

# Stable isotope values of carbon and nitrogen in Norwegian brown bear, wolf, lynx and wolverine tissue and their significance for understanding diets

D.J. Halley







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## Abstract

Halley, D.J. 2017. Stable isotope values of carbon and nitrogen in Norwegian brown bear, wolf, lynx and wolverine tissue and their significance for understanding diets - NINA Report 1341. 41 pp.

Analysis of stable isotope values of carbon and nitrogen in body tissues of a consumer allow inferences to be drawn about the dietary sources of the tissues (ie, the foods) from which that body tissue was made. Muscle tissue of the four large mammalian predators found in Norway – brown bear, lynx, wolverine, and wolf – was analysed and compared with the isotope values of plants and animals in the Norwegian terrestrial food chain.

This method cannot distinguish between the proportion of food consumed that was taken directly as live prey or indirectly by scavenging.

Mean values for each predator species were similar. As a result, they did not allow inferences to be made between species about the relative balance of food sources in their diets. This was because the differences between the four species were well within the known inter-species variation in systematic change in isotope ratios caused by digestive processes ('dietary fractionation').

The overall values of all species were in the ranges expected for animals consuming a diet dominated by the food chain from plants (ie, not lichens), through wild mammal herbivores excluding wild and semi-domestic reindeer. Reindeer have very distinctive isotope profiles, mainly because they eat much lichen, which is isotopically distinct from plant species. Values are not compatible with reindeer tissue being a major source of the assimilated diet of any of the species; though they may have been a significant subsidiary source for some individual wolverines in wild reindeer areas of south Norway, and some individual lynx living in semi-domestic reindeer areas.

For wolverine especially this result is at variance with dietary studies using other methods such as scat analysis, and suggest that those methods may overestimate the significance of reindeer in wolverine diets. Further research would be useful to clarify this issue.

Sheep isotope values are closely similar to those of the large predators themselves. This appears to be an effect of the high values for carbon and nitrogen in marine protein. Marine protein is an element in the artificial feeds sheep consume in winter in Norway. The result is that the proportion of sheep in the diet in Norway is very difficult to interpret using this method. However, if sheep were a very large proportion of the diet, predator stable isotope values would be expected to be even higher than they were observed to be.

In brown bears, no significant differences in isotope values between males and females; or between bears in areas with semi-domestic reindeer and without, were found; indicating that by this method there was no evidence of variation in diet between these groups.

In lynx, female lynx in areas without semi-domestic reindeer had stable isotope values that distinguished them from other groups; indicating a significantly different balance of diet from those other groups. The nature of this difference was unclear.

In wolverine, carbon isotope values differed significantly between males and females, and between areas with semi-domestic reindeer and other areas; indicating relative dietary differences between males and females; and between areas with domestic reindeer and those without. However, this was within an assimilated diet dominated by wild mammalian herbivores excluding reindeer.

In wolves, only one sample was available from areas with semi-domestic reindeer. In areas with no semi-domestic reindeer, there was no significant difference between sexes in stable isotope

values. Values were consistent with an assimilated diet dominated by wild mammalian herbivores excluding reindeer; and reindeer could not have been a significant element. The proportion of sheep in the assimilated diet was hard to interpret, but could not have been dominant.

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## Sammendrag

Halley, D.J. 2017. Stable isotope values of carbon and nitrogen in Norwegian brown bear, wolf, lynx and wolverine tissue and their significance for understanding diets - NINA Rapport 1341. 41 s.

Ved å analysere stabil-isotopverdier av karbon og nitrogen fra kroppsvev hos dyr kan man trekke slutninger om hvilke kilder (i form av mat) kroppsvevet har. «I denne studien ble» muskelvev fra Norges fire store rovdyr: brunbjørn, gaupe, jerv, og ulv, analysert og sammenlignet med verdiene hos planter, lav og andre dyr i den norske terrestriske næringskjeden.

Metodikken kan ikke skille mellom føde som kommer fra levende byttedyr og fra åtsel.

Resultatene viser at rovdyrartene har ganske like gjennomsnittsverdier, så like at de ikke tillater å trekke slutninger om den relative balansen av fødekilden mellom artene. Dette er fordi forskjellene mellom de fire artene er godt innenfor kjent variasjon mellom arter i systematiske endringer i isotopverdier forårsaket av fordøyelsesprosesser ('fordøyselsesfraksjonering').

Oppsummert plasserer verdiene til artene seg innenfor spekteret som er forventet for dyr som spiser en diett dominert av planteetende pattedyr (unntatt rein) som igjen spiser planter (dvs, ikke lav). Rein har veldige bestemte isotopprofiler som skiller seg fra andre pattedyr. Dette er hovedsakelig på grunn av at de spiser mye lav, som har karbonverdier som er veldig annerledes enn planter. Verdiene som ble funnet hos alle de fire artene stemmer for artene som helhet ikke overens med at reinsvev utgjør en vesentlig andel av den fordøyde dietten. Rein kan ha vært en signifikant bi-ressurs for noen individer av jerv i villreinområder i Sør-Norge, og for noen individer av gaupe som lever i områder med tamrein.

For jerv spesielt er resultatene ikke i samsvar med diettundersøkelser som bruker andre metoder, som f.eks. avforingsanalyse. Det antyder at metodikkene muligens overestimerer andelen av rein i jervens diett. Det er en fordel med videre forskning for å få klarhet i dette.

Isotopverdier som måles fra sau ligner veldig på isotopverdiene som måles fra de fire store rovdyrene. Dette synes å være forårsaket av veldig høye verdier av karbon og nitrogen i marint protein, som er en viktig bestanddel i kraftforet som sau fores med om vinteren i Norge. Resultatet er at andelen sau (i rovdyrdietten) er svært vanskelig å tolke ved bruk av metodikken. Likevel, dersom sau utgjorde en veldig stor andel av dietten, ville stabil-isotopverdier hos rovdyrene forventes å være enda høyere enn de som ble funnet.

Hos brunbjørn ble det ikke funnet betydelig statistiske forskjeller i isotopverdier mellom hanner og hunner, eller mellom områder med tamrein og uten tamrein. Dette indikerer at det mangler bevis for variasjon i dietten mellom gruppene med bruk av stabil-isotopteknikken.

Hos gaupe hadde hunner i områder uten tamrein stabil-isotopverdier som skilte de statistisk fra alle andre gruppene (hunner i områder med tamrein, samt hanner i både tamrein og ikke-tamreinområder). Dette indikerer en statistisk betydelig forskjell i balansen mellom diettkilder i denne gruppen i forhold til de andre gruppene. Årsaken til forskjellen er uklar. I områder med tamrein, men der rådyr er sjelden eller ikke funnet, var verdiene forenelig med en større, men ikke dominerende andel rein i dietten.

Hos jerv ble det funnet en statistisk betydelig forskjell i karbon-isotopverdier mellom hanner og hunner, og mellom områder med tamrein og områder uten. Likevel var den assimilerte dietten dominert, bortsett fra noen få individer, av ville planteetende pattedyr unntatt rein.

Hos ulv var det en bare en prøve fra tamreinområder tilgjengelig. I områder uten tamrein var det ikke noen statistisk betydelig forskjell mellom kjønnene i stabil-isotopverdier. Verdiene var i

overenstemmelse med en assimilert diett dominert av ville planteetende pattedyr, unntatt rein. Resultatene viste at det ikke var mulig at rein utgjorde en betydelig andel av dietten. Andelen sau er vanskelig å tolke, men kan ikke ha vært dominerende.

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# 1 Introduction

Analysis of stable isotopes, particularly (but not only) those of carbon and nitrogen, have in recent years been widely employed to investigate the assimilated diets of organisms, and trophic interactions (Kelly 2000; Post 2002; Newsome et al 2007; Crawford et al 2008 for reviews)

This method is not subject to some of the limitations of conventional diet study methods such as faecal analysis, analysis of stomach contents, rumen sampling, collection of prey remains in the field, etc. (see e.g. van Dijk et al 2007), as it provides information on the assimilated diet as incorporated into body tissues. As a result, the method has been increasingly widely used to reconstruct assimilated diets in taxonomically and ecologically diverse species (DeNiro & Epstein 1978, 1981; Hobson & Clark 1992; Dalerum & Angerbjörn 2005).

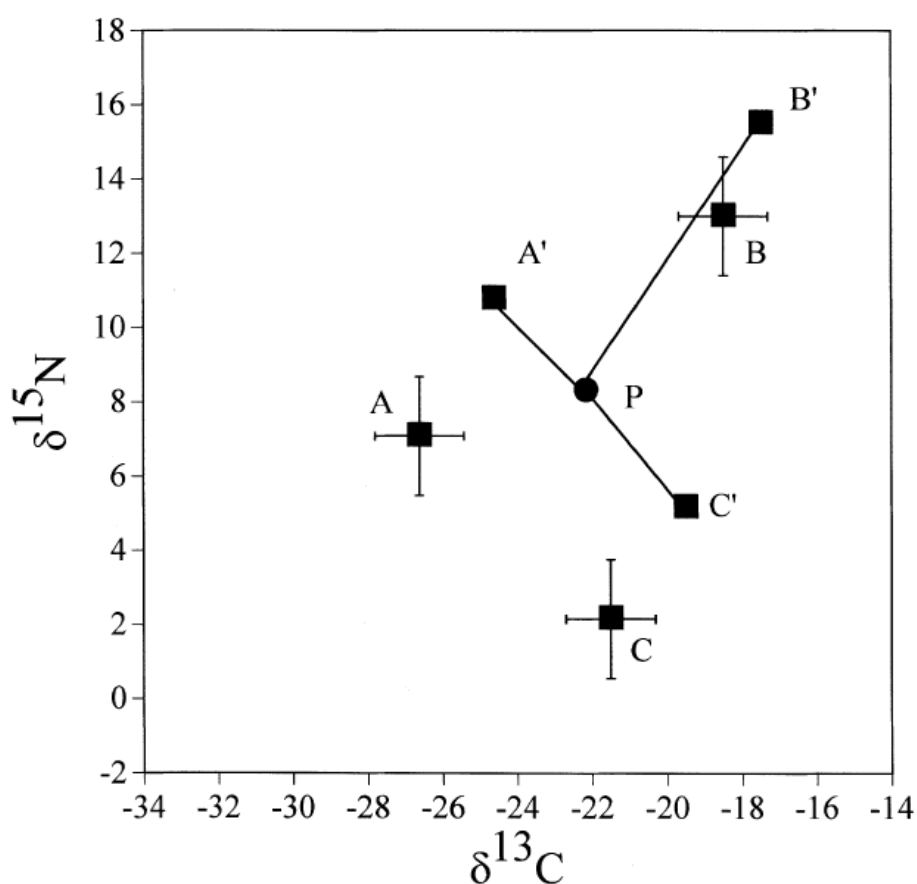
The diets of the four large predators of Norway, wolf *Canis lupus*, brown bear *Ursus arctos*, wolverine *Gulo gulo*, and lynx *Lynx lynx* have been the subject of investigations for many years. This is primarily due to the fact that each of the species predate to some extent on domestic livestock, and that compensation is paid for this confirmed or assumed predation.

Stable isotope analysis offers another method for gaining insight into this issue, which has not so far been widely used in Norway. Samples of the tissue of large predators killed or found dead in Norway have been routinely preserved, and this method of analysis requires only tiny amounts of tissue to be used. This allowed for the analysis of samples from a larger number of individuals than is normally practicable with work on large predators, which naturally occur at low densities and which in Norway are in addition well below the population density levels that the food resource could support.

In this report we present the results of this analysis, and discuss the meaning and limitations of the method and data for understanding the diet of large predators in Norway.

## 2 Methods

Investigating diets of animals through stable isotope analysis has, since the 1980s, become an established technique in dietary and ecosystem studies (e.g. Kelly 2000; Minagawa 1992; Minagawa *et al* 1991; Phillips & Gregg 2003; Halley & Minagawa 2005; Halley *et al.* 2006, 2008, 2010). The method relies on identifying systematic variations in dietary sources in the proportions of the main isotopes of elements, in the case of carbon  $^{12}\text{C}$  and  $^{13}\text{C}$ ; and nitrogen  $^{14}\text{N}$  and  $^{15}\text{N}$  (Brand 1996). The isotopic “signature” of the consumer tissue reflects the proportional intake of the various dietary sources (DeNiro & Epstein 1978, 1981), with the important proviso that a correction for preferential uptake / loss of given isotopes in the digestive process, often known as diet-tissue, or trophic fractionation, must be made. Trophic fractionation varies for different elements, species, and tissues (e.g. Hobson & Clark 1992; Halley *et al* 2010; Dalerum & Angerbjörn 2005 for review).



