

1 **Not only mosses – lemming winter diets as described by DNA metabarcoding**

2 Eeva M. Soininen¹, Lucie Zinger^{2,3}, Ludovic Gielly², Nigel G. Yoccoz¹, John-Andre Henden¹,

3 Rolf A. Ims¹

4

5 Author affiliations:

6 ¹ Department of Arctic and Marine Biology, UiT – The Arctic University of Norway, N-9037

7 Tromsø, Norway

8 ²Laboratoire d'Ecologie Alpine, UMR CNRS-UGA-USMB 5553, Université Grenoble Alpes, CS

9 40700, F-38058 Grenoble Cedex 9, France

10 ³ current affiliation: Université Toulouse 3 Paul Sabatier, CNRS, ENFA, UMR 5174 EDB, F-

11 31062 Toulouse, France.

12

13

14 *Corresponding author e-mail: eeva.soininen@uit.no

15 tel: +47 77620932

16 fax: +47 77 64 63 33

17 **Abstract**

18 The temporal dynamics of most tundra food webs are shaped by the cyclic population
19 dynamics of lemmings. While processes during winter may be behind the recent disruptions
20 of lemming cycles, lemming winter ecology is poorly known. We present here the first DNA
21 metabarcoding data on the winter diet of Norwegian lemmings (*Lemmus lemmus*), based on
22 feces collected after a winter of population increase. Prostrate willows, mosses, and
23 graminoids dominated the species winter diet, indicating that the conventional idea of
24 lemmings as moss-specialists should be revised. The behavior of lemming-plant models in
25 theoretical studies is conditional on the assumptions of mosses being their main winter food
26 item. As shrubs have been excluded from the framework of these models, incorporating
27 them in future modeling studies should nuance our understanding on how plants affect
28 lemmings. We also sampled diet of a few individuals found dead on top of the snow. These
29 individuals had relatively empty stomachs and had, prior to death, relied heavily on mosses.
30 This apparent lack of abundant good quality indicates spatial heterogeneity in local food
31 availability during the population increase phase.

32

33 **Key words:** Arctic, bryophyte, *Lemmus lemmus*, prostrate *Salix*, snowbed, winter

34 **Introduction**

35 The temporal dynamics of most tundra food webs are shaped by the cyclic population
36 dynamics of lemmings, considered as key species in the Arctic (Ims and Fuglei 2005).

37 Wintertime processes are crucial for lemming population dynamics (Gilg et al. 2009;
38 Bilodeau et al. 2013a) and changes in snow properties may be behind the recent disruptions
39 of lemming population cycles in Fennoscandia (Kausrud et al. 2008; Ims et al. 2011). Yet,
40 winter ecology of lemmings is poorly known as Arctic winters up to nine months long and
41 snow packs up to several meters thick, combined with often difficult access to remote field
42 sites, make data collection challenging.

43

44 Lemming grazing during the periodic peaks can have a profound effect on vegetation
45 (Virtanen 2000; Olofsson et al. 2012) and interactions with food plants have been suggested
46 to be behind the cyclic dynamics (Turchin et al. 2000; Oksanen et al. 2008). Interactions
47 between lemmings and their food resources can be expected to be most pronounced during
48 winter. No new plant growth occurs during this period, snow conditions may limit access to
49 some food items, and individuals tend to concentrate at locations with favorable snow
50 conditions such as snowbeds (Duchesne et al. 2011). However, descriptions of lemming
51 winter diet are scarce (but see Soininen et al. 2015b).

52

53 We present here the first DNA metabarcoding (Taberlet et al. 2012) analysis of the winter
54 diet of Norwegian lemmings (*Lemmus lemmus*). The species feeds on a range of mosses,
55 graminoids, forbs and shrubs during summer (Tast 1991; Saetnan et al. 2009; Soininen et al.
56 2013) but is thought to rely heavily on mosses during the winter (Kalela et al. 1961; Koshkina
57 1961; Calandra et al. 2015). Previous descriptions of the species winter diet are based on a

58 cafeteria experiment (Kalela et al. 1961), a combination of microhistological analyses of
59 stomach content and grazing signs on vegetation (Koshkina 1961) and stable isotopes
60 analyses of tooth tissue (Calandra et al. 2015). Compared to these methods, DNA
61 metabarcoding enables taxonomically detailed analyses of a large number of samples and
62 allows for more precise and spatially extensive assessments of variability of herbivore diets
63 (Soininen et al. 2009).

64

65 To describe Norwegian lemming winter diet in low Arctic landscapes, we analyzed feces
66 collected in their winter habitat during a year of population peak in Finnmark, northeastern
67 Norway. We complement these data with samples collected from individuals found dead on
68 top of the snowpack during the same winter. To achieve taxonomically detailed information
69 on both vascular plants and bryophytes, we used two different primer sets to identify the
70 ingested plants (Taberlet et al. 2007) and compared the recovered plant DNA in feces to
71 reference libraries of Arctic and boreal vascular plants (Sønstebø et al. 2010; Willerslev et al.
72 2014b) and bryophytes (Soininen et al. 2015b).

