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1 **Reproductive success and failure – the role of winter body mass in reproductive**
2 **allocation in Norwegian moose**

3

4 **Jos M. Milner^{1*}, Floris M. van Beest^{1†}, Erling J. Solberg² and Torstein Storaas¹**

5 ¹ *Faculty of Applied Ecology and Agricultural Sciences, Hedmark University College,*

6 *Evenstad, NO-2480 Koppang, Norway*

7 ² *Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway*

8 † current address: *Department of Animal and Poultry Science, College of Agriculture and*

9 *Bioresources, University of Saskatchewan, 51 Campus Drive, Saskatoon, SK, S7N 5E2,*

10 *Canada.*

11

12 * Corresponding author: jos.milner@gmail.com, tel. +44 (0)1339753854

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15

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16 Abstract

17 A life-history strategy that favours somatic growth over reproduction is well known for long-
18 lived iteroparous species, especially in unpredictable environments. Risk-sensitive female
19 reproductive allocation can be achieved by a reduced reproductive effort at conception, or the
20 subsequent adjustment of investment during gestation or lactation in response to unexpected
21 environmental conditions or resource availability. We investigated the relative importance of
22 reduced investment at conception compared with later in the reproductive cycle (i.e. prenatal,
23 perinatal or neonatal mortality) in explaining reproductive failure in two high density
24 populations in southern Norway. We followed 65 multiparous GPS-collared moose (*Alces*
25 *alces*) throughout the reproductive cycle and focused on the role of maternal nutrition during
26 gestation in determining reproductive success using a quasi-experimental approach to
27 manipulate winter forage availability. Pregnancy rates in early winter were normal (≥ 0.8) in
28 all years while spring calving rates ranged from 0.4 to 0.83, with prenatal mortality
29 accounting for most of the difference. Further losses over summer reduced autumn
30 recruitment rates to 0.23-0.69, despite negligible predation. Over-winter mass loss explained
31 variation in both spring calving and autumn recruitment success better than absolute body
32 mass in early or late winter. Although pregnancy was related to body mass in early winter,
33 overall reproductive success was unrelated to pre-winter body condition. We therefore
34 concluded that reproductive success was limited by winter nutritional conditions. However,
35 we could not determine whether the observed reproductive allocation adjustment was a bet-
36 hedging strategy to maximise reproduction without compromising survival or whether
37 females were simply unable to invest more resources in their offspring.

38

39 **Keywords:** deer, life-history, reproductive effort, supplementary feeding, trade-off.

40 **Introduction**

41 In many species there is a good understanding of the factors affecting reproductive
42 success, an important measure of ecological fitness (Clutton-Brock 1988). Body size is a key
43 element, which is typically mediated by intrinsic and extrinsic factors (Sæther 1997). While
44 reproductive failure is expected to be affected by some of the same factors in the opposing
45 direction, the mechanisms causing it and its timing are less well understood, partly due to the
46 inherent difficulties of detecting conception, foetal loss or perinatal mortality in wild
47 populations.

48 Within a given year, reproductive failure may be caused by a life-history strategy of
49 intermittent breeding, with individuals favouring somatic growth over reproduction (Williams
50 1966; Stearns 1992), and so skipping breeding, as a result of the trade-off between current
51 and future reproduction (Clutton-Brock et al. 1983; Stearns 1992; Testa 2004; Bårdsen et al.
52 2010). This is likely to be particularly true of capital breeders, which rely on stored energy
53 for reproduction, rather than income breeders which derive energy for reproduction from
54 short-term acquisition during the breeding season (Stearns 1992; Festa-Bianchet et al. 1998;
55 Stephens et al. 2009). Investment in somatic growth, such as fat reserves, coupled with a
56 conservative reproductive allocation, enhances adult over-winter survival chances. Such a
57 strategy should be expected in long-lived iteroparous species (Williams 1966) in which
58 survival is a key determinant of lifetime reproductive success (Clutton-Brock 1988; Newton
59 1989), and particularly among those living in unpredictable environments where reproductive
60 decisions must be made before resource availability or environmental conditions are known
61 (Bårdsen et al. 2010; Martin and Festa-Bianchet 2010). Among ungulates, most of which are
62 considered to be towards the capital breeding end of the capital-income breeder continuum,
63 reproductive pauses are common (Hamel et al. 2009). Individuals that fail to reach a certain
64 body condition in autumn do not ovulate (Albon et al. 1986; Sand 1996a). The threshold for