**Figure 1.** Schematic illustration of dietary fractionation. There are three food sources, A, B and C; and the observed values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for a predator, P. The values for A, B, and C are corrected for the enrichment in predator ratios compared with its diet (i.e., fractionation values): A', B', C'. The relative contribution of each prey to the predator's diet is inversely related to the distance between the corrected signature of the prey and that of the predator (i.e., the shorter the distance the greater the contribution). Adapted from Ben David *et al* (1997). / Skjematisk illustrering av fordøyselsesfraksjonering. Det viser 3 matkilder, A,B,C; og verdier for en rovdyr, P. Verdiene er korrigerede for berikelsen i rovdyrverdiene sammenlignet med dens diett (dvs, fraksjoneringverdier). Relativ kontribusjon av hver matkilde til rovdirets diett er omvendt proporsjonal til avstand mellom korrigeret signatur av byttedyret og av rovdiret (det kortere avstanden, det høyere andelen). Adapterte fra Ben David *et al* 1997.

Abundance of the isotopes of various chemical elements vary in primary producers (plants), depending initially mainly on metabolic pathways and on soils. The digestive processes of animals further modify these isotope ratios, a process known as 'diet-tissue fractionation' or 'dietary fractionation'. These processes in combination finally determine the isotopic 'signature' of the body tissue of a given consumer (e.g. grouse, moose, sheep) in an ecosystem, and in turn of the predators (e.g. wolf, brown bear, lynx, wolverine) which prey on them. The use of natural isotopic tracers has been shown to be effective in discriminating between different dietary sources, even in animals with diverse diets, such as modern humans (Minagawa 1992), bears *Ursus sp.* (Hildebrand *et al* 1996); and American martens *Martes americana* (Ben-David *et al* 1997); however, care must be taken not to over-interpret results, especially where the exact dietary fractionation of a tissue is not known (Nilsen *et al* 2012).

Muscle tissue of brown bear, wolf, lynx, and wolverine carcasses delivered to NINA for post-mortem monitoring through the Norwegian government large predator-monitoring programme has been preserved in ethanol for many years. Typically, >25g of muscle tissue is preserved. A sample of c. 5mg of preserved muscle tissue from 36 male and 18 female brown bears, 36 male and 38 female lynx, 36 male and 36 female wolverine, and 16 male and 12 female wolves was removed for analysis, with permission from the Norwegian Environment Agency. All individuals were adults. Location of sample was given as a placename and kommune. As many placenames were not found in the State Mapping Authority (Statens kartverk) register, in practice the location of the animals at time of death could only be determined to kommune level. Where the number of samples for a given species, age, and sex permitted, we sampled equally from areas with, and without, semi-domestic reindeer populations; and within that criterion used the most recent samples available. Semi-domestic reindeer areas were taken to be all kommuner where domestic reindeer husbandry is practiced.

Data indicates that preservation in ethanol does not affect tissue isotope ratios (Halley *et al* 2008). Samples were dried at 60°C for 24 hours to evaporate all ethanol and water. The dried tissue was powdered. c.0.5mg (range: 0.21-0.76mg), weighed to  $\pm 0.01$ mg, was loaded into standard 8mm x 5mm tin capsules (Elemental Microanalysis product no. D1008) and placed in 48-well plastic microplates. Mass spectrometry was conducted at the University of Copenhagen. The total carbon and nitrogen contents and isotopic ratios of  $^{13}\text{C}/^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$  were measured in solid samples by Dumas combustion (1050 °C) on an elemental analyser (CE 1110, Thermo Electron, Milan, Italy) coupled in continuous flow mode to a Finnigan MAT Delta PLUS isotope ratio mass spectrometer (Thermo Scientific, Bremen, Germany). Acetanilide (Merck, Darmstadt, Germany) was used for elemental analyser mass calibration. As working standard for isotope ratio analysis we used pure gases of  $\text{CO}_2$  and  $\text{N}_2$  calibrated against certified reference materials of  $^{13}\text{C}$ -sucrose and  $^{15}\text{N}$ - $(\text{NH}_4)_2\text{SO}_4$ , respectively (IAEA, Vienna, Austria). Performance of analysis (Qa/Qc) was assessed by the inclusion of reference samples of biological origin (Peach leaves (NIST 1547), National Institute of Standards and Technology, Gaithersburg, MD, USA).

Ratios of  $^{13}\text{C}$  and  $^{15}\text{N}$  isotopes are expressed as  $\delta$ , or variation in parts per thousand (‰) from a standard, according to the formula  $\delta X = ((R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}}) \times 1,000$ , with X as  $^{13}\text{C}$  or  $^{15}\text{N}$  and R as the corresponding ratio of  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$  of the sample or the standard. The standard is atmospheric nitrogen for  $\delta^{15}\text{N}$  and PDB limestone for  $\delta^{13}\text{C}$ .

In-house calibration standards are proline and tyrosine of known isotopic composition. The precision obtained is normally  $< \pm 0.1\%$  SD for both N and C.

Data was analysed for significant effects using univariate general linear modelling.

### 3 Results

Analysis yielded valid  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for 216 individuals: 35 male and 13 female brown bears, 35 male and 37 female lynx, 36 male and 36 female wolverine, and 13 male and 11 female wolves.

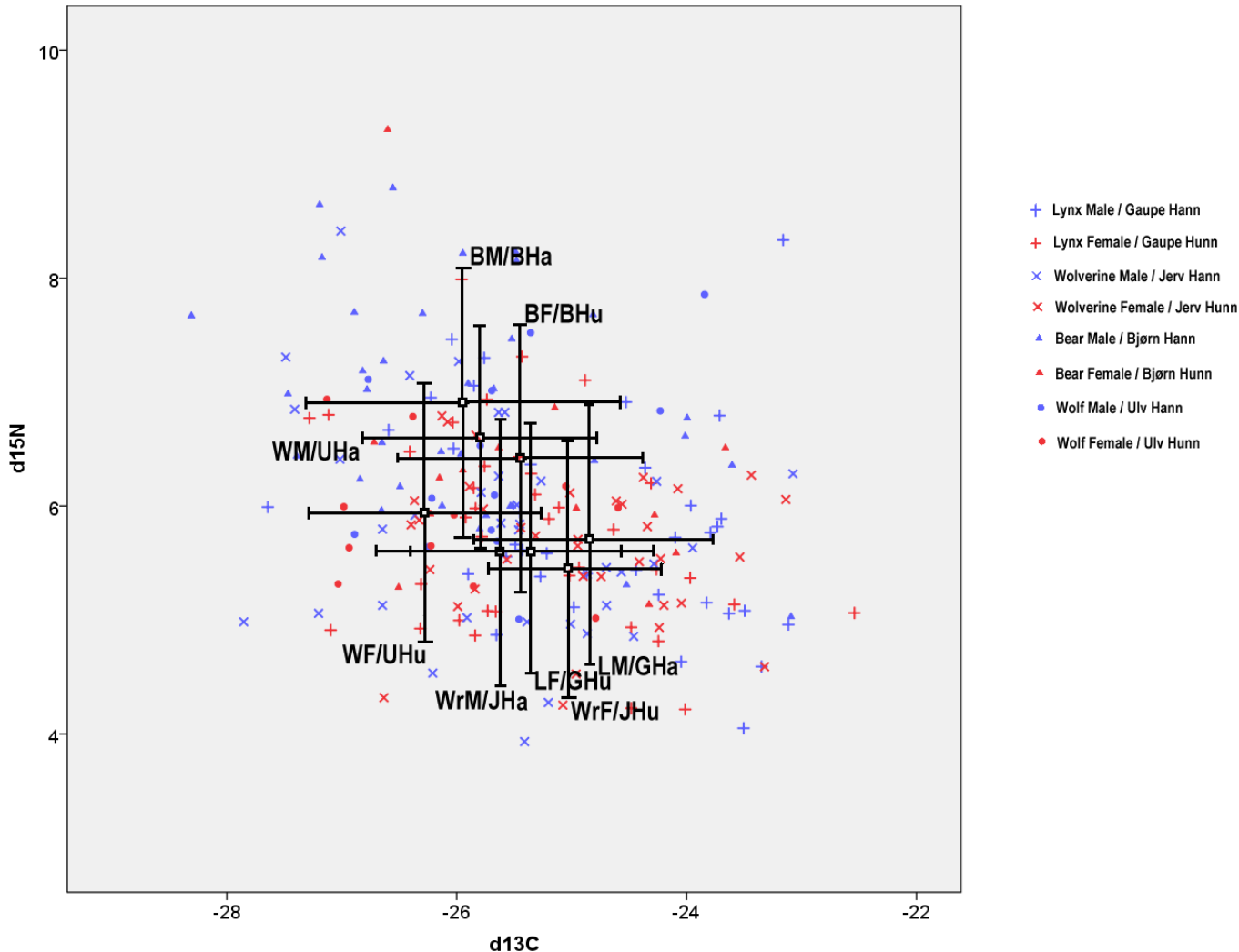
Male bear samples dated from 2008-2013; female bear 1991-2011 (10 of 13 2000-2011); male lynx 2005-2013; female lynx 2010-2013; male wolverine 2012-2013; female wolverine 2010-2013; male wolf 2005-2013; female wolf 2001-2013.

Table 1 indicates mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values with Standard Errors and Standard Deviations for males and females of each species.

Species/Art	Sex/Kjønn	Mean $\delta^{13}\text{C}$	SE	SD	Mean $\delta^{15}\text{N}$	SE	SD
Lynx / Gaupe	Male / Hann	-24.8	0.2	1.1	5.9	0.2	0.9
Lynx / Gaupe	Female / Hunn	-25.3	0.2	1.0	5.8	0.1	0.9
Wolverine / Jerv	Male / Hann	-25.6	0.2	1.1	5.8	0.2	0.9
Wolverine/Jerv	Female / Hunn	-25.0	0.2	1.0	5.6	0.1	0.6
Bear / Bjørn	Male / Hann	-25.9	0.1	1.2	6.9	0.2	0.9
Bear / Bjørn	Female / Hunn	-25.4	0.3	1.1	6.3	0.3	1.0
Wolf / Ulv	Male / Hann	-25.7	0.2	0.9	6.4	0.2	0.8
Wolf / Ulv	Female / Hunn	-26.1	0.3	0.9	5.9	0.2	0.6

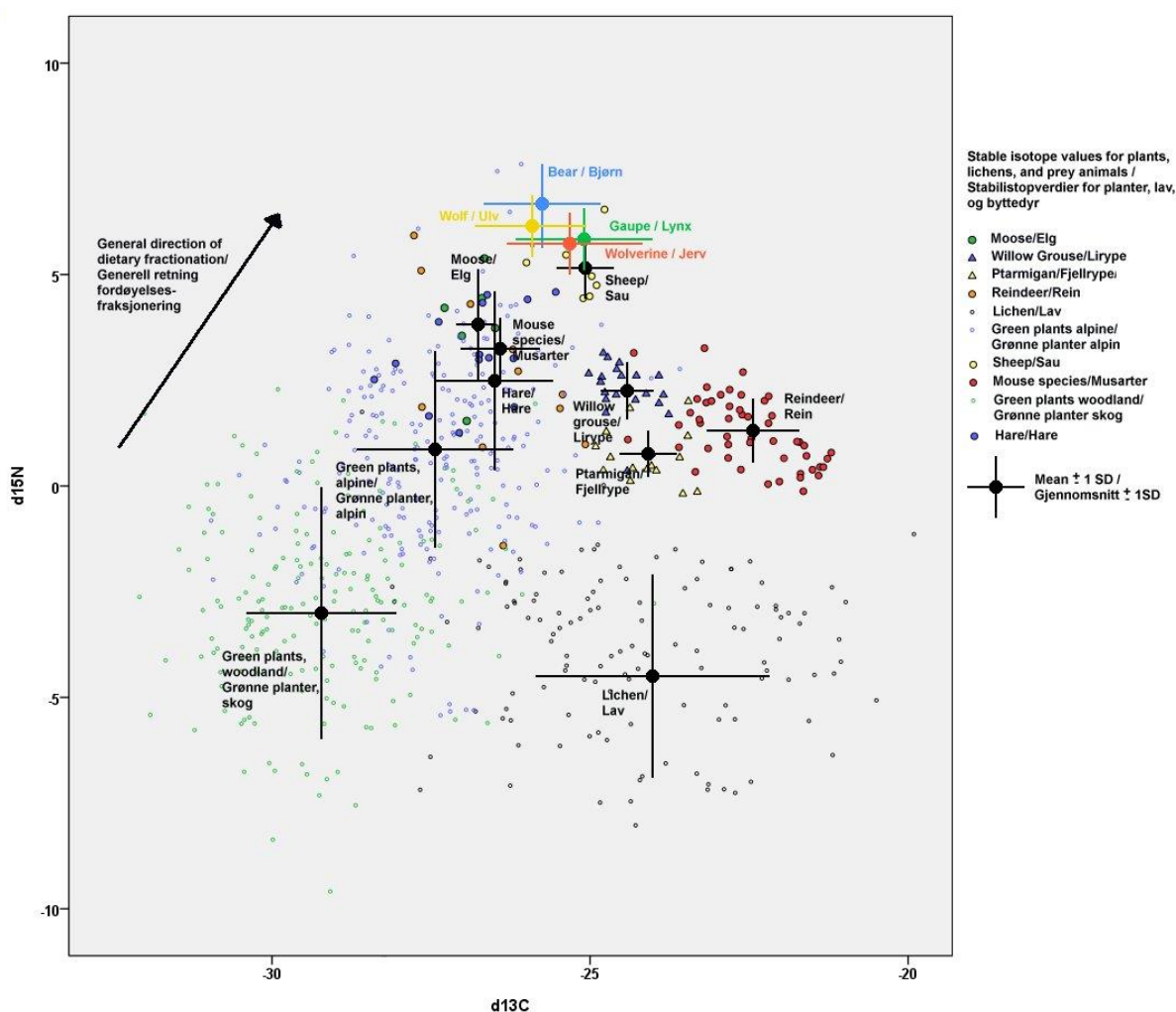
**Table 1.** Stable isotope values of carbon and nitrogen of muscle tissue of male and female lynx, wolverine, bears and wolves in Norway. / Stabilisotopverdier av karbon og nitrogen av muskelmasse hos hann og hunn gaupe, jerv, bjørn og ulv.