73

74 **Material and methods**

75 **Study area and samples**

76 All samples were collected in northeastern Norway (70-71° N, 28-31° E), from snowbed
77 habitats where monitoring of Norwegian lemmings has been conducted since 2009 using
78 feces removal plots. The snowbeds are distributed among three different watershed areas;
79 Komagdalen (KO), Vestre Jakobselv (VJ) and Ifjordfjellet (IF). Within the watersheds, the
80 sampled snowbeds are spread across an area of 32km², 18km², and 16 km² at KO, VJ and IF,
81 respectively. They cover an altitudinal gradient of approximately 150 to 200m, from valley

82 bottoms with willow thicket to barren highlands. Snowbeds occur in small-scale topographic
83 depressions, where the snowpack can be more than 4m thick in winter and persist until late
84 July. Characteristic plants are mosses (*Dicranum sp.* and *Polytrichum sp.*), a prostrate willow
85 (*Salix herbaceae*), graminoids (*Carex bigelowii*, *Avenella flexuosa*), and low statured forbs
86 (e.g. *Bistorta vivipara*).

87

88 Populations of Norwegian lemmings peaked in the area autumn 2011, followed by a
89 population crash during the winter 2011-2012 (Ims et al. 2013). To assess the species winter
90 diet during an increase phase of the population cycle (i.e. winter 2010-2011), we sampled
91 feces soon after snowmelt in 2011. In each snowbed (n= 18, 18, and 16 snowbeds for KO, VJ
92 and IF, respectively) we collected a sample of 5-20 pellets, aiming at five pellets from each
93 feces removal plot within a snowbed (n=4 plots per snowbed). However, this was
94 sometimes impossible as some snowbeds had few pellets. Thus, three of the samples had
95 only one pellet. The feces removal plots were cleaned the previous time in July 2010. We
96 assume that the feces collected in July 2011 represent winter 2011 instead of
97 summer/autumn 2010, because i) snowbeds are typically winter habitats of the Norwegian
98 lemming, and ii) we excluded feces that had clear signs of decomposition, i.e. feces
99 potentially originating from summer 2010. Further, we assume that the feces did not
100 originate from after snowmelt in 2011 as the sampling was conducted relatively soon after
101 snowmelt (on average 17 days, as the average snowmelt date of the sampled snowbeds was
102 June 23rd and the average sampling date July 10th). In addition, during snowmelt the
103 snowbed habitats are very wet, colder than the ambient air, provide little fresh plant foods,
104 and lemmings seem to move away from these habitats before the snow melts (Bilodeau et
105 al. 2013b).

106

107 We also collected dead individuals opportunistically in March 2011 (n=6 individuals found on
108 top of the snow, all from VJ). We initially aimed to sample stomach content of these
109 individuals, but as the stomachs were mainly empty we sampled pellets from the intestines
110 (n=1 stomach content and n=5 samples of pellets). The number of samples is summarized in
111 Online Resource 1, Supplementary Table S1.

112

113 **Diet analysis**

114 We analyzed 58 samples for this study as a part of a larger batch of samples (n=192), using
115 DNA metabarcoding. Other parts of the dataset have previously been described in Soininen
116 et al. (2013); Soininen et al. (2014); Soininen et al. (2015a). The method is based on
117 amplifying and high-throughput DNA sequencing a targeted plastid DNA region (P6-loop of
118 the chloroplast *trnL* (UAA) intron) with universal primers for plants. (Taberlet et al. 2007;
119 Soininen et al. 2009). We used two complementary primer pairs, *g-h* which targets seed
120 plants and *c-h* which is universal to plants, to get data on both vascular plants and
121 bryophytes (Taberlet et al. 2007). See details in Online Resource 1, Supplementary Text S1.

122

123 Sequence reads were analyzed using the OBITools software package (Boyer et al. 2016). As
124 taxonomic reference libraries for the primer pair *g-h*, we first used a combined library of 815
125 Arctic (Sønstebo et al. 2010) and 835 boreal vascular plant species (Willerslev et al. 2014b).
126 For the *c-h* primer pair, we used the same taxonomic reference libraries of Arctic and boreal
127 vascular plant species, supplemented with a library of 455 Arctic and boreal bryophyte
128 species (Soininen et al. 2015b). Sequences that matched poorly against these references
129 were further compared with references retrieved from the EMBL Nucleotide Sequence

130 Database (version 111, available at <http://www.ebi.ac.uk/embl/>). We then carefully checked
131 these taxonomic assignments using both the known regional flora and the reference libraries
132 coverage of all relevant taxa. See details in Online Resource 1, Supplementary Text S1.