65 ovulation varies spatially and temporally (Garel et al. 2009) depending on environmental
66 conditions such as climate (Sand 1996a), density (Albon et al. 1983), winter predictability
67 (Bårdsen et al. 2008) or between-year variation in forage availability (Parker et al. 2009). In
68 addition, it depends on individual phenotypic characteristics such as age and previous
69 reproductive history (Garel et al. 2009; Hamel et al. 2009).

70 Alternatively, reproductive failure may arise due to an adjustment of reproductive effort
71 later in the reproductive cycle (Testa and Adams 1998). While ovulation is commonly used
72 as a measure of fecundity (Markgren 1969; Albon et al. 1983; Langvatn 1992; Sand 1996a),
73 variance in female reproductive success in terms of the number of eggs ovulated is
74 considerably lower than the variance in terms of the number of offspring recruited (Clutton-
75 Brock 1988). Ovulation may occur without fertilisation and subsequent conception, although
76 this should be rare in polygynous species unless the adult sex ratio is extremely skewed
77 (Mysterud et al. 2002). More likely, conception occurs but with the subsequent loss of the
78 foetus (defined here as prenatal mortality), birth of non-viable offspring (i.e. perinatal
79 mortality) or mortality of the offspring within the first month (i.e. neonatal mortality) among
80 poor condition individuals and, particularly, in years with harsh environmental conditions
81 (Kruuk et al. 1999; Milner et al. 2003; Tveraa et al. 2003). Such a strategy of adjustment to
82 reproductive effort may allow a female to hedge its bets in the face of unknown future
83 conditions, conceiving in autumn but then reducing reproductive investment during winter or
84 spring if conditions are worse than expected and resources are needed to ensure over-winter
85 survival in the current or subsequent year (Gaillard et al. 2000; Bårdsen et al. 2008). As the
86 cost of gestation is low relative to the cost of lactation (Clutton-Brock et al. 1989), losing a
87 potential offspring before parturition is comparatively inexpensive. Discrepancies between
88 ovulation rates, pregnancy rates and recruitment rates have been reported at the population
89 level in several cross-sectional studies (e.g. Skogland 1984; Schwartz and Hundertmark

1993; Solberg et al. 2006), with most of the difference usually being attributed to neonatal mortality (Clutton-Brock 1988). Rarely have the extent and circumstances of prenatal mortality been determined using longitudinal studies (but see Testa and Adams 1998). As maternal nutrition affects foetal growth, particularly in late gestation (Skogland 1984; Parker et al. 2009), and maternal malnutrition is a predisposing factor for neonatal mortality in many ungulate populations (Skogland 1984; Clutton-Brock et al. 1987; Keech et al. 2000; Tveraa et al. 2003), we would expect prenatal mortality, as well as perinatal and neonatal mortality, to be related to winter nutrition.

198 A conservative reproductive allocation strategy may therefore manifest itself as a
199 reduction in reproductive effort at conception, during gestation or during lactation. In this
100 study, we firstly quantified failure at successive points of the reproductive cycle of adult
101 female moose (*Alces alces*) to determine the nature of the reproductive allocation strategy.
102 We then quasi-experimentally manipulated winter resource availability by forage
103 supplementation to determine the role of winter body mass in reproductive allocation
104 adjustment. If winter nutrition was limiting, we would expect a positive relationship between
105 the use of supplementary forage and reproductive success. Furthermore, among females of
106 similar pre-winter condition, those experiencing the worst nutritional conditions during
107 winter would lose more weight and be the most likely to adjust their reproductive investment.
108 We expect the probability of reproductive success to be inversely related to winter mass loss
109 in such females. As moose show consistently high adult calving rates across their range
110 (Testa and Adams 1998), we focused on individuals that we expected to face a high cost of
111 reproduction, namely adult females that had calved in the previous year (Testa 2004), living
112 in two high density populations in southern Norway. While both populations had
113 approximately similar densities during the study period (Fig. 1), the more southerly one
114 previously had a higher population density and has shown a significant decline in calving

115 rates over recent decades, in parallel with decreasing autumn slaughter weights (Solberg et al.
116 2006; Grøtan et al. 2009; Wam et al. 2010).

