5-m^2 plots). All species included except mosses and lichens. Abbreviations are study areas (see Table 1) and food inventory year (t). Calf recruitment is the average of year t, $t-1$, and $t+1$. R^2 and the solid black line represent the linear fit for region. The shaded area represents the 95% CI. The field-layer can sum to >100% because taller species (like raspberry or ferns) can grow horizontally above lower ones (especially grass). Note the different range of values on the x-axes.

high on rowan (57% ± 9.3% of shoots browsed), the most common of the selected tree forages. It varied more for birch (26% ± 18.0%), which is the most common tree in the diets of the study moose. Pine, predominantly a winter food and either common or very rare in the study areas (Table 1), had similar browsing intensities to birch (26% ± 14.7%).

Associations between browsing intensity and moose fitness

The browsing intensity on birch was more strongly related to the moose fitness than was the browsing intensity on rowan or pine, in all regions apart from in the West (Figure 4). Graphs specifying the results for each moose population are given in Appendix S1: Figures S7 and S8. In the West, there was an outlier for birch (VM-21 with record-low availability and record-high browsing intensity). Without this outlier, birch browsing in relation to calves per cow in the West had a R^2 close to 1 (0.99). The browsing intensities on all three focal tree forage species were negatively related to calves per cow (birch $t_{22} = -3.7$, $p = 0.001$, rowan $t_{22} = -3.7$, $p = 0.001$, pine $t_{22} = -3.5$, $p = 0.002$) (nested models, VM-21 included), apart from in the mid region. Browsing intensity was not related to calf body mass, although there were tendencies for some species in some regions (Appendix S1: Figure S8).

DISCUSSION

By combining detailed field inventories of food with hunting statistics, we documented strong associations between available food quantities, browsing intensity and moose fitness in 24 management units across southern Norway. We found clear support for our hypotheses 2–5, all of which related to how moose food selectivity affects the dynamics between their food availability and their performance in terms of calf body mass and calf production: The various tree forage species did not have the same value to moose fitness in all regions. Our study underlines that to fully capture and understand these complex food-fitness relationships, one needs measures that accurately target the various food types accessible to moose. We also found support for our first hypothesis, although this came with a surprising twist: Moose fitness