133

134 The resulting datasets consisted of a sequence count per taxon and sample, from which we
135 calculated the proportion of different taxa in each sample. Even though DNA metabarcoding
136 data for plants probably reflects herbivore diets well (Soininen et al. 2009; Willerslev et al.
137 2014a), the amount of DNA sequences per sample may be biased for some taxa (Soininen et
138 al. 2009; Pompanon et al. 2012). Hence, we also report the number of samples in which a
139 given taxon was found. We used the *c-h* dataset to compare the proportions of seed plants,
140 ferns and fern allies (i.e. vascular non-seed plants) and bryophytes (i.e. mosses and
141 liverworts) in the diet and to assess the proportions of different bryophyte taxa. We used
142 data from primer pair *g-h* to assess the proportions of seed plant taxa. Preliminary
143 multivariate analyses (PCA on centered log-ratio transformed proportions of families with
144 >1% mean proportion of the diet) revealed little differences in Norwegian lemming diets
145 between the three watershed areas. Furthermore, the difference in sample size between
146 snowbeds (n=50) and dead individuals (n=6) was large. For these reasons, we here focus on
147 descriptive analyses.

148

149 **Results**

150 *Taxonomic precision of diet data*

151 A total of 12 190 sequences were obtained with the *g-h* primer pair (210 sequences/sample
152 on average) and 19 199 sequences with the *c-h* primer pair (343 sequences/sample on
153 average). We removed two samples from the dataset because we were unable to amplify

154 any DNA with the *c-h* primer from them. Overall, 98.2% of the sequences were identified at
155 the family level, 60.1% at the genus level and 17.1% at the species level. The large amount of
156 sequences assigned to the family level were mainly assigned to Salicaceae, a common plant
157 family in the study area and for which the *g-h* region is almost identical between members
158 of this group (Sønstebø et al. 2010). Excluding this family, 77.0% of sequences were
159 identified to the genus level. However, as only the genus *Salix* is present in the study area,
160 we considered all sequences assigned to Salicaceae to belong to this genus.

161

162 *Composition of Norwegian lemming winter diet*

163 For the samples collected during the population cycle increase phase (i.e. snowbed samples),
164 we retrieved 17 species, 29 genera and 25 families of vascular plants, and 9 species, 18
165 genera and 13 families of bryophytes (Table 1; Online Resource 1, Table S2). Proportion of
166 vascular plants was on average 0.54 (range from 0.03 to 0.99) (Figure 1a). The most common
167 family was Salicaceae. Other common vascular plant families were Poaceae and
168 Polygonaceae. The vascular plant component of Norwegian lemming diets thus
169 encompassed deciduous shrubs, grasses and forbs (Figure 1a). The three most common
170 moss families were Polytrichaceae, Dicranaceae and Rhabdoweisiaceae. In the study area, all
171 of these families are mainly represented by acrocarpous species, with Polytrichaceae
172 growing as scattered stems, while the two other families usually form carpets. We obtained
173 very similar results by using the frequency of occurrence instead of relative abundance
174 (Table 1; Online Resource 1, Table S2). Plant family composition differed little between the
175 three watershed areas (Online Resource 1, Figure S1). In the samples collected from dead
176 individuals, bryophytes of the family Dicranaceae largely dominated the diet while the mean
177 proportion of vascular plants was 0.30 (range from zero to 0.97) (Figure 1b).

178

179 **Discussion**

180 We found that mosses, grasses, and willows dominated the winter diet of the Norwegian
181 lemming in snowbed habitats during the increase phase of the population cycle. This
182 indicates that vascular plants have a more prominent role in the species winter diet than
183 previously assumed. Use of food plants varied little between the sampled watershed areas.
184 In contrast, dead individuals sampled on top of the snow pack had relied heavily on mosses.
185 This suggests that Norwegian lemming winter diets may differ substantially between
186 individuals remaining in their normal subnivean habitat and individuals dispersing on the
187 snow surface.

188

189 Based on DNA metabarcoding, we were able to identify food items that have previously
190 been considered unimportant. Furthermore, we were able to describe Norwegian lemming
191 winter diet at an unprecedented level of taxonomic detail, showing a previously undescribed
192 diversity of food items. DNA metabarcoding has previously been used to successfully
193 describe diets in a semi-quantitative way in various herbivores (Kowalczyk et al. 2011;
194 Newmaster et al. 2013; Willerslev et al. 2014a), including lemmings (Soininen et al. 2013;
195 Soininen et al. 2015a). Still, DNA metabarcoding of faeces has several potential biases, in
196 particular differential PCR amplification between taxa and differential digestion between
197 plant taxa (Pompanon et al. 2012). The abundance of *Salix* in our results is unlikely to be an
198 artifact due to preferential amplification of short fragments. The DNA fragment amplified by
199 the primer pair *g-h* for *Salix* is of similar length (56bp) as that of the two most abundant
200 grass genera we identified (*Avenella* and *Festuca*, 52bp in the species occurring in the study
201 area; *A. flexuosa*, *F. rubra*, and *F. ovina*). Furthermore, differential digestion is unlikely a