117

118 **Methods**

119 *Study areas*

120 Our study areas were located in Siljan and Skien municipalities, Telemark county in
121 southern Norway, (59° 21' N, 9° 38' E) and in Stor-Elvdal municipality, Hedmark County, in
122 south-eastern Norway (~ 61° N, 11° E; Fig. 1). The Telemark study area (733 km²) ranged in
123 altitude from 20 to 800 m with the forest line at approximately 750 m. It was in the
124 boreonemoral zone, largely covered by commercially managed coniferous forest, dominated
125 by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). The Hedmark study area
126 (1370 km²) ranged in elevation from 250 to 1100 m, with the tree line at approximately 800-
127 900 m. It was dominated by lower productivity, commercially managed boreal forest with
128 pure or mixed stands of Scots pine and Norway spruce. Mixed stands including deciduous
129 species such as birch (*Betula pubescens* Ehrh. and *B. pendula* Roth.), rowan (*Sorbus*
130 *aucuparia* L.), willow (*Salix* spp.) and aspen (*Populus tremula* L.) occurred throughout both
131 areas and sub-alpine birch woodland occurred above the commercial forest line in both areas.

132 The climate differed between the study areas, being colder in the more continental
133 Hedmark area. Average daily minimum and maximum January temperatures during the study
134 period were -2.2 °C and 3.1 °C respectively in Telemark and -15.5 °C and -8.3 °C
135 respectively in Hedmark while average daily minimum and maximum July temperatures were
136 12.2 °C and 21.2 °C respectively in Telemark and 10.6 °C and 20.9 °C respectively in
137 Hedmark. Snow cover lasted from December to April in Hedmark and a somewhat shorter
138 period in Telemark with mean February snow depths of 68 cm and 73 cm respectively.

139 Current wintering densities were estimated at approximately 1.3 moose per km² in both
140 populations (Milner et al. 2012). Red deer (*Cervus elaphus* L.) and roe deer (*Capreolus*
141 *capreolus* L.) occurred in both areas at much lower densities, especially in Hedmark. No
142 resident large carnivore populations occurred in either area during the study period, although
143 wolves (*Canis lupus* L.) were occasionally present in the Hedmark study area (P. Wabakken,
144 *pers. comm.*) meaning that summer calf predation could not be completely ruled out. Human
145 hunting was the single most important cause of moose mortality in both areas.

146

147 *Experimental manipulation*

148 Supplementary winter forage, in the form of ensilaged round bales (~ 800 kg) of mixed
149 graminoids and herbs, was provided as part of longer-term feeding programmes in both study
150 areas (van Beest et al. 2010a; van Beest et al. 2010b; Milner et al. 2012). Our study was
151 carried out in 2007 and 2008 in Telemark and in 2009 and 2010 in Hedmark when an average
152 of 198 t silage / winter and 1538 t / winter respectively was provided. Use of supplementary
153 feeding stations differed between individuals, within and between study areas (see below).
154 However, use of supplementary feed was unrelated to body mass in early winter ($F_{1,66} = 1.70$,
155 $P = 0.197$). During this study we followed the reproductive success of marked individuals
156 from across the spectrum of individual variation in feeding station use.

157

158 *Moose data*

159 Between 16 and 20 adult female moose a year, each accompanied by a calf from the
160 previous year, were immobilised from a helicopter (see Arnemo et al. 2003 for full details) in
161 early winter (January) 2007 - 2010 (van Beest et al. 2010c; Milner et al. 2012). All moose
162 were fitted with GPS collars with a VHF radio transmitter and motion sensor (Tellus Remote