Figure 2 indicates  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for males and females of the four species, with means and standard deviations for each indicated. Standard deviations for all groups indicated considerable variation in the relative isotopic composition of the diet between individuals within each group.



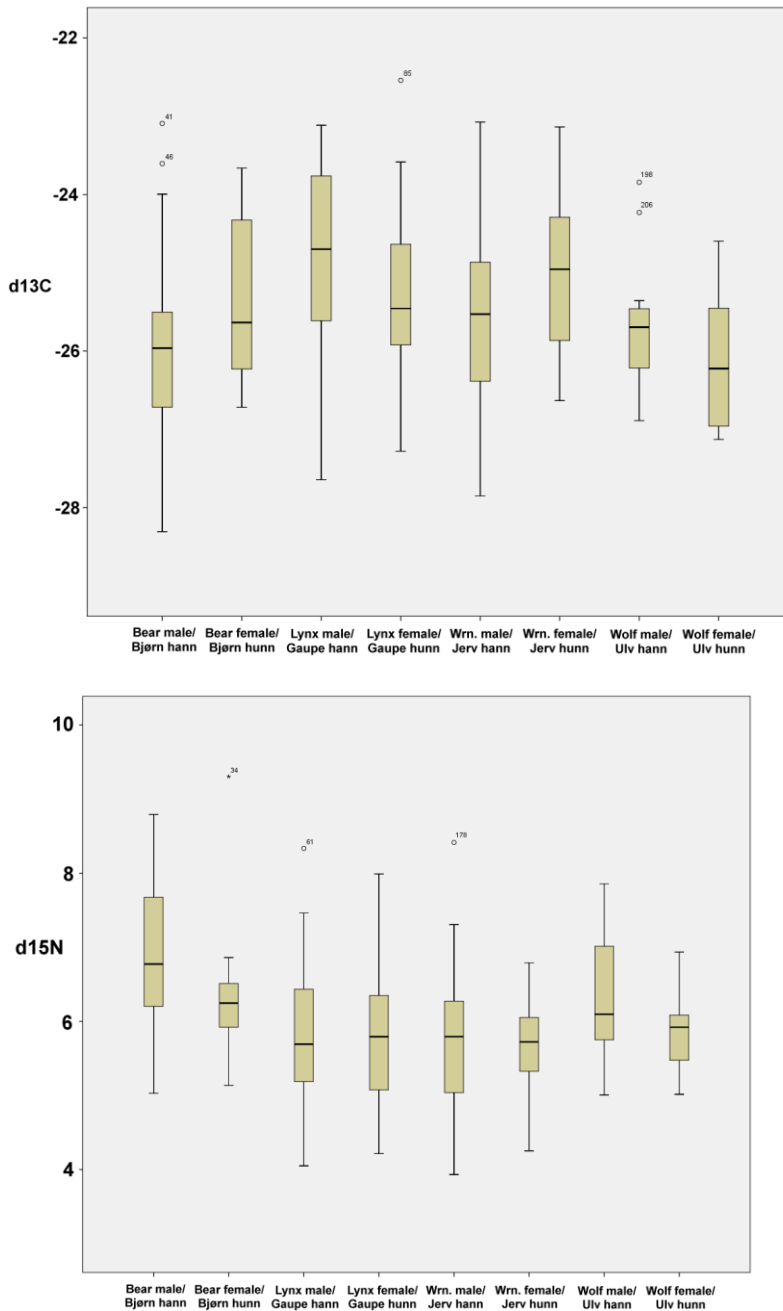
**Figure 2.** Stable isotope values of carbon and nitrogen of muscle tissue of male and female lynx, wolverine, bears and wolves in Norway; with means and standard deviations indicated. LM = lynx male; LF = lynx female; WrM = wolverine male; WrF = Wolverine female; BM = bear male, BF = bear female; WM = wolf male; WF = wolf female. / Stabilisotopverdier av karbon og nitrogen av muskelmasse hos hann og hunn gaupe, jerv, bjørn og ulv; med gjennomsnittverdier og standardavvik indikerte. GHa = gaupe hann; GHu = gaupe hunn; JHa = jerv hann; JHu = jerv hunn; BHa = bjørn hann; BHu = Bjørn hunn; UHa = ulv hann; UHu = ulv hunn.

Figure 3 places values for each species in the context of known values for plants and herbivorous mammals in the Norwegian terrestrial food chain. In some parts of the world, marine protein from anadromous fish such as salmon are important in the diet of brown bears; but that is not the case in Norway (Bojarka & Selva 2012). Dietary fractionation between trophic levels varies in intensity between species; however, in general with each trophic step (e.g. plants to herbivores or herbivores to carnivores), both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  tend to increase in value (i.e., the proportion of that isotope in the resulting tissue becomes greater than that of the diet); and in general  $\delta^{15}\text{N}$  increases more quickly than  $\delta^{13}\text{C}$ . A 'rule of thumb' for this, where exact fractionation values are not known, is ca. +3-3.4‰ for  $\delta^{15}\text{N}$  and +1‰ for  $\delta^{13}\text{C}$  (Kelly 2000; Post 2002); however (see above), variation between species is significant and care must be taken not to over-interpret results when exact fractionation values for the species are not known (Post 2002; Nilsen *et al.* 2012)



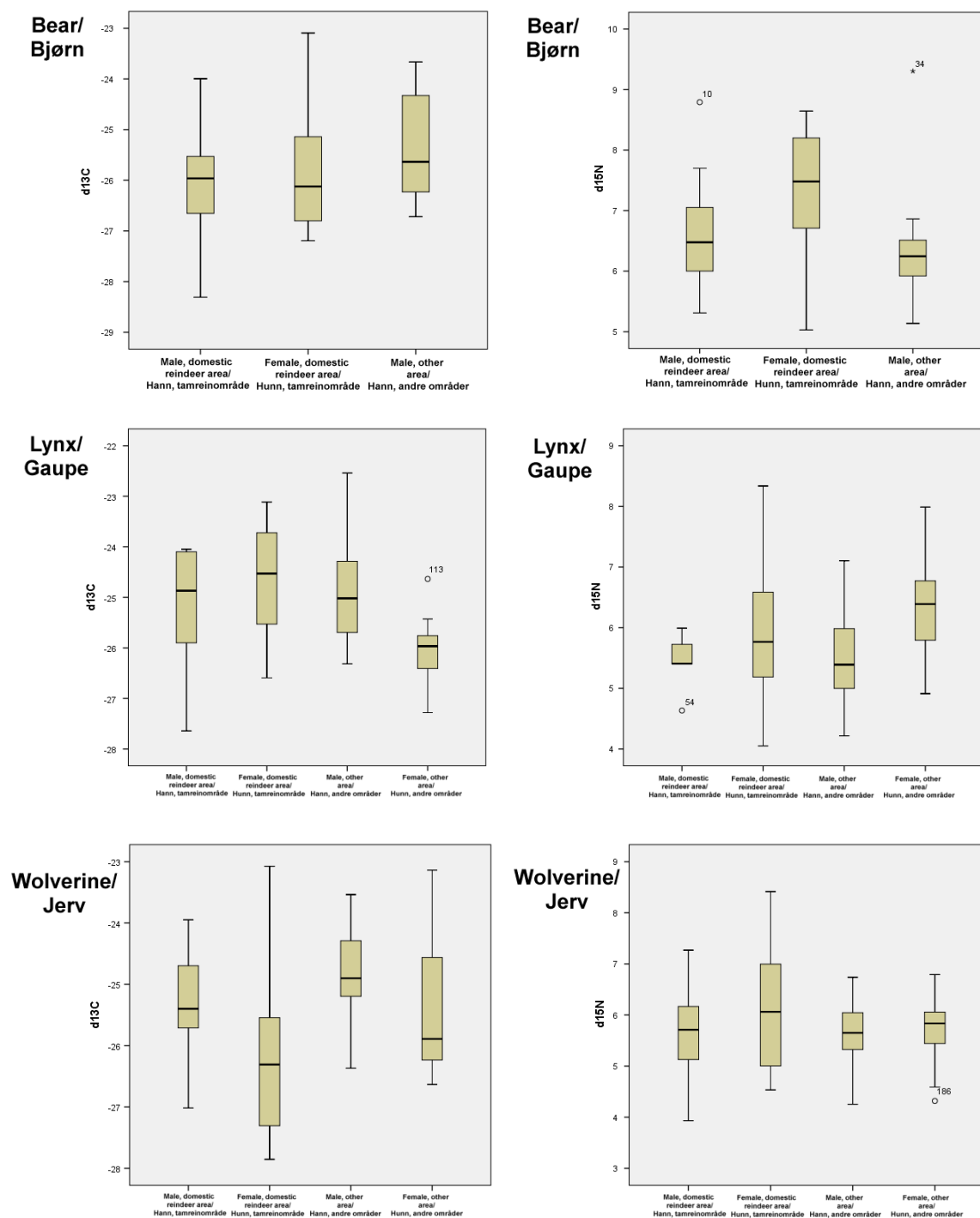
**Figure 3.** Stable isotope values of muscle tissue of each species of large carnivore in relation to values of plant (homogenized leaves and stems), lichen (homogenized), and herbivore species (muscle tissue) in the Norwegian terrestrial food chain. Non-carnivore data from Halley *et al.* (in prep). Large circles indicate the mean value for the species/group; error bars  $\pm 1$  Standard Deviation. The general trend in dietary fractionation from dietary source to consumer is indicated; exact values vary from species to species. Stabilisotopverdier av muskelvev fra store rovdyr i forbindelse med plante (homogenisert blad og stilk), lav (homogenisert), og plantetende arter (muskelvev) i det norske terrestriske næringskjede. Ikke-rovdyr data fra Halley *m.fl.* i preparasjon. Store sirkler indikerer gjennomsnittsverdien for arten/gruppen; avviklinjer 1 standardavvik.

Trenden i fordøyelsesfraksjonering fra kilde til konsument er indikerte; nøyaktige verdier varierer fra art til art.



**Figure 4a & 4b.** Boxplots of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for males and female bear, lynx, wolverine, and wolf. Black horizontal bar within box is median value. Box indicates limits of upper and lower quartiles (ie, 25% of values lie within the box above, and 25% within the box below, the median). Vertical black bars are upper and lower limits of values excluding outliers. Outliers (marked as points) are values at least 1.5 interquartile ranges above or below the limit of the box. Boxplotter av  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  verdier for hann- og hunnbjørn, gaupe, og jerv og ulv. Boksen indikerer grensene av øvre og nedre kvartilene (dvs, 25% av verdiene ligger innen boksen over, og under medianverdien merket). Vertikale svarte linjer viser øvre og nedre grenser bortsett fra utliggende verdier. Utliggende verdier (punkter) er verdier mer enn 1,5 interkvartiler over eller under boksen.





**Figure 5a-f.** Boxplots of  $\delta^{13}C$  and  $\delta^{15}N$  values for male and female bear, lynx, and wolverine, in relation to areas with and without domestic reindeer. All except one wolf sample were from areas without domestic reindeer. Box indicates limits of upper and lower quartiles (ie, 25% of values lie within the box above, and below the median). Vertical black bars are upper and lower limits of values excluding outliers. Outliers (marked as points) are values at least 1.5 interquartile ranges above or below the limit of the box. Boxplotter av  $\delta^{13}C$  and  $\delta^{15}N$  verdier for hann- og hunnbjørn, gaupe, og jerv i forbindelse med tamrein/ikke tamreinområder. Boksen indikerer grensene av øvre og nedre kvartilene (dvs, 25% av verdiene ligger innen boksen over, og under

medianverdien merket). Vertikal svarte linjer viser øvre og nedre grenser bortsett fra utliggende verdier. Utliggende verdier (punkter) er verdier mer enn 1,5 interkvartiler over eller under boksen.

Data was analysed for significant effects using univariate general linear modelling (IBM SPSS Statistics 23 software). Results of pairwise comparisons between species for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  are shown in Table 2a & 2b.