202 major problem in small rodents, as there is a good correspondence of DNA metabarcoding
203 data between samples collected from stomach and rectum of the same individuals (Soininen
204 2012). In ruminants, DNA metabarcoding has been compared with known diets, recorded by
205 animal-born video footage Newmaster et al. (2013) or by controlling the diet of a captive
206 individual (Willerslev et al. 2014a; Nakahara et al. 2015). While population-level average
207 diets were found to have good correspondence (Newmaster et al. 2013), the
208 correspondence of individual-level diets appears to be variable (Willerslev et al. 2014a;
209 Nakahara et al. 2015). For small rodents, the method has been evaluated in terms of its
210 correspondence with microhistology, the two methods yielding a taxonomically similar
211 picture of small rodent diets (Soininen et al. 2009). We thus believe that our results reflect
212 actual diet proportions of Norwegian lemmings rather well, although assessing the
213 quantitative correspondence between food intake and DNA metabarcoding would be
214 required to confirm this.

215

216 The most common food item of the Norwegian lemmings' winter diet was the vascular plant
217 family Salicaceae. Although we could not identify the species with DNA metabarcoding, we
218 do know that the predominant species within the family Salicaceae in the snowbed habitats
219 in northern Norway is the prostrate *Salix herbaceae*. Our findings thus contrast most
220 previous studies on Norwegian lemming diets, which have highlighted the importance of
221 mosses and grasses during winter (Kalela et al. 1961; Koshkina 1961; Calandra et al. 2015)
222 and summer (Stoddart 1967; Hansson 1969; Tast 1991; Saetnan et al. 2009). Yet, the
223 biomass of prostrate willows in snowbeds is affected by Norwegian lemmings (Moen et al.
224 1993; Virtanen 2000), supporting our interpretation of these plants as important winter food
225 for the species. Accordingly, a recent DNA metabarcoding study of winter diets of two other

226 lemming species from Arctic Canada showed that *Salix* was an important winter food item
227 for both the collared lemming, *Dicrostonyx groenlandicus*, and brown lemming, *Lemmus*
228 *trimucronatus* (Soininen et al. 2015a). The conventional wisdom that lemmings are “ moss-
229 eaters, in particular so during the critical winter period” (cf. Turchin et al. 2000) has had a
230 profound implication for how their dynamics have been modelled in theoretical studies
231 (Turchin et al. 2000; Turchin and Batzli 2001). In these studies, the destabilizing effect of
232 plants on lemmings is conditional on the plants re-growth corresponding to logistic growth.
233 This has been argued to apply for mosses but not graminoids, whereas woody plants were
234 excluded from this modeling framework (Turchin and Batzli 2001). Hence, further
235 development of rodent-plant interaction models would benefit from considering how the
236 functional diversity of vascular plants in lemming diets would best be incorporated.

237

238 We found three moss families to be common in the Norwegian lemmings’ winter diet,
239 namely Rhabdoweisiaceae, Polytrichaceae and Dicranaceae. This contrasts with the summer
240 diet, where Dicranaceae has been found to be the dominant moss in the same study area
241 (Soininen et al. 2013). In addition, the species appears also to use more mosses during
242 winter than summer, as indicated by a higher mean proportion of bryophytes (50% in this
243 study vs 32% in Soininen et al. 2013). The use of mosses seems thus to be more important
244 and diversified during winter. The winter diet differs from the summer diet in terms of the
245 diversity and importance of vascular plants: winter diet contains i) larger proportion of *Salix*,
246 ii) a lower vascular plant diversity, and iii) lower proportion of the grass *A. flexuosa*.
247 Norwegian lemmings thus appear to compensate for the low availability of herbaceous
248 plants in winter by feeding more on woody plants and mosses. Such seasonality contrasts
249 the findings by Calandra et al. (2015) who found little differences between summer and

250 winter diets based on stable isotope analyses of Norwegian lemming teeth. However, the
251 isotopic signatures of for instance mosses, forbs and shrubs overlap largely (Calandra et al.
252 2015). Thus, seasonal differences in diet taxonomic composition do not necessarily result as
253 a change in the isotopic diet. Even though we found no clear indication of regional
254 differences in diets, it is possible that some of the variation (e.g. the proportion of vascular
255 plants that ranged almost between zero and one [0.03 and 0.99]) could be caused by local
256 differences in available vegetation. Yet, a proper assessment of active selection or
257 alternatively, avoidance, of plants and potential seasonal patterns in it, would require
258 comparisons of available biomass and ingested biomass.