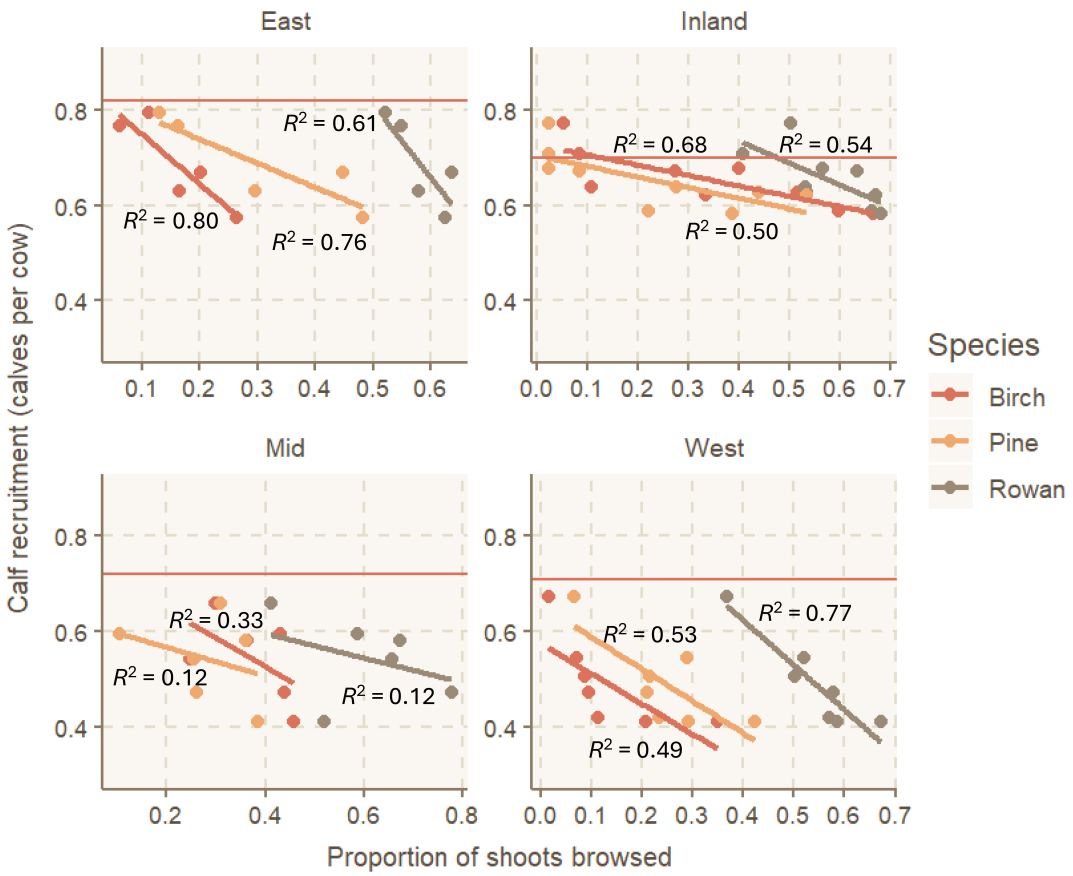

FIGURE 4 Region-wise associations between moose calf recruitment in 24 study areas in Norway (calves observed per cow during the autumn hunt) and proportion of shoots browsed (accumulated browsing over several years) on the three most common tree species used by moose. Shoot represents the current annual growth (CAG) starting from old growth on twigs, irrespective of CAG diameter, length and its further branching, or old twigs (no CAG) browsed in previous years. Calf recruitment is the average of year t, $t-1$ and $t+1$. R^2 and the solid lines represent the linear fit for the species in the region. Horizontal red lines indicate the average baseline calf recruitment within the region, that is, the average of 1986–1990 (1990–1994 in the Inland), which is prior to the general historic peak in moose abundance in Norway.

was strongly related to food availability, but less so per capita than per unit area. One likely explanation is that regional differences in past overabundance of moose had created a persistent legacy, which we discuss below. Browsing intensity likewise explained more of the variation in moose fitness in the regions with the presumed highest levels of past overabundance. Another related key finding is that there were regional differences in the amount of food that seemed sufficient to maintain moose within their baseline fitness, that is, the generally high fitness levels in the management unit before any historic overabundance.

Our results contribute to filling a research gap regarding food and fitness relations in northern cervid species, for which data are needed to both verify basic animal ecology and aid applied management. We discuss how our study can facilitate proactive management that adjusts densities of moose in Norway, and possibly moose in other areas or other cervid species, relative to trends in food availability and browsing intensity and thereby avoid detrimental effects of animal overabundance.

Tree forage selected for mattered the most, but not equally so everywhere

The availability of tree forage selected for by the study moose (rowan, aspen, sallow, oak) was more strongly associated with moose fitness than was the availability of total tree forage, apart from in the Mid region. This is in line with our findings in southern Sweden, where the amount of *Salix* spp. and *Populus* spp. in the moose diet (both selected for) was associated with higher calf body mass (Felton et al., 2020). However, only a comparatively small amount of these plant species was needed for some of the Norwegian study areas to maintain higher fitness. For example, in the East region their availability was only about 10% of the amount available to the moose in the

West region (per area, Figure 3B; per capita, Appendix S1: Figure S4). Similarly, moose in the Inland region had about 25% as much selected tree forage compared to moose in the West. Nevertheless, the moose in the East and the Inland had retained much higher levels of fitness than moose in the West. This illustrates and supports hypotheses 2 and 3: Some food types were more important than others, but the same amount of a given food type had different value for moose fitness in different regions (see more on this in *The complex foodscape behind moose fitness*).

Total field-layer availability was negatively related to moose fitness, and there were no significant positive associations between fitness and the availability of the various field-layers selected for (bilberry, raspberry and "selected herbs"). This was unexpected. We have previously shown that moose with higher levels of selected field-layers in their summer diet (e.g., raspberry) have higher fecal nitrogen content (Wam & Herfindal, 2018), which likely indicates a higher protein intake (Hodgman et al., 1996) (but see also Verheyden et al., 2011). A higher protein intake benefits calf production if protein is limiting (Parker et al., 2009). In the exploratory multivariate modeling of our data, which included both tree forage and field-layer forage in the same candidate models, none of the best models included field-layer forage. For our study moose, the winter food (only tree forage available) thus appears to have been generally more limiting than food in the growing season (including field-layer forage). This seems plausible, given that the study regions generally have long winters with deep snow relative to moose capacity to access snow-covered vegetation (Table 1). We cannot, however, rule out a possible positive influence of some field-layer forage for our study moose at certain times of the year (Hjeljord & Histol, 1999). The tendency of a negative association between the availability of total field-layer forage and total tree forage may have contributed statistically to cancel out such a positive seasonal influence.