		Mean Difference	Standard Error	Sig.
Bear/Bjørn	Lynx/Gaupe	-,811	,194	,000*
	Wolverine/Jerv	-,531	,194	,007*
	Wolf/Ulv	-,469	,281	,096
Lynx/Gaupe	Bear/Bjørn	,811	,194	,000*
	Wolverine/Jerv	,279	,170	,102
	Wolf/Ulv	,342	,258	,186
Wolverine/Jerv	Bear/Bjørn	,531	,194	,007*
	Gaupe/Lynx	-,279	,170	,102
	Wolf/Ulv	,062	,260	,810
Wolf/Ulv	Bear/Bjørn	,469	,281	,096
	Lynx/Gaupe	-,342	,258	,186
	Wolverine/Jerv	-,062	,260	,810

**Table 2a.** Pairwise comparisons of  $\delta^{13}\text{C}$  values between species. Significant differences ( $p > 0.05$ ) are indicated \*. Parvis sammenligninger av  $\delta^{13}\text{C}$  verdier mellom arter. Signifikante forskjeller ( $p < 0.05$ ) indikerte \*.

		Mean Difference	Standard Error	Sig.
Bear/Bjørn	Lynx/Gaupe	,926*	,160	,000*
	Wolverine/Jerv	1,016*	,160	,000*
	Wolf/Ulv	,864*	,231	,000*
Lynx/Gaupe	Bear/Bjørn	-,926*	,160	,000*
	Wolverine/Jerv	,090	,140	,521
	Wolf/Ulv	-,062	,212	,771
Wolverine/Jerv	Bear/Bjørn	-1,016*	,160	,000*
	Lynx/Gaupe	-,090	,140	,521
	Wolf/Ulv	-,152	,214	,478
Wolf/Ulv	Bear/Bjørn	-,864*	,231	,000*
	Lynx/Gaupe	,062	,212	,771
	Wolverine/Jerv	,152	,214	,478

**Table 2b.** Pairwise comparisons of  $\delta^{15}\text{N}$  values between species. Significant differences ( $p > 0.05$ ) are indicated \*. Parvis sammenligninger av  $\delta^{15}\text{N}$  verdier mellom arter. Signifikante forskjeller ( $p < 0.05$ ) indikerte \*.

Brown bears were significantly higher in  $\delta^{15}\text{N}$  values compared to the other three species; and higher than lynx and wolverine, but not wolves, in  $\delta^{13}\text{C}$  values.

Male/female differences and differences between areas with domestic reindeer populations and those without, are shown in Table 3a & 3b.

$\delta^{13}\text{C}$ Species		B	Std. Er- ror	t	Sig.
Bear	Male/female	,619	,395	1,566	,124
	Area with/without domestic reindeer	,246	,405	,608	,546
Lynx	Male/female	-,548	,209	-2,624	,011*
	Area with/without domestic reindeer	-1,196	,216	-5,533	,000*
Wolverine	Male/female	,626	,231	2,704	,009*
	Area with/without domestic reindeer	-,662	,243	-2,724	,008*
Wolf	Male/female	-,284	,341	-,835	,413
	Area with/without domestic reindeer	-1,963	,849	-2,312	,031*

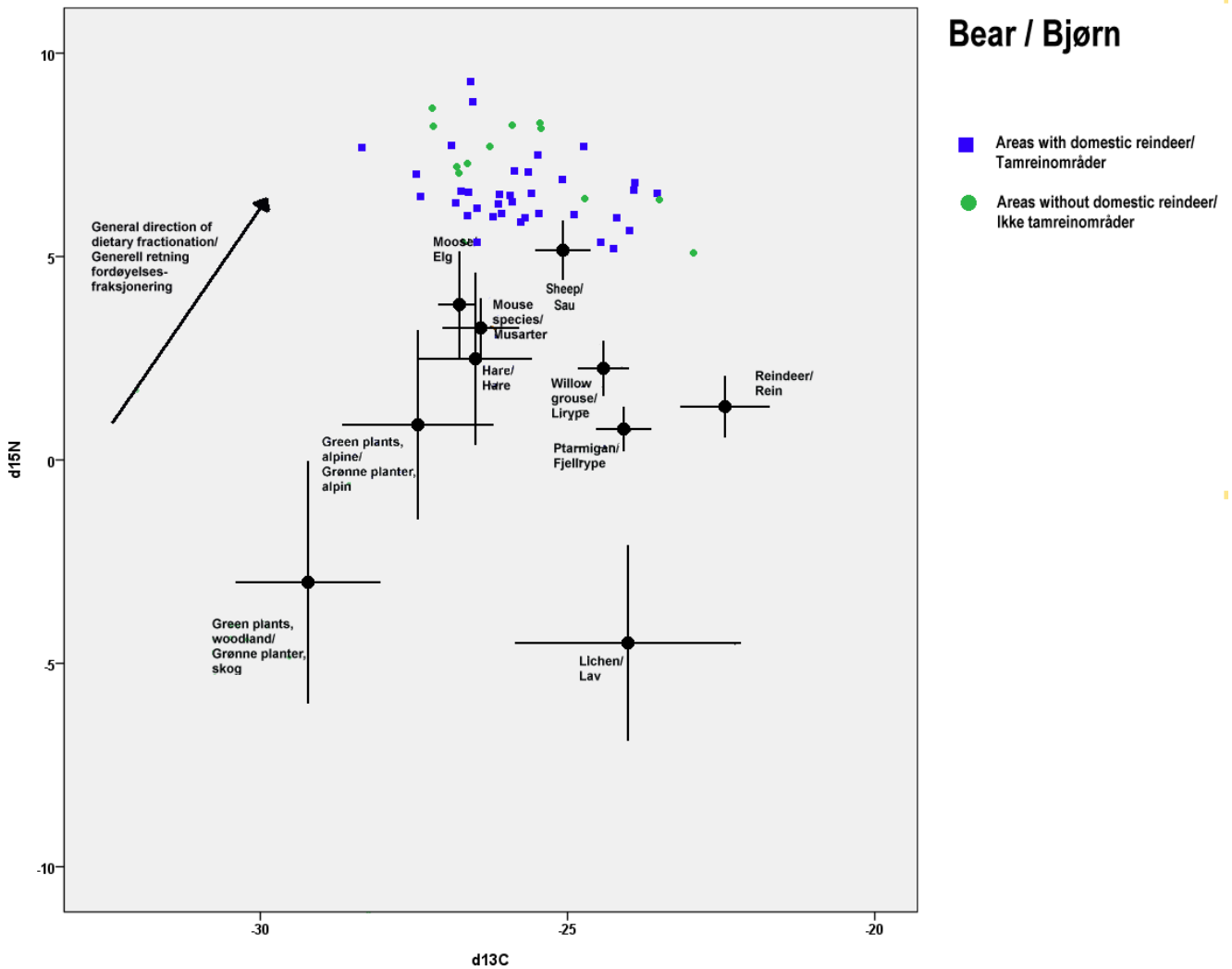
**Table 3a.** Relationship between sex, and presence or absence of domestic reindeer, and  $\delta^{13}\text{C}$  values for each species. Significant differences ( $p > 0.05$ ) are indicated \*. Forbindelsen mellom kjønn, tamrein/ikke tamreinområder, og  $\delta^{13}\text{C}$  verdier. Signifikante forskjeller ( $p < 0.05$ ) indikerte \*.

$\delta^{15}\text{N}$ Species	Parameter	B	Std. Error	t	Sig.
Bear	Male/female	-,337	,323	-1,043	,303
	Area with/without domestic reindeer	,709	,332	2,136	,038*
Lynx	Male/female	-,072	,199	-,362	,719
	Area with/without domestic reindeer	,574	,206	2,780	,007*
Wolverine	Male/female	-,151	,188	-,802	,425
	Area with/without domestic reindeer	,253	,198	1,282	,204
Wolf	Male/female	-,372	,283	-1,313	,203
	Area with/without domestic reindeer	-1,602	,706	-2,268	,034*

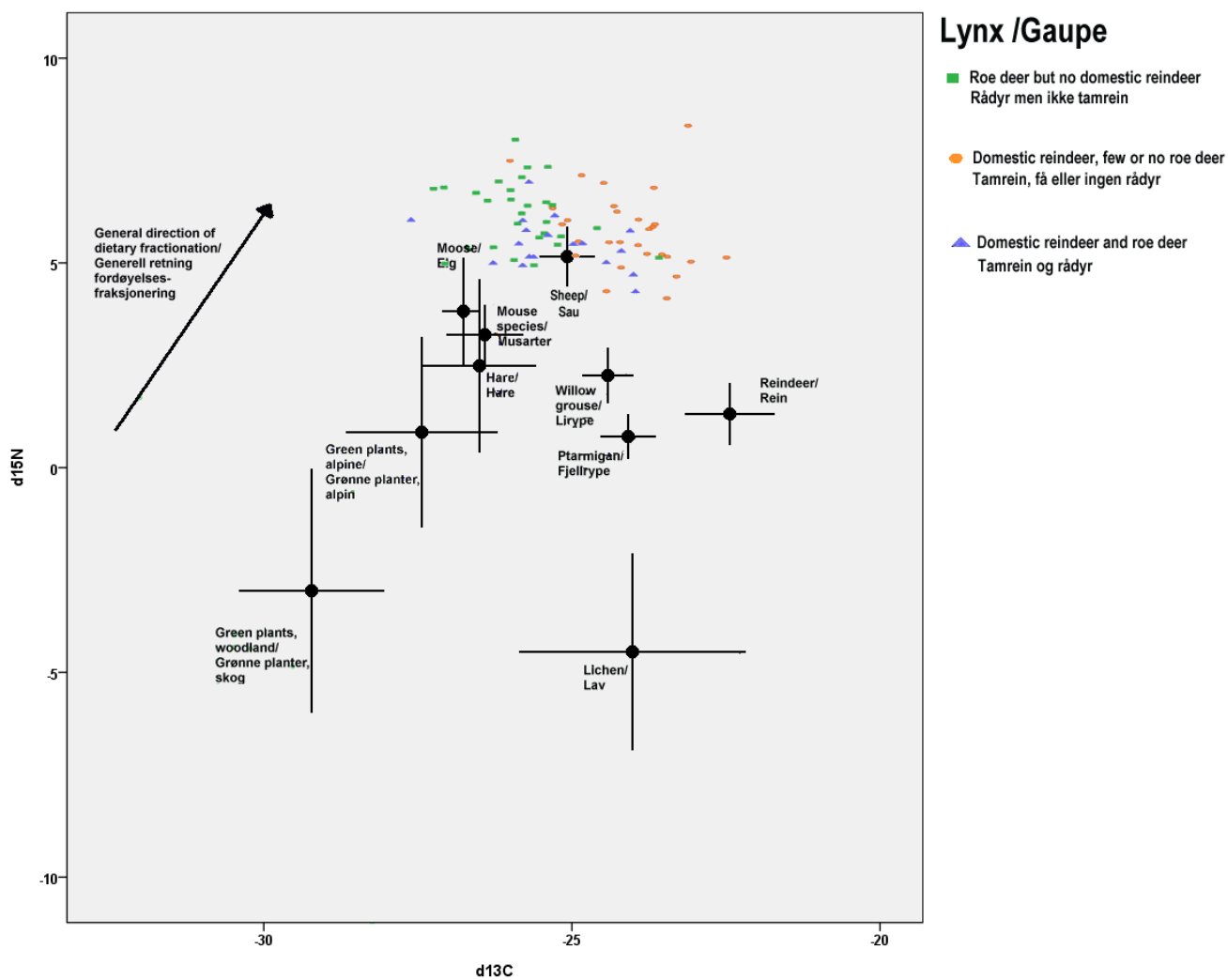
**Table 3b.** Relationship between sex, and presence or absence of domestic reindeer, and  $\delta^{15}\text{N}$  values for each species. Significant differences ( $p > 0.05$ ) are indicated \*. Forbindelsen mellom kjønn, tamrein/ikke tamreinområder, og  $\delta^{15}\text{N}$  verdier. Signifikante forskjeller ( $p < 0.05$ ) indikerte \*.

The data for lynx appeared to indicate a particularly strong effect between areas with and without semi-domestic reindeer. On closer analysis (Figure 6b), the values found were lowest for  $\delta^{13}\text{C}$ , and even more so for  $\delta^{15}\text{N}$ , in animals from Troms and Finnmark. Roe deer are not generally present in these provinces, and where they are found are not in large numbers. For Nordland and the two Trøndelag provinces, the five values lying clearly within the 'Troms-Finnmark group' came from Snåsa, Lierne, Vefsn, Saltdal and Tjeldsand kommunes. Of these, Vefsn, Saltdal and Tjeldsand have low or no roe deer populations. Lierne and Snåsa have roe deer, but they do not appear to be common ([www.artsdatabanken.no](http://www.artsdatabanken.no)). All have sheep to varying degrees. Differences between the three regions (Figure 6b) were highly significantly different for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (Kruskal-Wallis  $p < 0.001$ ).