259

260 Interestingly, the samples collected from dead individuals that were found on top of the
261 snow pack show a contrasting diet composition. These relied heavily on *Dicranum* mosses,
262 while other food items were scarce in their diets. The samples collected from the snowbeds
263 represent an average diet of several individuals, across a longer time window and larger
264 spatial scale, in the normal subnivean winter habitat of Norwegian lemmings. In contrast,
265 the diet description of the dead individuals represents the last meal of these individuals that
266 were likely searching for better grazing grounds as we found them on top of the snow. In
267 particular, the mostly empty stomachs and the difference in diet composition compared to
268 the feces samples from snowbeds suggest a lack of abundant good quality food prior to
269 death. Indeed, limited access to food due to poor snow conditions (Kausrud et al. 2008) and
270 overgrazing of food resources (Turchin et al. 2000) have been assumed to cause population
271 crashes in lemmings, and similar causes could explain the movement of individuals on top of
272 the snow during the increase phase. Although some of the differences in the diet between
273 the two sets of samples could be due to lower sample size, they indicate spatial

274 heterogeneity in local food availability during the population increase phase. Consequently,
275 lemming-plant interactions may show substantial spatial heterogeneity during a given
276 population cycle phase.

277

278 **Acknowledgements**

279 We thank Siw Killengreen, Geir Vie, Sandra Hamel, Kristoffer H. Juell, Francisco Javier Ancin
280 Murguzur, and Ingrid Jensvoll for collecting samples in the field; Christian Miquel, Delphine
281 Rioux and Alice Valentini help with the laboratory; Eric Coissac for help with the
282 bioinformatics analyses; and Eivind Flittie Kleiven for help with checking snow melt dates.
283 The work of Eeva M. Soininen was supported by Oskar Huttunen foundation and the Fram
284 Centre through the Climate-Ecological Observatory for Arctic Tundra (COAT). Sample
285 collection was funded by the Research Council of Norway (project EcoFinn).

286

287 **Conflict of interest**

288 We would like to mention that Ludovic Gielly is one of the co-inventors of a patent
289 concerning *g-h* primers and the subsequent use of the P6 loop of the chloroplast *trnL* (UAA)
290 intron for plant identification using degraded template DNA. These patents only restrict
291 commercial applications and have no impact on the use of this locus by academic
292 researchers.

293

294 **References**

295 Bilodeau F, Gauthier G, Berteaux D (2013a) Effect of snow cover on the vulnerability of lemmings to
296 mammalian predators in the Canadian Arctic. *J Mammal* 94 (4):813-819
297 Bilodeau F, Kenney AJ, Gilbert BS, Hofer E, Gauthier G, Reid DG, Berteaux D, Krebs CJ (2013b)
298 Evaluation of a technique to trap lemmings under the snow. *Arctic* 66 (1):32-36
299 Boyer F, Mercier C, Bonin A, Le Bras Y, Taberlet P, Coissac E (2016) OBITOOLS: a UNIX-inspired
300 software package for DNA metabarcoding. *Mol Ecol Resour* 16 (1):176-182

301 Calandra I, Labonne G, Mathieu O, Henttonen H, Leveque J, Milloux MJ, Renvoise E, Montuire S,
302 Navarro N (2015) Isotopic partitioning by small mammals in the subnivium. *Ecol Evol* 5:4132-
303 4140

304 Duchesne D, Gauthier G, Berteaux D (2011) Habitat selection, reproduction and predation of
305 wintering lemmings in the Arctic. *Oecologia* 167 (4):967-980

306 Gilg O, Sittler B, Hanski I (2009) Climate change and cyclic predator-prey population dynamics in the
307 high Arctic. *Glob Change Biol* 15 (11):2634-2652

308 Hansson L (1969) Spring Populations of Small Mammals in Central Swedish Lapland in 1964-68. *Oikos*
309 20:431-450

310 Ims RA, Fuglei E (2005) Trophic interaction cycles in tundra ecosystems and the impact of climate
311 change. *BioScience* 55:311-322

312 Ims RA, Jepsen JU, Stien A, Yoccoz NG (2013) Science plan for COAT: Climate Ecological Observatory
313 for Arctic Tundra. Fram Centre Report Series, vol. 1. Fram Centre, Norway

314 Ims RA, Yoccoz NG, Killengreen ST (2011) Determinants of lemming outbreaks. *P Natl Acad Sci USA*
315 108:1970-1974

316 Kalela O, Koponen T, Lind EA, Skarén U, Tast J (1961) Seasonal change of habitat in the Norwegian
317 lemming *Lemmus lemmus* (L.). *Ann Acad Sci Fenn A4* 55