163 GSM, Followit AB, Lindesberg, Sweden), programmed with a 1-h relocation schedule.
164 Where possible, animals were recaptured in late March of the same year. A total of 74 adults
165 were marked of which 9 were excluded from analyses (2 died during winter and 1 prior to
166 calving (due to injury), 1 died during capture in March, 3 collars failed during winter and 2
167 collars were lost). A further 3 individuals lost collars during the summer, reducing the sample
168 size for the summer calf mortality study to 62 individuals. The body mass of 68 individuals
169 was measured using a net and helicopter in January, when body mass of female moose is at
170 its annual peak (Schwartz et al. 1987), and 52 were re-weighed in March. Blood samples
171 were collected on both capture occasions each year and screened for serum progesterone
172 (Sentrallaboratoriet 2011). Pregnancy was diagnosed by rectal palpation of most females in
173 January 2007 but this procedure was not continued in subsequent years for fear it had
174 adversely influenced calving rates (Solberg et al. 2003). We used the proportion of time (i.e.
175 fixes) between January and March captures spent within a 100 m buffer around feeding
176 stations as an index of the use of supplementary feed by each adult female (van Beest et al.
177 2010b).

178 All marked adult females were located and approached carefully on foot in early June
179 to determine the presence of one or more new-born calves. If no calf was observed, the
180 process was repeated at intervals of several days until we were confident of calving status.
181 Field data were compared with expectations based on winter serum progesterone levels and
182 the analysis of GPS data to detect a birth signal by reduced ranging behaviour and increased
183 residence time (Van Moorter et al. unpublished ms; Long et al. 2009). Although progesterone
184 is not a pregnancy-specific indicator, in an earlier study, calving was associated with
185 progesterone levels ≥ 4 nmol/L in 66 out of 79 moose, while 0 out of 8 females with
186 progesterone levels < 4 nmol/L were observed with a calf in June (J.M. Arnemo and M.
187 Heim, unpublished data). We therefore assumed that females with progesterone levels < 4

188 nmol/L were not pregnant (Fig. 2). None of these females showed a positive birth signal in
189 the GPS data (Table 1). Twelve additional females showed no GPS birth signal but had a
190 progesterone level ≥ 4 nmol/L on one or both sampling occasions and of those palpated in
191 2007 all were diagnosed as pregnant. It was therefore assumed that these females were
192 pregnant in early winter but lost their foetus before parturition, although misdiagnosis due to
193 continued oestrus cycling in January was possible among those not palpated. All remaining
194 females ($n = 42$) showed a positive birth signal and, with one exception, had progesterone
195 levels ≥ 4 nmol/L on both sampling occasions (Fig. 2). Summer calf survival was assessed in
196 the autumn by locating all collared females on one or more occasion and checking the
197 lactation status of individuals shot during the hunting season.

198 A subset of shot moose were aged (25 in Telemark [mean age at marking = 7.5 years,
199 range 2.5 - 14.5 years]; 11 in Hedmark [mean age at marking = 8.5 years, range 3.5 – 15.5
200 years]) by counting annuli in the cementum of incisor root tips (Rolandsen et al. 2008). At
201 this latitude in Scandinavia, 99% of adult females can be expected to have reached full adult
202 body mass by the age of 3 years (Sand et al. 1995). Only 3 of 36 aged individuals were less
203 than 3 years old. We found no significant effects of age on body mass within our sample.

204

205 *Statistical analysis*

206 Reproductive success was divided into 3 steps. First, we determined the factors
207 associated with pregnancy in early winter, secondly the factors determining successful spring
208 calving among pregnant females and, thirdly, factors affecting summer calf survival and
209 hence autumn recruitment among females that calved successfully.

210 We used generalised linear models with a logit link function (i.e. logistic regression) to
211 determine factors influencing binomially distributed pregnancy, calving success and autumn

212 recruitment, scored as 0 (not pregnant, no calf observed, or calf died during the summer,
213 respectively) and 1 (pregnant, at least one calf observed or calf/calves survived the summer).
214 Explanatory variables for pregnancy were year (4 level factor) or study area (2 level factor:
215 Hedmark/Telemark), early winter live mass (log transformed), sex of calf in the previous year
216 and their second order interactions. The following additional covariates were also included in
217 the models of spring calving and autumn recruitment: live mass in March, relative winter
218 mass change ($\log[\text{March mass} / \text{January mass}]$), an index of use of supplementary forage
219 (proportion of time spent within 100m of feeding stations) and second order interactions. As
220 calving rates were lower than expected we also assessed the effects of our own handling in
221 terms of rectal palpation (2 level factor: yes vs. no) and number of times captured (2 level
222 factor: 1 vs. 2), although the latter could not be fitted in models that included relative mass
223 change as 2 captures were required to calculate mass change. Relative winter mass change
224 was not corrected for individual differences in the number of days between January and
225 March captures (range 64 – 78 days) as this explained less than 1% of the variation in relative
226 winter mass change and was not statistically significant ($F_{1,50} = 0.208$, $P = 0.651$). Final
227 models for pregnancy, spring calving and autumn recruitment were re-run on the subset of
228 individuals for which age was available.