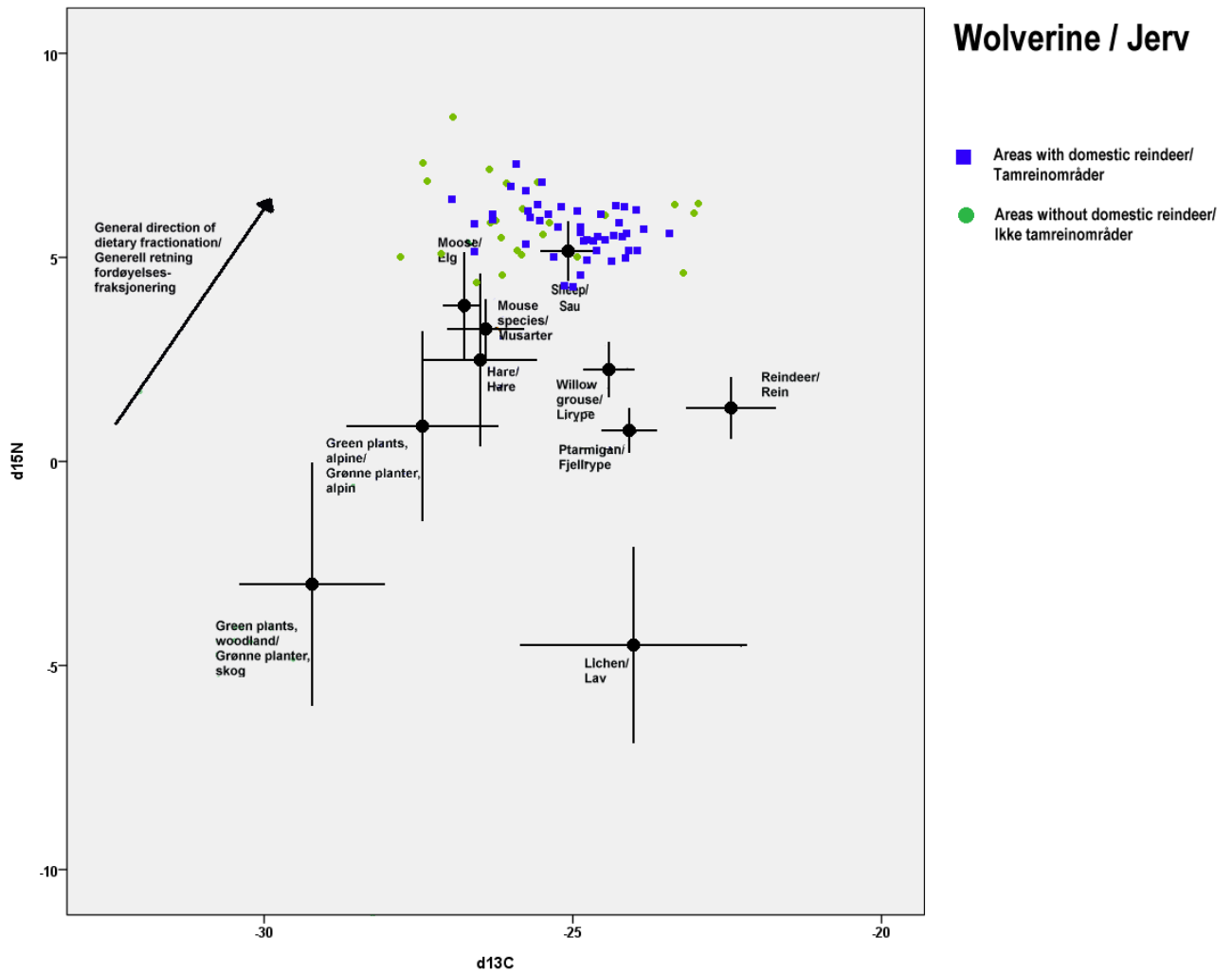
Mean values for groups can conceal important variations between individuals. Figures 5a-d present data for bears, lynx, wolverine, and wolf with presence or absence of domestic reindeer (and for lynx, roe deer; their main, and strongly preferred, prey in most areas where available (Odden et al 2014)) indicated.



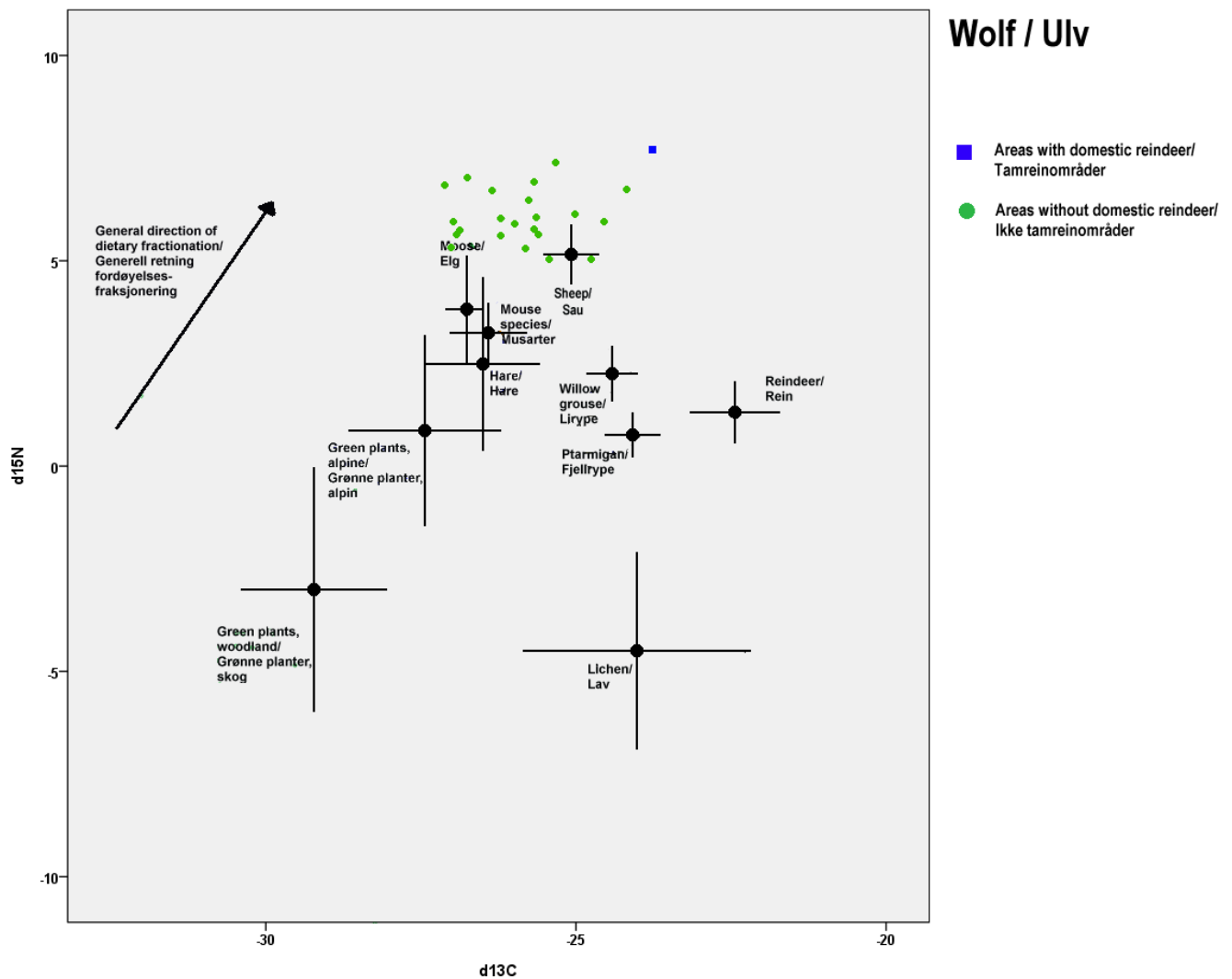
**Figure 6a.** Bear stable isotope values in relation to presence or absence of semi-domestic reindeer in the region (see discussion). *Bjørn stabilisotopverdier i forbindelse med tamrein/ikke tamreinområder (se diskusjon).*



**Figure 6b.** Lynx stable isotope values in relation to presence or absence of semi-domestic reindeer and roe deer in the region (see discussion). Gaupe stabilisotopverdier i forbindelse med tamrein/ikke tamreinområder (se diskusjon).



**Figure 6c.** Wolverine stable isotope values in relation to presence or absence of semi-domestic reindeer in the region (see discussion). Jerv stabilisotopverdier i forbindelse med tamrein/ikke tamreinområder (se diskusjon).



**Figure 5d.** Wolf stable isotope values in relation to presence or absence of semi-domestic reindeer in the region (see discussion). Ulv stabilisotopverdier i forbindelse med tamrein/ikke tamreinområder (se diskusjon).

## 4 Discussion

Stable isotope values provide information on the *assimilated diet* of the animal, that is, the sources of food which were digested and used to form tissue. They do not provide direct evidence on how many individuals of a prey species were consumed (the amount of a carcass which the animal eats can vary a lot depending on circumstances); or the proportion of food killed by the predator, or eaten from animal carcasses found dead by the predator.

Mean values for each carnivore species lie close to one another, within 1.3‰ for  $\delta^{13}\text{C}$  and 1.1‰ for  $\delta^{15}\text{N}$ . This range is well within the range that differences in trophic fractionation between species consuming identical diets can produce (Sponheimer *et al.* 2003, Nilsen *et al.* 2012). Fractionation may also differ between different types of food, particularly vegetable and animal food. This has been demonstrated for bears (Philips and Koch 2002), and is plausible to a lesser extent for wolverine, which to a lesser extent also consume vegetable food in some quantity (Banci 1994)

As a result, the values obtained in this study are too close to one another to be safely interpreted as resulting from differences in diet between species. This is reinforced by the observation that male and female brown bears, which are known to consume a diet containing a large proportion of vegetable matter, have the two highest  $\delta^{15}\text{N}$  values obtained; even though  $\delta^{15}\text{N}$  values increase with each trophic stage (e.g. from plant, to herbivore, to predator). We cannot, therefore, from this data, make safe inferences *between* the Norwegian large carnivore species in diet makeup, as we could if observed differences were of greater magnitude.

Wild herbivores (moose, hare, small rodents) feeding mainly on plants (i.e. not on lichens) have very similar isotope profiles, with large overlaps between species. This means that these species cannot be separated using this methodology, and accordingly are treated as one dietary source in the discussion below.

The two grouse species, willow grouse *Lagopus lagopus* and (rock) ptarmigan *Lagopus mutus* eat varied diets, and are each separable from each other and from other sources.

Reindeer, as noted, are strongly distinctive in isotope profile due mainly to the large element of lichen in their diet (Figure 2); and possibly also in part due to their unusual digestive processes; and, as a result, have a very distinct isotope profile.

Sheep in Norway, because of supplemented winter diets including concentrate made in part from marine food chain carnivore protein (e.g. fish meal), have observed stable isotope values very unlike those of plant-eating herbivores consuming a natural diet, and which are similar to those for terrestrial predators. Marine food chains are longer than terrestrial food chains at Norwegian latitudes, and start from primary producers (phytoplankton) with different baseline values from those of terrestrial plants or lichens. Marine fish values are very much higher in both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  than those of terrestrial predators. This means that tissues formed even of a small proportion of marine protein relative to the terrestrial plant element would yield high values, by non-tropical terrestrial ecosystem standards.

It should also be noted that while the sheep from which these values were calculated were fed on typical Norwegian diets, but the sample size was limited. Formulas used in supplemented winter diets on which sheep are fed may vary in their marine protein content. A wider survey of sheep tissue would be necessary to determine how representative the values indicated in Figures 2 and 5 are. Sheep fed entirely on terrestrial temperate ecosystem plant material would be expected to have isotope profiles in the same range as for hares, moose, and rodents; and so be indistinguishable from them using this method of analysis.

Assuming they are typical for sheep in Norway generally (see above), the observed isotopic values of sheep tissue nevertheless make the proportion of sheep in the diet in Norway very



hard to interpret using this method, as they lie so close to those of the carnivores themselves. This makes assessing their importance in the diet particularly sensitive to the exact values of dietary fractionation – small variations in which would have large consequences for the inferred proportion of sheep in the diet of large carnivores. (Post 2002; Nilsen *et al* 2012). However, a carnivore consuming a large proportion of sheep tissue would be expected to have isotope values rather higher than those of sheep, while values for  $\delta^{13}\text{C}$  in general straddle the values for sheep, with lower means in all cases. All carnivore species are only slightly higher in  $\delta^{15}\text{N}$  than are sheep. This suggests that sheep are not a large proportion of the diet, but cannot be regarded as strong evidence.

A mixed diet of sheep and wild herbivorous mammals excluding reindeer (reindeer will be discussed below) is compatible with the values obtained, with sheep possibly being a significant, although not a main, dietary source. This could be calculated more closely if the exact fractionation values for each carnivore species were known through a direct experiment. This has so far not been attempted. As it would require feeding a number of animals of each species a diet of exactly known isotopic composition for an extended period it would be both challenging and expensive. Without such data, ‘average fractionation values’, when the potential dietary sources lie so close together in isotope values, would yield diet proportion estimates dominated by small differences in the assumed values, and with error terms too large to be of practical use (Post 2002; Nilsen *et al* 2012).

Males and females of the same species do not differ in digestive fractionation, except in cases where sexual dimorphism is very extreme; nor do individuals of the same species living in different regions (such as areas with domestic reindeer and other areas). It can therefore be assumed that systematic differences between sexes or between different areas, in the same species, do result from differences in the isotopic composition of the diet rather than differences in digestive fractionation. The implications of the values observed for each large carnivore species are discussed below.