318 Kausrud KL, Myrseth A, Steen H, Vik JO, Ostbye E, Cazelles B, Framstad E, Eikeset AM, Myrseth I,
319 Solhøy T, Stenseth NC (2008) Linking climate change to lemming cycles. *Nature* 456:93-97

320 Koshkina TV (1961) New data on the nutrition of the Norwegian lemming (*Lemmus lemmus*) (in
321 Russian). *Byulletin Moskouskogo Obschestva Ispytalei Prirody Otdel Biologicheskii* 66:15-
322 31

323 Kowalczyk R, Taberlet P, Coissac E, Valentini A, Miquel C, Kaminski T, Wójcik JM (2011) Influence of
324 management practices on large herbivore diet - case of European bison in Białowieża
325 primeval forest (Poland). *Forest Ecol Manag* 261:821-828

326 Moen J, Lundberg PA, Oksanen L (1993) Lemming grazing on snowbed vegetation during a population
327 peak, Northern Norway. *Arctic Alpine Res* 25:130-135

328 Nakahara F, Ando H, Ito H, Murakami A, Morimoto N, Yamasaki M, Takayanagi A, Isagi Y (2015) The
329 applicability of DNA barcoding for dietary analysis of sika deer. *DNA Barcodes* 3:200-206

330 Newmaster SG, Thompson ID, Steeves RAD, Rodgers AR, Fazekas AJ, Maloles JR, McMullin RT, Fryxell
331 JM (2013) Examination of two new technologies to assess the diet of woodland caribou:
332 video recorders attached to collars and DNA barcoding. *Can J Forest Res* 43 (10):897-900.
333 doi:10.1139/cjfr-2013-0108

334 Oksanen T, Oksanen L, Dahlgren J, Olofsson J (2008) Arctic lemmings, *Lemmus* spp. and *Dicrostonyx*
335 spp.: integrating ecological and evolutionary perspectives. *Evol Ecol Res* 10:415-434

336 Olofsson J, Tommervik H, Callaghan TV (2012) Vole and lemming activity observed from space. *Nat*
337 *Clim Change* 2 (12):880-883

338 Pompanon F, Deagle BE, Symondson WOC, Brown DS, Jarman SN, Taberlet P (2012) Who is eating
339 what: diet assessment using next generation sequencing. *Mol Ecol* 21:1931-1950

340 Saetnan ER, Gjershaug JO, Batzli GO (2009) Habitat use and diet composition of Norwegian lemmings
341 and field voles in Central Norway. *J Mammal* 90 (1):183-188

342 Soininen EM (2012) Interactions between small rodents and their food plants in tundra habitats (PhD
343 thesis). University of Tromsø, Tromsø, Norway

344 Soininen EM, Ehrlich D, Lecomte N, Yoccoz NG, Tarroux A, Berteaux D, Gauthier G, Gielly L,
345 Brochmann C, Gussarova G, Ims RA (2014) Sources of variation in small rodent trophic niche:
346 new insights from DNA metabarcoding and stable isotope analysis. *Isot Environ Healt S* 50
347 (3):361-381

348 Soininen EM, Gauthier G, Bilodeau F, Berteaux D, Gielly L, Taberlet P, Gussarova G, Bellemain E,
349 Hassel K, Stenøien HK, Epp L, Schröder-Nielsen A, Brochmann C, Yoccoz NG (2015a) Highly
350 overlapping winter diet in two sympatric lemming species revealed by DNA metabarcoding.
351 *PLoS ONE* 10 (1):e0115335. doi:10.1371/journal.pone.0115335