Why was moose fitness more related to food availability per area than per capita?

The significant relationship between food availability and moose fitness was somewhat lower using values per capita (per moose) compared to per unit area. This indicates at least two sources of noise in the data: (1) inaccuracy in the moose density estimates, and (2) a legacy of differences across the study areas in past overabundance of moose relative to its food resources.

Regarding the first source of noise, our moose density estimates based on hunting statistics were probably not equally accurate across all study areas. Studies have found moderate to high correlations between density estimates based on hunting statistics and aerial counts, of which the latter is considered to be the most accurate if sufficient time in the air is spent in good enough weather conditions (but see LeResche & Rausch, 1974). For example, correlations were 0.76 in Rönnegård et al. (2008), 0.74 in Courtois and Crête (1993), 0.58–0.69 in Ericsson and Wallin (1999, depending on moose density), and ranged from negative to 0.70 in Sylvén (2000) depending on the size of the area. A few of our study areas were too small according to these references, although these small areas do not appear to be the source of the noise. The small areas were mainly in the West region, where there was not a lack of per capita associations to fitness. The accuracy of density estimates from hunting statistics is influenced by a range of factors that vary between populations, such as the observability of moose, hunting efforts, and migration. Migration likely affected our density estimates for three study areas in the Inland region and one to two study areas in the Mid region (see *Methods*: *Estimation of moose densities*), which partly explains their lesser fit for per capita rates (e.g., Appendix S1: Figure S5A). The presence of newly immigrating red deer may also have confounded the per capita rates of food availability for moose in the Inland and Mid regions (Table 1). We opted not to adjust the moose densities for red deer presence, because the density estimates of the red deer are still so imprecise due to low sample sizes (see *Methods*: *Study areas*).

Regarding the second source of noise, that is a legacy of past overabundance, we suggest that some of the study areas with higher moose fitness had not yet reached or only recently reached the first peak in their historic density (Figure 1), while most of the areas with lower fitness, particularly in the West, had experienced a longer period of high densities with declining fitness. This indicates a history of overabundance in the West, which could have created a persistent lag in the fitness response of moose to changes in food availability, despite recent reductions in moose density. Smaller born female moose in Norway tend to stay smaller as adults and produce smaller and fewer calves (at least early in life) (Solberg et al., 2008). Even their daughters may then produce smaller and fewer calves (Markussen et al., 2018). Simultaneously, the regions without past overabundance contributed to less strong associations for per capita food, because moose in most of these areas likely were not food limited. In the long time series from the Isle Royale, patterns between available and consumed forage for moose became decoupled at low moose densities (De Jager et al., 2009), indicating the obvious but rarely documented fact that the per capita rates of food availability become irrelevant when food is in excess.

Why was food availability more related to calf production than to calf body mass?

In our study, calf production was more strongly associated with the available food quantities than calf body mass. It is reasonable to assume that hunters are more precise in weighing dead calves than in observing live ones. So, in a practical sense, calf body mass should be a more accurate index than calf production. On the other hand, calf production may be more sensitive to food limitation. Depletion of maternal resources can to an extent buffer the loss of calf body mass through gestation and lactation, but the food-depleted cow is highly likely to first reduce her number of fertilized eggs (review across species by Gaillard et al., 2000). One can therefore expect that food limitation will first manifest in calf production.

The complex foodscape behind moose fitness

The stronger associations to fitness for selected tree forage compared to total tree forage reflect a crucial aspect of moose nutritional ecology: not all forage is equal. The seminal paper by White (1983) shows how animals that are able to achieve even small shifts toward a diet richer in food selected for can greatly enhance their fitness. For northern cervids, traditional hypotheses emphasized the maximization or limitation of any one nutrient as the primary driver of foraging decisions (Felton et al., 2018). However, over the last decade, there has been increasing evidence that foraging decisions in a wide range of organisms are instead driven by nutrient-specific appetites that guide the individual toward a target balance of a few key macronutrients, typically protein, carbohydrates, and fat (Simpson & Raubenheimer, 2012). Feeding experiments on captive moose suggest that moose aim for a nutritional target similar to the one in *Salix* spp. twigs (Felton et al., 2016); a finding which has recently gained further support from studies of wild moose (Spitzer et al., 2023, 2024).