229 We used likelihood-ratio tests, distributed as χ^2 , to assess whether removing terms
230 affected the model fit or not. Non-significant terms were sequentially dropped (Murtaugh
231 2009).

232

233 **Results**

234 *Pregnancy*

235 Pregnancy rates in early winter averaged 0.83 in Telemark and 0.95 in Hedmark (Table
236 2). These rates did not differ significantly although the probability of pregnancy in Hedmark
237 in 2010 was significantly higher than in other years ($\chi^2 = 5.082$, $df = 65$, $P = 0.024$). This
238 difference in pregnancy probability was largely due to between-year differences in body
239 mass, and was not significant when modelled together with live mass in January. Non-
240 pregnant females had significantly lower live mass in January than other females (mean \pm SE;
241 299.7 ± 16.8 kg and $350.4 \pm SE 4.9$ kg respectively; $F_{1,60} = 10.07$, $P = 0.002$; Fig. 3). Age
242 was not a contributory factor to differences in January body mass between non-pregnant and
243 pregnant females and did not differ between pregnancy classes ($F_{1,33} = 0.029$, $P = 0.865$).
244 Neither the sex of the calf in the previous year ($\chi^2 = 1.504$, $df = 47$, $P = 0.220$) nor age had
245 any effect on the probability of pregnancy ($\chi^2 = 0.126$, $df = 34$, $P = 0.723$) after accounting
246 for January mass. Pregnancy status was unrelated to subsequent use of supplementary winter
247 forage ($\chi^2 = 0.272$, $df = 64$, $P = 0.602$).

248

249 *Calving*

250 Calving rates were considerably lower than pregnancy rates in all years and especially
251 in Telemark (Table 2). Differences were due to both foetal losses during mid to late
252 pregnancy (i.e. prenatal mortality) and, to a lesser extent, perinatal mortality (Table 1).
253 Pregnancy failure was associated with a drop in serum progesterone levels in March
254 compared with January and with significantly lower March progesterone levels compared
255 with in females that went on to give birth ($F_{1,44} = 21.84$, $P < 0.001$; Fig. 2). By contrast,
256 March serum progesterone levels appeared to be particularly high among females
257 experiencing perinatal mortality (Fig. 2), although the sample size was too small to analyse
258 statistically.

259 Calving success among pregnant females was not related to body mass in early winter
260 (Fig. 3). However, as expected if winter conditions were limiting, relative change in body
261 mass over winter significantly affected calving probability which was highest amongst the
262 individuals that lost least weight ($\chi^2 = 5.56$, $df = 44$, $P = 0.018$; Fig. 4a). Neither absolute nor
263 relative winter mass change were related to January body mass ($r = -0.132$; $P = 0.350$ and $r =$
264 -0.010 ; $P = 0.944$ respectively). Nor was relative winter mass change correlated to age ($r = -$
265 0.158 ; $P = 0.452$). Whilst females in Telemark had a greater tendency for pregnancy failure
266 than females in Hedmark (Table 1), this was associated with their greater absolute and
267 relative winter mass loss between January and March (mean \pm SE: 33.8 ± 4.9 kg (10.2 %)
268 mass loss in Telemark compared with 27.7 ± 4.2 kg (7.6 %) in Hedmark). There was
269 therefore no study area effect after accounting for body mass change. Relative winter mass
270 change was a better predictor of calving probability than absolute mass in March, which was
271 only marginally significant ($\chi^2 = 3.709$, $df = 44$, $P = 0.054$; Fig. 3). Calving success was
272 unrelated to age once winter mass change was accounted for ($\chi^2 < 0.001$, $df = 22$, $P = 0.997$).