352 Soininen EM, Gauthier G, Bilodeau F, Berteaux D, Gielly L, Taberlet P, Gussarova G, Bellemain E,
353 Hassel K, Stenøien HK, Epp L, Schröder-Nilsen A, Brochmann C, Yoccoz NG (2015b) Data from:
354 Highly overlapping winter diet in two sympatric lemming species revealed by DNA
355 metabarcoding. Dryad Data Repository. doi:10.5061/dryad.4rr39
356 Soininen EM, Valentini A, Coissac E, Miquel C, Gielly L, Brochmann C, Brysting AK, Sonstebo JH, Ims
357 RA, Yoccoz NG, Taberlet P (2009) Analysing diet of small herbivores: the efficiency of DNA
358 barcoding coupled with high-throughput pyrosequencing for deciphering the composition of
359 complex plant mixtures. *Front Zool* 6:16. doi:10.1186/1742-9994-6-16
360 Soininen EM, Zinger L, Gielly L, Bellemain E, Bråthen KA, Brochmann C, Epp LS, Gussarova G, Hassel K,
361 Henden J-A, Killengreen ST, Rämä T, Stenøien HK, Yoccoz NG, Ims RA (2013) Shedding new
362 light on the diet of Norwegian lemmings: DNA metabarcoding of stomach content. *Polar Biol*
363 36:1069-1076
364 Stoddart DM (1967) A note on the food of the Norway lemming. *J Zool* 151:211-213
365 Sønstebo JH, Gielly L, Brysting A, Elven R, Edwards M, Haile J, Willerslev E, Coissac E, Roiux D, Sannier
366 J, Taberlet P, Brochmann C (2010) Using next-generation sequencing for molecular
367 reconstruction of past Arctic vegetation and climate. *Mol Ecol Resour* 10:1009-1018
368 Taberlet P, Coissac E, Hajibabaei M, Rieseberg LH (2012) Environmental DNA. *Mol Ecol* 21:1789-1793
369 Taberlet P, Coissac E, Pompanon F, Gielly L, Miquel C, Valentini A, Vermet T, Corthier G, Brochmann
370 C, Willerslev E (2007) Power and limitations of the chloroplast *trnL* (UAA) intron for plant
371 DNA barcoding. *Nucleic Acids Res* 35 (3):e14
372 Tast J (1991) Will the Norwegian lemming become endangered if climate becomes warmer? *Arctic*
373 *Alpine Res* 23:53-60
374 Turchin P, Batzli G (2001) Availability of food and the population dynamics of arvicoline rodents.
375 *Ecology* 82 (6):1521-1534
376 Turchin P, Oksanen L, Ekerholm P, Oksanen T, Henttonen H (2000) Are lemmings prey or predators?
377 *Nature* 405:562-565
378 Virtanen R (2000) Effects of grazing on above-ground biomass on a mountain snowbed, NW Finland.
379 *Oikos* 90 (2):295-300
380 Willerslev E, Davison J, Moora M, Zobel M, Coissac E, Edwards ME, Lorenzen ED, Vestergard M,
381 Gussarova G, Haile J, et al. (2014a) Fifty thousand years of Arctic vegetation and megafaunal
382 diet. *Nature* 506 (7486):47-51
383 Willerslev E, Davison J, Moora M, Zobel M, Coissac E, Edwards ME, Lorenzen ED, Vestergård M,
384 Gussarova G, Haile J, et al. (2014b) Data from: Fifty thousand years of arctic vegetation and
385 megafaunal diet. Dryad Data Repository. doi:10.5061/dryad.ph8s5

386

387

388

389

390

391

392

393

394

395

396

397

398

399

400 **Table 1.** Composition of winter diets of Norwegian lemmings (*Lemmus lemmus*) during a population
 401 cycle increase phase (mean proportion of DNA sequences of fecal pellets analyzed primer pairs *g-h*
 402 and *c-h*) in northern Norway (n=50 snowbeds). At each taxonomic level, also the proportions from
 403 lower levels are included. Only taxa with mean proportion >0.01 are included. Column frequency
 404 refers to the number of samples in which the taxa were found. When this differed between family
 405 and genus resolution data, both values are given.
 406

Family	Genus	Species	Mean (\pm SE)	Frequency
Vascular plants				
Salicaceae	<i>Salix</i>		0.21 (\pm 0.03)	45
Poaceae			0.10 (\pm 0.02)	46
	<i>Avenella</i>	<i>Avenella flexuosa</i>	0.04 (\pm 0.01)	40
	<i>Festuca</i>		0.01 (\pm 0.00)	15
Polygonaceae			0.09 (\pm 0.02)	27
	<i>Rumex</i>		0.02 (\pm 0.01)	18
	<i>Bistorta</i>	<i>Bistorta vivipara</i>	0.07 (\pm 0.02)	20
Juncaceae			0.05 (\pm 0.02)	23
	<i>Juncus</i>		0.04 (\pm 0.02)	16
	<i>Luzula</i>		0.01 (\pm 0.01)	11
Asteraceae			0.03 (\pm 0.01)	25
Ericaceae	<i>Empetrum</i>	<i>Empetrum nigrum</i>	0.01 (\pm 0.00)	26/20
Cyperaceae	<i>Carex</i>		0.01 (\pm 0.00)	22/21
Rosaceae			0.01 (\pm 0.00)	12
Ranunculaceae	<i>Ranunculus</i>		0.01 (\pm 0.00)	12
Bryophytes				
Polytrichaceae				
	<i>Polytrichum</i>		0.16 (\pm 0.02)	47
	<i>Polytrichum</i>		0.08 (\pm 0.01)	44
	<i>Psilopilum</i>		0.03 (\pm 0.01)	12
Dicranaceae				
	<i>Dicranum</i>		0.15 (\pm 0.03)	42
	<i>Dicranum</i>		0.14 (\pm 0.03)	40
Rhabdoweisiaceae				
	<i>Kiaeria</i>		0.14 (\pm 0.03)	37
	<i>Kiaeria</i>		0.10 (\pm 0.02)	36
	<i>Kiaeria</i>	<i>Kiaeria glacialis</i>	0.01 (\pm 0.01)	9
Hylocomiaceae				
	<i>Pleurozium</i>	<i>Pleurozium schreberi</i>	0.01 (\pm 0.00)	5/4

407
 408
 409
 410
 411
 412
 413
 414
 415
 416
 417
 418
 419
 420

421 **Figure captions**

422 **Figure 1.** Proportion of plant families in winter diets of Norwegian lemmings (*Lemmus lemmus*).
423 Families are arranged with increasing mean proportion towards the right. Families with mean
424 proportion < 0.01 are omitted from the figure. Families to the left of the vertical line are vascular
425 plants, to the right mosses.