- 1) *Brown bears*: Bears did not differ significantly in stable isotope values, either between sexes or between bears living in areas with semi-domestic reindeer populations and those elsewhere. This does not necessarily mean that diets did not differ, as different combinations of food sources may lead to the same stable isotope values of tissue.

Bears have a very wide dietary range, including a wide range of plants, insects, honey, and other items; for some of which stable isotope values are not available. Also, dietary fractionation of isotopes can vary between plant and animal foods (Philips and Koch 2002). This makes interpretation of their diet, given the observed values, difficult.

However, the position of overall bear isotope values appears to position them, allowing for dietary fractionation, on the axis leading from plants (as opposed to e.g. lichens), through wild mammalian herbivores excluding reindeer (which have a very different isotope profile owing to the large element of lichen in the diet). They are not compatible with grouse species or reindeer as significant elements in the diet, unless bears also had a significant dietary source of higher  $\delta^{13}\text{C}$  values than the known sources, which in combination with the low values for reindeer could yield the values found.

Many of the bears in the sample, especially males, may have originated from and spent most of their lives in Sweden. This might affect availability of, especially, sheep in the diet at the time they were living there, relative to availability of sheep in Norway. Reindeer are widely herded in northern Sweden at the same latitudes and in the same way as they are in Norway, and so would have been in broad terms similarly available. In addition, as most bears in the sample were shot as predators of domestic stock, or a threat to such stocks, their diets and so isotopic signatures may not be representative of the species as a whole. Nevertheless, the isotope profiles are not compatible with either sheep or reindeer as a significant proportion of the assimilated diet. For sheep, it is possible to

interpret the data as resulting from the bears in the sample did not living long enough in Norway before their deaths, to develop a large isotopic trace of sheep in their body tissues.

- 2) *Lynx*: Lynx differed significantly in  $\delta^{13}\text{C}$  values both for males and females, females having significantly lower values; and for domestic reindeer vs. other areas, animals from areas without domestic reindeer having significantly lower values.

Lynx also differed significantly in  $\delta^{15}\text{N}$  values, but only for domestic reindeer vs. other areas.

Closer examination of patterns within lynx in relation to semi-domestic reindeer herding areas and roe deer (Figure 5b) indicates a pattern consistent with a higher element of reindeer and/or grouse species in the diet in areas where semi-domestic reindeer are established but roe deer are uncommon or absent, a lower element in those areas of Nordland and Trøndelag where both roe deer and semi-domestic reindeer are found, and lowest where semi-domestic reindeer are absent.

A number of individuals from reindeer herding areas with few or no roe deer have isotope profiles consistent with a diet roughly equally split between reindeer and wild mammal herbivores other than reindeer. However, the data does not appear to be consistent with reindeer being the *dominant* food source even in areas where both roe deer and sheep are uncommon.

In broad terms, this data is consistent with detailed research on radio-collared lynx, including in those parts of northern Norway where semi-domestic reindeer are common and roe deer rare or absent (Odden et al 2014). There, “semi-domestic reindeer are the main prey of lynx” (*op.cit.*), comprising about two thirds of *prey items*. However, it would suggest that reindeer are unlikely to form as much as 2/3 of the *assimilated* diet except for one individual, if lynx fractionation values are not very different from those of other predatory mammals. The explanation for this is unclear; the work in Odden *et al.* was very detailed, involving examination of carcasses found by following radio-collared lynx, when their stationary behaviour indicated a kill had been made. A possibility is that diet elements of species like hares, grouse and rodents might be underestimated by the tracking methodology if the lynx’s movements were not strongly affected by preying them. They are small prey items that would not take long for a lynx to consume entirely. However, the method involved investigating any spot where lynx were active for more than 30 minutes, so for this to be the case consumption of such prey must have been rapid for this hypothesis to be plausible; or the prey consumed so entirely as to leave no detectable trace.

It is also possible that lynx shot in these areas, whose carcasses were sent to NINA and muscle mass preserved; and which formed the data set for this study, were systematically biased in diet. This might be the case if lynx living in lower-lying areas, with more forest and a prey base less composed of reindeer, were disproportionately likely to be hunted. This cannot be excluded, but the differences in dietary estimate by the two methods are so large that the bias would have to be very strong; not a single lynx in the data set had a diet that appeared, from stable isotope analysis, to be consistent with reindeer as a dominant source of the assimilated diet.

Nevertheless, given the uncertainties in all methods of assessing diet, the results from stable isotope analysis are in broad agreement with other methods of assessing the diet of lynx.

If there were sex differences in the proportion of reindeer consumed in these areas (as live prey and/or carrion), it would be expected that this would be visible in stable isotope

values. From this data, therefore, one cannot conclude that there are differences in the consumption of semi-domestic reindeer between male and female lynx living in these areas. This conclusion is consistent with data from tracking radio collared lynx (Odden et al 2006, 2014).

The dietary difference in non-reindeer areas is consistent with, though not necessarily caused by, females eating relatively more sheep tissue and relatively fewer grouse than males, while both sexes appear to have the bulk of their diet sourced from plant-eating herbivores (see above).

- 3) *Wolverine*: Wolverine  $\delta^{13}\text{C}$  values differed significantly between males and females, and between areas with domestic reindeer and other areas.  $\delta^{15}\text{N}$  values did not differ significantly. Examination of Figure 5c indicates that  $\delta^{13}\text{C}$  values were higher in areas with semi-domestic reindeer; and in each area, female values were lower than those of males. There were also four individuals from outside domestic reindeer herding areas with very high  $\delta^{13}\text{C}$  values, higher than all other values. This is likely to be because wild reindeer can be a large element in the diet of this species.

Allowing for isotopic fractionation, values lie within the range expected for a diet dominated by wild mammal herbivores such as moose, hares, and small rodents; while some animals to the right of the distribution may have had reindeer as up to roughly half of their assimilated diet.

Landa *et al* (1997) found for wolverine in southern Norway (Dovrefjell plateau) that reproduction was strongly correlated with small rodent abundance (and also included many hares), but nevertheless considered reindeer the 'basic prey' in the denning period, based on analysis of identifiable remains in wolverine excrement. Van Dijk *et al* 2008 found semi-domestic reindeer and moose almost equal as the main source of identifiable remains in wolverine excrement in tundra habitats in southern Norway (moose 38.6%, reindeer 40.2%), and moose a major source in forest habitats in the same region, with reindeer relatively subsidiary (moose 51.9%, reindeer 27.9%; *op.cit.* Table 1).

There is reason to suspect that the importance of small rodents may be underestimated by either analysis of prey remains, or analysis of remains in excrement ('scat analysis'). Small rodents are normally eaten whole by this species, and digestive processes in the species are powerful; so that there would be few prey remains of rodents, and scat analyses would likely strongly underestimate small rodents, as even bones would be completely digested. Perhaps similarly, the use of time-lapse video photography at the nests of large raptors such as goshawks revealed small prey items to be much more important in the diet than earlier methods suggested (Grønnesby & Nygård 2000; Lewis et al. 2004)

Stable isotope data thus indicates that wild mammal herbivores other than reindeer are a larger part of the assimilated diet than other techniques indicate. This would be consistent with the data on reproductive success, and the hypothesis that scat analysis underestimates the importance of rodents in the diet. Magoun (1987) found that wolverine in arctic Alaska lived mainly on rodents throughout the year, except for midwinter.

Wolverine also eat plant material, mainly berries (Banci 1994). These have the isotope profiles expected for plants, and so are at the lower end of the trophic axis of isotope values of the plant – wild herbivorous mammal – carnivore food chain. This makes them difficult to distinguish from herbivorous mammals in wolverine diet, as increasing proportions of berries would 'move' the profile of wolverine tissue along the same axis, in the direction of the profiles of wild herbivorous mammals. Variable combinations of wild herbivorous mammals and plants might thus produce similar wolverine isotope profiles. A

diet *dominated* by plant material would be expected to be similar to those for wild herbivorous mammals. The higher values observed, however, indicate plants are not a large source of wolverine tissue. A diet combination of mainly sheep and plants is also compatible with the observed isotope values for this species; however as noted, the plant element would have to be unrealistically high for this to be plausible.

Stable isotope values would be expected to be significantly higher in both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  if sheep were a major proportion of the diet, due to dietary fractionation. However, the values are consistent with sheep being a significant element in a diet where wild herbivores other than reindeer were the main source.

Overall, together with data on the positive influence of rodent populations on wolverine reproduction, the overall isotope data suggests that rodents (or other wild herbivores, excluding reindeer), are a larger proportion of the wolverine diet than is normally considered to be the case.

- 4) *Wolf*: Although values of both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  vary significantly between areas with semi-domestic reindeer and other areas, only one sample of a wolf (a male) was available from an area with domestic reindeer. That individual was a vagrant animal, not native to or holding territory in the area. Wandering wolves can travel very large distances.

It is unsafe to draw conclusions from a single data point, even if it is statistically significantly different from the remainder of the data set. We can only conclude from the data that too little stable isotope data is available from areas with semi-domestic reindeer to draw conclusions from it about what the diet might be if wolves were resident in such areas.

Overall, allowing for dietary fractionation, the isotope values for wolves fall clearly in the range expected for a diet dominated by non-reindeer wild herbivorous mammals. As for the other large predators, stable isotope values would be expected to be higher in both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  if sheep were a major proportion of the diet, due to the effect of dietary fractionation. However, the values are consistent with sheep being a significant element in a diet where herbivores other than reindeer were the main source.

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## 7 Appendix: Data

Year/År	Journal-nr	Rovbase-no	Sex/Kjønn	Species/Art	Location/Fellingssted	Tamrein area	Kommune Number	Age/Alder	δ13C	δ15N
1993	103	MQ40022	Female/Hunn	Bear/Bjørn	Lierne	Yes/Ja	1738	6	6,32	-25,95
1997	106	MT60069	Female/Hunn	Bear/Bjørn	Sagdammen	Yes/Ja	2030	0	9,30	-26,60
2000	83	M301087	Female/Hunn	Bear/Bjørn	Lierne	Yes/Ja	1738	3	6,56	-26,72
2000	127	M205267	Female/Hunn	Bear/Bjørn		Yes/Ja	2021	4	5,92	-24,28
2001	133	M301089	Female/Hunn	Bear/Bjørn	Skjelbred	Yes/Ja	1738	9	5,93	-26,23
2003	109	M302590	Female/Hunn	Bear/Bjørn	Sørli	Yes/Ja	1738	3	5,29	-26,51
2005	100	M307029	Female/Hunn	Bear/Bjørn	Fjelløya	Yes/Ja	1738	4	5,98	-24,96
2005	103	M307006	Female/Hunn	Bear/Bjørn	Mostadfjellet	Yes/Ja	2030	3	6,51	-23,66
2007	160	M401397	Female/Hunn	Bear/Bjørn	Inderdalen	Yes/Ja	1738	3	5,59	-24,09
2008	165	M403448	Female/Hunn	Bear/Bjørn	Munkelv	Yes/Ja	2030	0	6,51	-25,64
2010	272	M404755	Female/Hunn	Bear/Bjørn	Andematte dalen	Yes/Ja	2030	3	6,86	-25,15
2011	12	M404757	Female/Hunn	Bear/Bjørn	Folmerfjellet	Yes/Ja	1742	9	6,25	-26,15
2011	276	M405143	Female/Hunn	Bear/Bjørn	Sørdalen	Yes/Ja	1924	3	5,14	-24,33
2009	218	M404416	Male/Hann	Bear/Bjørn	Myrabekken	No/Nei	1664	3	7,69	-26,30
2011	234	M405130	Male/Hann	Bear/Bjørn	Grundsetsætra	No/Nei	0427	5	6,40	-24,80



2011	233	M405135	Male/Hann	Bear/Bjørn	Flendalen	No/Nei	0428	9	8,15	-25,48
2011	232	M405129	Male/Hann	Bear/Bjørn	Tørråsen	No/Nei	0428	4	5,03	-23,09
2011	235	M405136	Male/Hann	Bear/Bjørn	Bjøråkjølen	No/Nei	0430	10	8,24	-25,49
2012	88	M405494	Male/Hann	Bear/Bjørn	Fjælabuhøgda	No/Nei	0429	5	8,65	-27,19
2012	216	M405661	Male/Hann	Bear/Bjørn	Mykleby	No/Nei	0430	5	8,18	-27,17
2012	215	M405837	Male/Hann	Bear/Bjørn		No/Nei	0430	12	8,22	-25,95
2012	73	M405455	Male/Hann	Bear/Bjørn	Horta	No/Nei	0430	5	6,36	-23,60
2012	74	M405466	Male/Hann	Bear/Bjørn	Fåberg	No/Nei	0501	8	7,19	-26,82
2012	69	M405439	Male/Hann	Bear/Bjørn	Tokke	No/Nei	0833	4	7,27	-26,64
2013	199	M406287	Male/Hann	Bear/Bjørn	Samdalen	No/Nei	0520	2	7,02	-26,78
2007	188	M401620	Male/Hann	Bear/Bjørn	Elgryggen	Yes/Ja	2030	2	5,80	-25,80
2008	137	M403148	Male/Hann	Bear/Bjørn	Vaggatem	Yes/Ja	2030	2	6,44	-27,39
2009	156	M404386	Male/Hann	Bear/Bjørn	Strompedalen	Yes/Ja	1740	1	6,00	-26,13
2009	214	M404421	Male/Hann	Bear/Bjørn	Lindsetfjellet	Yes/Ja	1740		5,92	-25,74
2009	194	M404390	Male/Hann	Bear/Bjørn	Klokkerelva	Yes/Ja	2030	3	6,98	-27,47
2009	201	M404400	Male/Hann	Bear/Bjørn	Norheim samdrift	Yes/Ja	2030	4	5,96	-26,65
2009	202	M404401	Male/Hann	Bear/Bjørn	Timesholmen	Yes/Ja	2030	2	6,46	-25,96
2010	268	M404786	Male/Hann	Bear/Bjørn	Tamneset	Yes/Ja	1640	4	7,47	-25,52
2010	271	M404770	Male/Hann	Bear/Bjørn	Tømmernes	Yes/Ja	2030	0	6,61	-24,01