273 Relative winter mass change was positively correlated with use of supplementary
274 winter forage ($r = 0.543$, $P < 0.001$). Individuals not using feeding stations lost the most mass
275 over winter while those using feeding stations heavily lost significantly less mass, although it
276 appeared that the relationship was non-linear, such that mass change leveled off at high
277 feeding station use (GAM: $F = 10.94$, $edf = 1.84$, $P < 0.001$; Fig. 5). In accordance with
278 expectations if winter conditions were limiting, calving success amongst pregnant females
279 increased with use of supplementary forage ($\chi^2 = 8.720$, $df = 56$, $P = 0.003$).

280 Only 3 females produced twins, precluding a statistical analysis. However, all twin-
281 bearing cows were in Hedmark, and on average they tended to be older (9.0 vs. 7.2 years),
282 heavier (in January 368 vs. 348 kg, but particularly in March 366 vs. 324 kg) and used

283 supplementary forage more (28% vs. 14% of time within 100m of feeding stations) than
284 females producing a singleton.

285 Females that were both rectally palpated to determine pregnancy status (2007 only) and
286 caught twice had spring calving rates of 0.14 ($n=7$). This compared with 0.5 in palpated
287 females caught once ($n=4$) and 0.75 and 0.78 in non-palpated females caught once ($n=9$) and
288 twice ($n=46$) respectively. Palpated females had a marginally lower calving probability after
289 accounting for relative winter mass change than non-palpated females ($\chi^2 = 2.94$, $df = 45$, $P =$
290 0.086). Neither the number of captures nor the interaction between number of captures and
291 palpation significantly affected calving probability.

292

293 *Summer calf survival*

294 Of 38 females that were observed with calves in June, seven lost their calves over
295 summer, 4 in Telemark (1 in 2007 and 3 in 2008) and 3 in Hedmark (all in 2010), giving low
296 autumn calf: cow ratios (Table 2). Although the autumn recruitment rate appeared
297 particularly poor in 2007, this arose from the much lower spring calving rate than in other
298 years, rather than from low summer calf survival.

299 Average summer calf survival increased with use of supplementary feed during winter
300 ($\chi^2 = 4.288$, $df = 37$, $P = 0.038$), being ≥ 0.90 amongst females that spent $\geq 20\%$ of their time
301 near feeding stations compared with 0.68 among those not using supplementary feed.
302 Relative winter mass change significantly affected calf summer survival probability ($\chi^2 =$
303 6.860 , $df = 30$, $P = 0.009$; Fig. 4b), but once this was accounted for there was no additional
304 effect of study area ($\chi^2 = 0.737$, $df = 30$, $P = 0.391$) or age ($\chi^2 = 0.002$, $df = 14$, $P = 0.961$).
305 Among females that gave birth in June, those that successfully reared their calf to autumn
306 tended to be heavier at the end of winter than those that lost their calf over summer (Fig. 3;

307 mean March live mass \pm SE: 330 ± 7.5 kg vs. 304 ± 15.0 kg), although differences were not
308 statistically significant ($F_{1,29} = 1.968$, $P = 0.171$). As with spring calving probability, over-
309 winter mass change was a better predictor of autumn recruitment than absolute mass in late
310 winter.

311

312 *Total calf production*

313 Across all females studied, the number of calves (0, 1 or 2) reared to autumn was
314 significantly related to both relative winter mass change and use of supplementary forage
315 ($F_{1,46} = 15.85$, $P < 0.001$; Fig. 6 and $F_{1,59} = 18.25$, $P < 0.001$ respectively) but unrelated to
316 January mass ($F_{1,58} = 2.50$, $P = 0.12$) or age ($F_{1,21} = 0.030$, $P = 0.864$).

317

318 **Discussion**

319 Our study has clearly demonstrated that while pregnancy was related to pre-winter
320 body condition in two high density Scandinavian moose populations, reproductive failure of
321 pregnant females was related to winter nutritional conditions and body mass change, but
322 unrelated to pre-winter conditions. Pregnancy rates were comparable with expected ovulation
323 rates for mature females in Scandinavia (Sand 1996a; Garel et al. 2009) but we found
324 evidence of losses at multiple points later in the reproductive cycle. Such losses have never
325 been reported for Scandinavian moose populations before but have been observed in a low
326 productivity Alaskan moose population (Testa and Adams 1998). However, in that study,
327 reproductive losses were correlated with autumn body condition (Testa and Adams 1998).
328 Moose calf summer mortality rates in Scandinavian populations with low predation rates vary
329 between years and populations from $< 10\%$ to almost 25% (Sand 1996b; Stubsjøen et al.