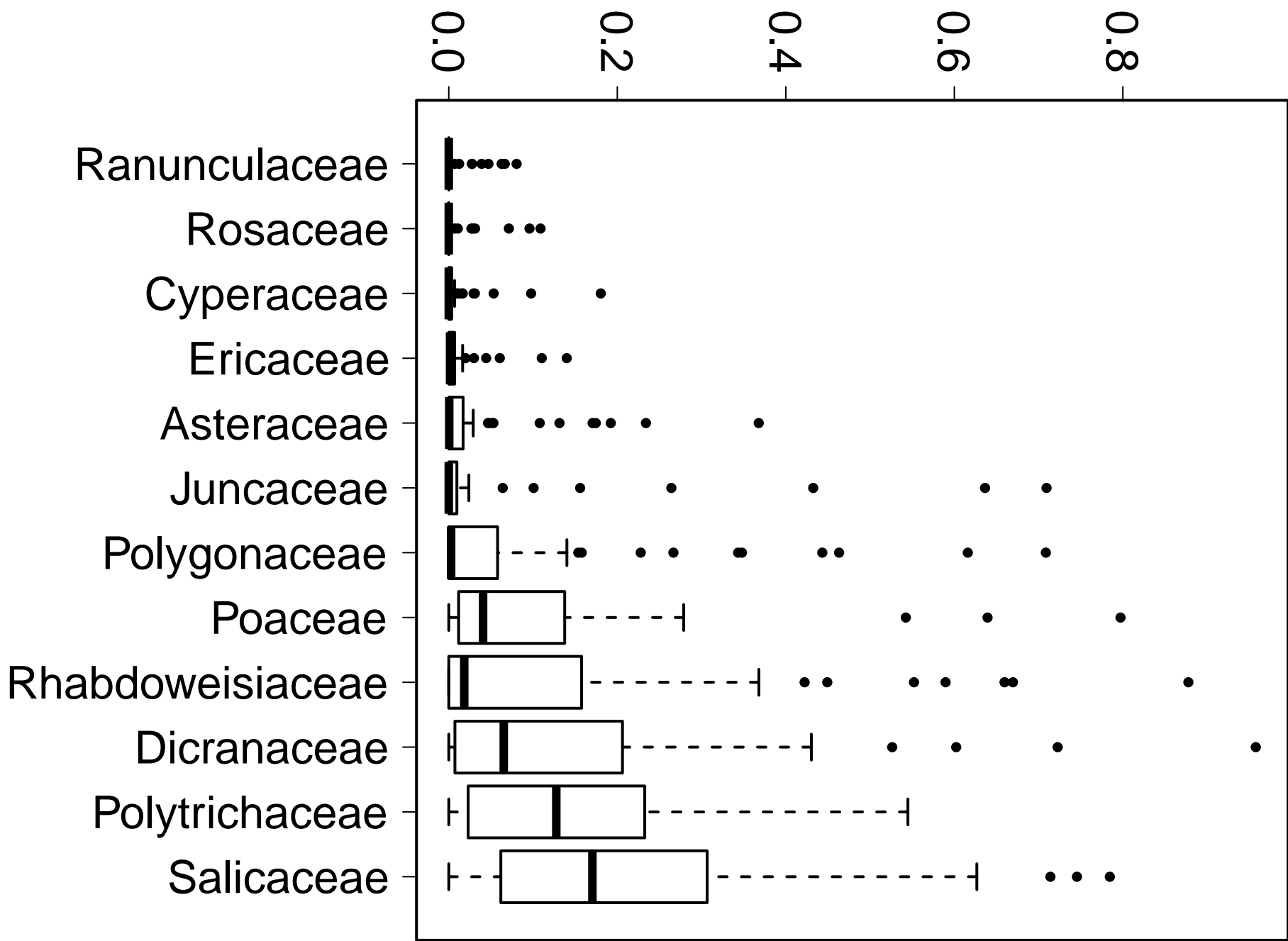
426 **a.** Feces samples from snowbeds (n= 50 snow beds).

427 **b.** Samples from intestines (n=5) and stomachs (n=1) of dead lemmings.

428

429

Proportion of sequences per sample



Proportion of sequences per sample