2011	213	M405133	Male/Hann	Bear/Bjørn	Kleivseterfjellet	Yes/Ja	1736	2	6,56	-26,65
2011	103	M405098	Male/Hann	Bear/Bjørn	Lurudalen	Yes/Ja	1736	4	7,08	-25,90
2011	212	M405132	Male/Hann	Bear/Bjørn	Gaundalen	Yes/Ja	1736	22	6,00	-25,53
2011	211	M405137	Male/Hann	Bear/Bjørn	Storsteintjønna	Yes/Ja	1738	12	7,70	-26,89
2011	297	M405145	Male/Hann	Bear/Bjørn	Maskevarre	Yes/Ja	2025	2	6,48	-26,14
2011	209	M405128	Male/Hann	Bear/Bjørn	Gjøkhotellet	Yes/Ja	2030	13	7,03	-25,68
2011	210	M405118	Male/Hann	Bear/Bjørn	Bukholmen	Yes/Ja	2030	0	7,68	-24,81
2012	196	M405538	Male/Hann	Bear/Bjørn	Nordre Raubeinklumpen	Yes/Ja	1736	18	7,67	-28,31
2012	85	M405465	Male/Hann	Bear/Bjørn	Pantdalen	Yes/Ja	1826	3	8,79	-26,56
2012	179	M405542	Male/Hann	Bear/Bjørn	Skardalen	Yes/Ja	1940	3	6,00	-25,51
2012	208	M405751	Male/Hann	Bear/Bjørn	Badjevuoppenjarga	Yes/Ja	2021	2	6,24	-26,84
2012	171	M405529	Male/Hann	Bear/Bjørn	Bordevarre	Yes/Ja	2030	11	6,17	-26,49
2012	153	M405504	Male/Hann	Bear/Bjørn	Neiden	Yes/Ja	2030	3	5,31	-24,52
2013	148	M406275	Male/Hann	Bear/Bjørn	Reinsjøfjellet	Yes/Ja	2030	3	6,77	-24,00
2012	198	M405346	Female/Hunn	Lynx/Gaupe	Elgålva	No/Nei	0434	8	5,79	-24,64
2012	164	M405442	Female/Hunn	Lynx/Gaupe	Liagardene	No/Nei	0617	13	6,77	-27,28
2012	160	M405441	Female/Hunn	Lynx/Gaupe	Barsgård	No/Nei	0833	6	6,43	-25,46
2013	166	M406037	Female/Hunn	Lynx/Gaupe	Rønes	No/Nei	0119	4	7,99	-25,96
2013	6	M405362	Female/Hunn	Lynx/Gaupe	Bolnesberget	No/Nei	0402	3	6,35	-25,76

2013	70	M406082	Female/Hunn	Lynx/Gaupe	Baklia	No/Nei	0520	4	7,31	-25,43
2013	74	M406034	Female/Hunn	Lynx/Gaupe	Onsberget	No/Nei	0532	6	6,16	-25,85
2013	162	M406020	Female/Hunn	Lynx/Gaupe	Pytte	No/Nei	0604	7	5,00	-25,98
2013	95	M406069	Female/Hunn	Lynx/Gaupe	Dramdal	No/Nei	0624	2	5,32	-26,31
2013	164	M406028	Female/Hunn	Lynx/Gaupe		No/Nei	0826	2	6,80	-27,11
2013	33	M406023	Female/Hunn	Lynx/Gaupe	Tuddal	No/Nei	0827	3	6,48	-26,41
2013	187	M406027	Female/Hunn	Lynx/Gaupe		No/Nei	0829	6	5,90	-25,92
2013	7	M405978	Female/Hunn	Lynx/Gaupe	Tussvika	No/Nei	1566	2	6,73	-26,03
2013	96	M406000	Female/Hunn	Lynx/Gaupe	Fosen	No/Nei	1624	4	4,91	-27,10
2010	194	M404697	Female/Hunn	Lynx/Gaupe	Stuorra Russujavri	Yes/Ja	2020	5	5,46	-24,94
2010	191	M404574	Female/Hunn	Lynx/Gaupe	Buggefjord	Yes/Ja	2030	2	6,28	-25,35
2011	193	M405021	Female/Hunn	Lynx/Gaupe	Buvarp	Yes/Ja	1725	7	5,98	-25,84
2011	63	M405031	Female/Hunn	Lynx/Gaupe	Oppland	Yes/Ja	1749	4	5,39	-25,02
2011	121	M404936	Female/Hunn	Lynx/Gaupe	Fagervika	Yes/Ja	1822	3	6,10	-25,32
2011	79	M405062	Female/Hunn	Lynx/Gaupe	Skibotn	Yes/Ja	1939	14	5,06	-22,54
2011	59	M404993	Female/Hunn	Lynx/Gaupe	Naranas	Yes/Ja	2011	3	5,37	-23,97
2011	163	M405004	Female/Hunn	Lynx/Gaupe	Adamselv	Yes/Ja	2022	3	5,14	-23,58
2011	123	M405023	Female/Hunn	Lynx/Gaupe	Guovdagarjavri	Yes/Ja	2025	5	5,89	-25,20
2011	116	M405030	Female/Hunn	Lynx/Gaupe	Eliasavzi	Yes/Ja	2025	3	4,81	-24,25

2012	106	M405405	Female/Hunn	Lynx/Gaupe	Morkamoen	Yes/Ja	1725	10	6,93	-25,74
2012	127	M405499	Female/Hunn	Lynx/Gaupe	Russelva	Yes/Ja	1840	3	4,94	-24,48
2012	82	M405422	Female/Hunn	Lynx/Gaupe	Lille Raipas	Yes/Ja	2012	2	5,99	-25,11
2012	101	M405397	Female/Hunn	Lynx/Gaupe	Tarmfjord	Yes/Ja	2025	2	4,23	-24,48
2013	184	M406045	Female/Hunn	Lynx/Gaupe	Karienet	Yes/Ja	1725	4	5,73	-25,78
2013	18	M406008	Female/Hunn	Lynx/Gaupe	Sagfossen	Yes/Ja	1736	4	4,22	-24,01
2013	185	M405991	Female/Hunn	Lynx/Gaupe	Devikkklumpen	Yes/Ja	1738	5	4,93	-26,32
2013	5	M405966	Female/Hunn	Lynx/Gaupe	RV760 Veium	Yes/Ja	1742	3	4,86	-25,84
2013	9	M405993	Female/Hunn	Lynx/Gaupe	Munnarhågen	Yes/Ja	1832	2	5,07	-25,66
2013	99	M406011	Female/Hunn	Lynx/Gaupe	Risfjell	Yes/Ja	1833	3	5,08	-25,73
2013	159	M405950	Female/Hunn	Lynx/Gaupe	Porsa	Yes/Ja	2017	17	7,10	-24,88
2013	153	M406051	Female/Hunn	Lynx/Gaupe	Trollberget	Yes/Ja	2022	2	6,20	-24,31
2013	102	M406120	Female/Hunn	Lynx/Gaupe	Geassanjarga	Yes/Ja	2025	7	5,44	-24,26
2012	163	M405425	Male/Hann	Lynx/Gaupe	Sandvik	No/Nei	1003	2	5,38	-25,27
2012	166	M405424	Male/Hann	Lynx/Gaupe	Berland	No/Nei	1021	2	5,66	-25,49
2013	57	M406039	Male/Hann	Lynx/Gaupe	Kroksund	No/Nei	0119	2	7,30	-25,76
2013	168	M406080	Male/Hann	Lynx/Gaupe	Stai	No/Nei	0430	3	6,36	-25,36
2013	72	M405996	Male/Hann	Lynx/Gaupe	Vika	No/Nei	0516	4	6,95	-26,23
2013	71	M405997	Male/Hann	Lynx/Gaupe	Øftsgard	No/Nei	0520	5	6,50	-26,03

2013	79	M405998	Male/Hann	Lynx/Gaupe	Syverud	No/Nei	0520	2	7,06	-25,85
2013	73	M406035	Male/Hann	Lynx/Gaupe	Hesjabakkollen	No/Nei	0540	4	6,67	-26,59
2013	2	M405900	Male/Hann	Lynx/Gaupe	Velstad kro	No/Nei	0621	2	4,87	-25,65
2013	29	M406029	Male/Hann	Lynx/Gaupe	Høymyr	No/Nei	0807	5	5,95	-25,45
2013	32	M406022	Male/Hann	Lynx/Gaupe	Hovin	No/Nei	0826	2	5,59	-25,22
2013	94	M406024	Male/Hann	Lynx/Gaupe	Flatdal	No/Nei	0828	5	5,56	-25,57
2013	47		Male/Hann	Lynx/Gaupe	Bygland	No/Nei	0938	2	5,06	-23,63
2005	16	M305865	Male/Hann	Lynx/Gaupe	Kråkelvdalen	Yes/Ja	2012	4	5,82	-23,73
2006	94	M305988	Male/Hann	Lynx/Gaupe	Harrecåkka	Yes/Ja	2020	7	5,89	-23,70
2007	88	M400831	Male/Hann	Lynx/Gaupe	Sør Varanger	Yes/Ja	2030	5	6,79	-23,71
2009	117	M404339	Male/Hann	Lynx/Gaupe	Leavdnjavarre	Yes/Ja	2020	4	4,05	-23,50
2009	116	M404353	Male/Hann	Lynx/Gaupe	Myggvatn	Yes/Ja	2030	2	5,77	-23,79
2010	77	M404608	Male/Hann	Lynx/Gaupe	Nevervik	Yes/Ja	2012	5	7,46	-26,04
2010	216	M404683	Male/Hann	Lynx/Gaupe	Peskanuten	Yes/Ja	2012	3	6,00	-23,96
2010	193	M404705	Male/Hann	Lynx/Gaupe	Gussajeaggi	Yes/Ja	2020	2	4,59	-23,35
2010	26	M404462	Male/Hann	Lynx/Gaupe	Holmsjøen	Yes/Ja	2030	4	6,91	-24,53
2011	207	M405042	Male/Hann	Lynx/Gaupe	Einrem	Yes/Ja	1824	2	4,63	-24,05
2011	174	M405034	Male/Hann	Lynx/Gaupe	Holmslett	Yes/Ja	1832	6	5,61	-25,43
2011	275	M404978	Male/Hann	Lynx/Gaupe	Nedrevann	Yes/Ja	2020	4	5,44	-24,44

2011	128	M404983	Male/Hann	Lynx/Gaupe	Marsavarri	Yes/Ja	2025	5	5,08	-23,49
2012	211	M405844	Male/Hann	Lynx/Gaupe	Lystad stigningen	Yes/Ja	1826	2	5,99	-27,64
2012	151	M405445	Male/Hann	Lynx/Gaupe	Kalvhauet	Yes/Ja	1924	2	5,11	-24,98
2013	181	M405376	Male/Hann	Lynx/Gaupe	Furutangvika	Yes/Ja	1738	2	5,40	-25,90
2013	178	M406158	Male/Hann	Lynx/Gaupe	Tunnsjøen	Yes/Ja	1738	2	5,72	-24,10
2013	20	M405426	Male/Hann	Lynx/Gaupe	Juvika	Yes/Ja	1804	9	5,41	-24,87
2013	156	M406085	Male/Hann	Lynx/Gaupe		Yes/Ja	1852	4	5,22	-24,24
2013	83	M405427	Male/Hann	Lynx/Gaupe	Brenna	Yes/Ja	1922	3	6,34	-24,36
2013	61	M406228	Male/Hann	Lynx/Gaupe	Oalgevarri	Yes/Ja	1933	5	4,96	-23,11
2013	125	M406205	Male/Hann	Lynx/Gaupe	Burfjorddalen	Yes/Ja	1943	2	8,34	-23,16
2013	198	M406119	Male/Hann	Lynx/Gaupe	Geassanjarga	Yes/Ja	2025	3	5,15	-23,83
2001	55	M203943	Female/Hunn	Wolf/Ulv	Klonkeneset	No/Nei	0432	4	5,32	-27,03
2003	19	M301800	Female/Hunn	Wolf/Ulv	Velta SØ	No/Nei	0425	14	5,63	-26,94
2003	137	M303061	Female/Hunn	Wolf/Ulv		No/Nei	0427	3	5,65	-26,22
2005	40	M305532	Female/Hunn	Wolf/Ulv	Tresdalen	No/Nei	0430	2	6,17	-25,05
2005	41	M305583	Female/Hunn	Wolf/Ulv	Åkerstraumen	No/Nei	0432	5	5,92	-26,02
2005	36	M306013	Female/Hunn	Wolf/Ulv	Vinstra (E6)	No/Nei	0516	2	5,30	-25,85
2006	56	M305638	Female/Hunn	Wolf/Ulv		No/Nei	0429	3	6,94	-27,13
2007	162	M401377	Female/Hunn	Wolf/Ulv	Gammelsætertjønna	No/Nei	0432	3	5,99	-24,60