Our results suggest that further research into these aspects should focus not only on the nutritional properties of selected forage (e.g., *Salix* spp.), but also on the possible nutritional complementarity of foods which are less selected for individually (e.g., birch). Although selected food had the strongest link to fitness in our study, the availability of total tree forage as well as browsing on the staple food (birch) was also highly explanatory. Habitats in which the nutritional target can easily be reached either via nutritionally balanced forage or through nutritionally complementary forage may constitute better fitness foodscapes than those where individual unbalanced food items are abundantly available, but the only items on the menu. Examples of nutritionally complementary forages for moose include pine and *Vaccinium* spp. during winter (Spitzer et al., 2023) or meadowsweet and bogbean (*Menyanthes trifoliata*) during summer (Spitzer et al., 2024). How the interrelated availability of such complementary food affects fitness is worth addressing in future studies, and the data provided in our current study are a highly relevant source for such investigations.

Management implications: Proactive monitoring

Essential to any wildlife monitoring is first to set the limits that safeguard the management goals. For moose management in Scandinavia, examples of goals are keeping the calf body mass above set levels, or the browsing damage to production forests below set levels. Our study can be used as a guide for managers to use food monitoring to reach these goals, also beyond Scandinavia. International readers should keep in mind that our study areas had relatively low primary production and that moose densities were high in the global context (Jensen et al., 2020). In regions with higher primary production, the vegetation can support and tolerate more cervids (e.g., Cromsigt & Kuijper, 2011; Rowland et al., 2018). The design and principal outcomes of our food monitoring can also be useful for the management of other cervids with a lot of browse in their diet, although the relative importance of specific plant species will be different (as will the management goals). For example, Mysterud et al. (2010) found that browsing on bilberry was most strongly correlated with red deer densities on the west coast of Norway, and therefore most focal to monitor. Likewise, Morellet et al. (2001) found that browsing on *Rubus* spp. but not *Quercus* spp. (one of the selected for tree forage in our moose study) was correlated with roe deer densities in France.

As a rough guideline for moose in our and similar study regions, our results suggest that the browsing intensity accumulated over recent winters should not exceed 10%–15% of the number of shoots with CAG on the staple foods birch or pine, and approximately 40% on the selected for and rarer rowan, if the management goal is to maintain moose within their baseline fitness. These thresholds were surprisingly consistent across our study areas and regions. In each region, all the area(s) with the highest moose fitness (all close to their historic baseline, see Figure 2) had browsing intensities below the threshold values. Interestingly, similar browsing intensities (10%–15% on the staple food) have been found

sustainable for moose calf production in Alaska too (Seaton et al., 2011), where the moose have winter diets comparable to Norway.

Our study suggests, however, that food availability and browsing intensity are complementing indices for monitoring that aims to ensure that cervid populations do not become overabundant. While it may seem more efficient to only monitor the browsing intensity, this requires that one already has in-depth knowledge of the cervid's foodscape in the area and knows which monitored plants are key determinants of fitness outcomes. It may also be difficult to use browsing intensity proactively where it is already very high, because stagnated plant growth due to overbrowsing can take time to revert (Myking et al., 2013; Tremblay et al., 2005). It will be likewise difficult in areas where food availability is changing, because this will affect the relative value of the various food types. Forest logging and silvicultural treatments are factors that intensively affect the foodscape of forest cervids throughout their geographical range (Bergquist et al., 2003; Johnson & Rea, 2023; Koetke et al., 2023; Leblond et al., 2015; Mumma et al., 2021; Schwegmann et al., 2023; Wam et al., 2010), as do fires in some regions of the world (Proffitt et al., 2016), while climate change seems to become of increasing importance (Felton et al., 2024; Holmes et al., 2023; Parmesan & Hanley, 2015).

AUTHOR CONTRIBUTIONS

Hilde Karine Wam: Conceptualization; methodology; investigation; resources; data curation; formal analyses; validation; writing—original draft. **Annika M. Felton**, **Adam Felton**, **Robert Spitzer** and **Märtha Wallgren:** Validation; writing—editing and review.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Wam et al., 2025) are available from Dryad: https://doi.org/10.5061/dryad.37pvmcvxn.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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