2010	14	M404544	Female/Hunn	Wolf/Ulv	Storsjøen	No/Nei	0432	2	5,99	-26,98
2011	273	M405148	Female/Hunn	Wolf/Ulv	Bergsida	No/Nei	0423	3	6,79	-26,38
2013	132	M406234	Female/Hunn	Wolf/Ulv	Sølenholet	No/Nei	0432	2	5,02	-24,79
2005	90	M306782	Male/Hann	Wolf/Ulv	Søndre Lønset	No/Nei	0429	7	5,69	-25,65
2006	57	M306791	Male/Hann	Wolf/Ulv	Nydalen	No/Nei	0301	3	6,07	-26,22
2006	110	M308818	Male/Hann	Wolf/Ulv	Joramo	No/Nei	0512	3	7,52	-25,36
2007	161	M401417	Male/Hann	Wolf/Ulv	Letjerndalen	No/Nei	0427	3	5,75	-26,89
2008	203	M403080	Male/Hann	Wolf/Ulv	Lystad	No/Nei	0226	2	6,10	-25,67
2011	171	M404749	Male/Hann	Wolf/Ulv	Elgåhogna	No/Nei	0434	2	5,79	-25,70
2011	238	M404750	Male/Hann	Wolf/Ulv	Sulebergsletta	No/Nei	0520	4	6,53	-25,80
2011	294	M404988	Male/Hann	Wolf/Ulv	Ytre Laurak	No/Nei	0919	2	5,01	-25,46
2012	36	M405318	Male/Hann	Wolf/Ulv	Narsetra	No/Nei	0415	3	7,11	-26,77
2012	51	M405432	Male/Hann	Wolf/Ulv	Opphus FV606	No/Nei	0430	2	5,64	-26,25
2013	149	M405871	Male/Hann	Wolf/Ulv	Skjervagen	No/Nei	0434	2	6,84	-24,23
2013	59	M406238	Male/Hann	Wolf/Ulv	Ausetsetra	No/Nei	1622	2	7,01	-25,70
2005	37	M306026	Male/Hann	Wolf/Ulv	Mikkelvatnet	Yes/Ja	2030	3	7,86	-23,84
2012	94	M405489	Female/Hunn	Wolverine/Jerv	Elgåhogna	No/Nei	0434	3	6,79	-26,13
2012	136	M405509	Female/Hunn	Wolverine/Jerv	Forellhogna	No/Nei	0437	5	6,06	-23,14
2012	91	M405486	Female/Hunn	Wolverine/Jerv	Mørkridsdalen	No/Nei	1426	4	5,81	-25,44

2012	135	M405512	Female/Hunn	Wolverine/Jerv	Isvatnet	No/Nei	1426	2	4,59	-23,32
2012	222	M405850	Female/Hunn	Wolverine/Jerv	Skyttholet	No/Nei	1664	2	6,02	-24,56
2013	52	M405927	Female/Hunn	Wolverine/Jerv	Tørberget	No/Nei	0428	5	5,12	-25,99
2013	175	M405872	Female/Hunn	Wolverine/Jerv	Varmbekkroa	No/Nei	0434	5	4,32	-26,63
2013	98	M405875	Female/Hunn	Wolverine/Jerv	Skjærbekkdalen	No/Nei	0434	3	5,88	-26,33
2013	176	M405873	Female/Hunn	Wolverine/Jerv	Tverrfjellsetra	No/Nei	0434	4	5,44	-26,23
2013	188	M405946	Female/Hunn	Wolverine/Jerv	Kvitdalen	No/Nei	0439	5	6,27	-23,44
2013	23	M405983	Female/Hunn	Wolverine/Jerv	Langsua	No/Nei	0519	4	5,53	-25,56
2013	137	M406187	Female/Hunn	Wolverine/Jerv	Geisdalen	No/Nei	1426	2	6,17	-25,89
2013	90	M406269	Female/Hunn	Wolverine/Jerv	Trollhetta	No/Nei	1567	3	5,84	-26,40
2010	37	M404549	Female/Hunn	Wolverine/Jerv	Gjelhaugen	Yes/Ja	2003	2	5,82	-24,34
2010	258	M404717	Female/Hunn	Wolverine/Jerv	Havvannet	Yes/Ja	2018	3	5,71	-24,95
2010	157	M404709	Female/Hunn	Wolverine/Jerv	Unjarga	Yes/Ja	2027	5	5,27	-25,84
2011	23	M404934	Female/Hunn	Wolverine/Jerv	Gagga	Yes/Ja	2020	2	6,15	-24,08
2011	114	M405077	Female/Hunn	Wolverine/Jerv	Mattefæijohka	Yes/Ja	2025	3	4,25	-25,08
2011	113	M405073	Female/Hunn	Wolverine/Jerv	Bårshejohka	Yes/Ja	2025	6	5,13	-24,20
2012	103	M405458	Female/Hunn	Wolverine/Jerv	Skipskjølen	Yes/Ja	2003	6	5,15	-24,04
2012	52	M405390	Female/Hunn	Wolverine/Jerv	Vuoldeavzzi	Yes/Ja	2012	2	6,04	-24,61
2012	31	M405371	Female/Hunn	Wolverine/Jerv	Raggonjarga	Yes/Ja	2025	3	6,05	-26,37



2012	105	M405454	Female/Hunn	Wolverine/Jerv	Syltefjorddalen	Yes/Ja	2028	2	5,54	-24,23
2013	193	M406031	Female/Hunn	Wolverine/Jerv	Tissvatnet	Yes/Ja	1738	4	4,53	-24,96
2013	53	M405957	Female/Hunn	Wolverine/Jerv	Perhaugen	Yes/Ja	1824	2	5,74	-25,31
2013	108	M405932	Female/Hunn	Wolverine/Jerv	Innerdal	Yes/Ja	1832	2	6,62	-25,83
2013	103	M405877	Female/Hunn	Wolverine/Jerv	Sjørdalen	Yes/Ja	1840	10	6,74	-26,08
2013	160	M405881	Female/Hunn	Wolverine/Jerv	Skeiti	Yes/Ja	1840	6	5,38	-24,74
2013	85	M405891	Female/Hunn	Wolverine/Jerv	Vesle Nuten	Yes/Ja	1924	10	5,97	-25,77
2013	115	M406272	Female/Hunn	Wolverine/Jerv	Jerta	Yes/Ja	1924	5	6,12	-25,02
2013	62	M405976	Female/Hunn	Wolverine/Jerv	Dividalen	Yes/Ja	1924	4	4,93	-24,24
2013	64	M405977	Female/Hunn	Wolverine/Jerv	Jules	Yes/Ja	1924	5	5,55	-23,54
2013	146	M406073	Female/Hunn	Wolverine/Jerv	juvvanroavri	Yes/Ja	1942	8	5,38	-24,90
2013	65	M406058	Female/Hunn	Wolverine/Jerv		Yes/Ja	1942	2	6,25	-24,38
2013	120	M405989	Female/Hunn	Wolverine/Jerv	Vesterelv	Yes/Ja	2012	8	5,51	-24,41
2013	14	M405974	Female/Hunn	Wolverine/Jerv	Sieppat	Yes/Ja	2025	4	5,65	-24,95
2012	177	M405541	Male/Hann	Wolverine/Jerv	Bergmillom	No/Nei	0516	2	8,41	-27,01
2012	90	M405485	Male/Hann	Wolverine/Jerv	Slufsedalen	No/Nei	1424	2	4,96	-25,01
2013	172	M405914	Male/Hann	Wolverine/Jerv	Strålsetra	No/Nei	0415	2	5,84	-25,45
2013	151	M406251	Male/Hann	Wolverine/Jerv	Sør for Vemunden	No/Nei	0425	5	5,06	-27,20
2013	15	M405912	Male/Hann	Wolverine/Jerv	Bjønnerget	No/Nei	0428	3	4,53	-26,21

2013	174	M405878	Male/Hann	Wolverine/Jerv	Flermoen	No/Nei	0428	2	5,02	-25,91
2013	1	M405812	Male/Hann	Wolverine/Jerv	Atndalen	No/Nei	0430	3	6,82	-25,64
2013	173	M405929	Male/Hann	Wolverine/Jerv	Sorken	No/Nei	0434	2	4,98	-27,85
2013	131	M405830	Male/Hann	Wolverine/Jerv	Hynnlia	No/Nei	0521	2	7,14	-26,41
2013	136	M406188	Male/Hann	Wolverine/Jerv	Srongdalen	No/Nei	1426	2	7,31	-27,49
2013	134	M406242	Male/Hann	Wolverine/Jerv	Holmavatnet	No/Nei	1426	3	6,28	-23,07
2013	129	M405979	Male/Hann	Wolverine/Jerv	Nedstestølen	No/Nei	1524	6	6,85	-27,41
2012	54	M405391	Male/Hann	Wolverine/Jerv	Vuoldeavzzi	Yes/Ja	2012	2	5,92	-26,36
2013	114	M405905	Male/Hann	Wolverine/Jerv	Fjellskardet	Yes/Ja	1824	3	3,93	-25,41
2013	113	M405931	Male/Hann	Wolverine/Jerv	Jamtfjelldalen	Yes/Ja	1825	2	5,79	-25,46
2013	106	M405901	Male/Hann	Wolverine/Jerv	Forshaugen	Yes/Ja	1825	4	4,98	-25,39
2013	112	M405938	Male/Hann	Wolverine/Jerv	Trollhaugan	Yes/Ja	1840	2	5,46	-24,70
2013	109	M405960	Male/Hann	Wolverine/Jerv	Østre Rundvatn	Yes/Ja	1840	2	5,49	-24,28
2013	48	M405925	Male/Hann	Wolverine/Jerv	Lappfjell	Yes/Ja	1845	3	4,88	-24,87
2013	208	M405959	Male/Hann	Wolverine/Jerv	Småtindan	Yes/Ja	1920	2	5,40	-24,86
2013	86	M405934	Male/Hann	Wolverine/Jerv	Istindlia	Yes/Ja	1922	2	5,85	-25,61
2013	63	M406059	Male/Hann	Wolverine/Jerv	Skakterelva	Yes/Ja	1924	3	6,22	-25,27
2013	161	M405885	Male/Hann	Wolverine/Jerv	Manndalen	Yes/Ja	1940	5	6,22	-24,26
2013	67	M406002	Male/Hann	Wolverine/Jerv	Stor Ana	Yes/Ja	1942	2	7,27	-25,98

2013	157	M406057	Male/Hann	Wolverine/Jerv	Punten	Yes/Ja	1942	5	6,01	-25,48
2013	121	M405980	Male/Hann	Wolverine/Jerv	Vuovdevarri	Yes/Ja	2011	2	5,42	-24,57
2013	122	M405984	Male/Hann	Wolverine/Jerv	Guormovuobmi	Yes/Ja	2012	3	5,13	-24,70
2013	139	M406150	Male/Hann	Wolverine/Jerv	Lavkoavvi	Yes/Ja	2020	3	6,41	-27,02
2013	77	M406134	Male/Hann	Wolverine/Jerv	Godduoavvi	Yes/Ja	2020	2	5,80	-26,65
2013	76	M406142	Male/Hann	Wolverine/Jerv	Halkavarri	Yes/Ja	2020	4	6,26	-25,64
2013	3	M405916	Male/Hann	Wolverine/Jerv	Indre Billefjord	Yes/Ja	2020	10	6,82	-25,58
2013	12	M405968	Male/Hann	Wolverine/Jerv	Vuomavarri	Yes/Ja	2020	2	4,28	-25,20
2013	141	M406138	Male/Hann	Wolverine/Jerv	Galmat	Yes/Ja	2021	3	4,86	-24,46
2013	144	M406141	Male/Hann	Wolverine/Jerv	Reatkajohka	Yes/Ja	2022	2	6,12	-25,79
2013	78	M406107	Male/Hann	Wolverine/Jerv	Hanaskaidi	Yes/Ja	2025	2	5,13	-26,65
2013	145	M406106	Male/Hann	Wolverine/Jerv	Nyelvdalen	Yes/Ja	2027	6	5,63	-23,95







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