2000; Ericsson et al. 2001). Our observations of perinatal and summer calf mortality fall within this range.

Moose demography is generally believed to be a balance between the quantity of winter food and the quality of summer food (Danielsen 2001). Our finding that non-pregnant females had lower early winter body masses than pregnant females agreed with the well established pattern among ungulates of conception being determined primarily by summer conditions and autumn body mass (Albon et al. 1983; Sand 1996a; Garel et al. 2009; Parker et al. 2009). We found high January pregnancy rates in Hedmark (95%) suggesting that summer forage imposed no constraints on reproductive success in that area. Pregnancy rates were lower in Telemark (83%), in common with the lower ovulation rates found in other south-western Norwegian moose populations (Solberg et al. 2006), despite high availability but unknown nutritional quality of preferred summer forage species (van Beest et al. 2010c; Wam et al. 2010; Milner et al. 2012).

Foetal loss and, to a lesser extent, calf mortality were more serious causes of recruitment failure in both populations. Our autumn recruitment rates for Telemark were low compared with those expected from hunter observations of calf: cow ratios (Solberg et al. 2006; Grøtan et al. 2009; Fig. 1b), considering our sample did not include primiparous females (first-time breeders). However, as all individuals in our sample had calved successfully in the previous year, the average recruitment rates over two years were in line with expectations. This suggests a cost of reproduction among some females experiencing over-winter resource limitation, particularly in Telemark and among those not using supplementary feed. Costs of reproduction are well documented in ungulates (Clutton-Brock et al. 1983; Sand 1998; Hamel et al. 2010) with the cost of lactation (borne during the growing season) being substantially greater than the cost of gestation during winter time (Clutton-Brock et al. 1989). However, costs vary with environmental conditions (Clutton-

355 Brock et al. 1983; Clutton-Brock et al. 1996; Hamel et al. 2010) and individual quality
356 (Tavecchia et al. 2005; Hamel et al. 2009). In a low productivity Alaskan moose population,
357 Testa and Adams (1998) showed that while ovulation rates were unaffected by current
358 reproductive status, pregnancy rates were lower and embryos smaller in females that had
359 reared a calf in the previous year than in those that had not. Calving and twinning rates also
360 tended to be lower and pregnancy failure higher in females that had reared a calf the previous
361 year (Testa and Adams 1998). By contrast, previous studies of reproductive costs in
362 Scandinavian moose have shown that current reproductive status did not negatively affect
363 future fecundity (Sæther and Haagenrud 1983; Sand 1998). However, these studies
364 considered future fecundity in terms of the number of eggs ovulated while our study
365 suggested that reproductive failure occurred post ovulation.

366 In general, once pregnancy reaches the second trimester, the foetus is expected to be
367 robust and well protected against nutritional deficiencies, being prioritised over less essential
368 maternal tissues (Markgren 1969). However, re-partitioning of nutrients from the foetus to
369 the mother may occur as a result of harsh winter weather (Simms et al. 2007). This is an area
370 requiring further research, although it is well known that harsh weather conditions can restrict
371 access to forage (Parker et al. 1999; Visscher et al. 2006) and increase maternal costs of
372 locomotion and thermoregulation (Parker et al. 1999). Foetal loss has been inferred or
373 detected in several wild ungulates (Thorne et al. 1976; Skogland 1984; Testa and Adams
374 1998; Kruuk et al. 1999; Keech et al. 2000; Milner et al. 2003; Barnowe-Meyer et al. 2011),
375 peaking in years or populations of high nutritional stress (Skogland 1984; Milner et al. 2003).

376 Winter mass loss is part of the normal annual cycle for temperate ungulates. Individuals
377 experiencing the greatest losses are generally the largest (Parker et al. 2009), and may be
378 those that gained the most mass in summer, were in the best pre-winter condition, had the
379 highest expenditure during gestation (Festa-Bianchet 1998) and/or had the highest fitness

380 (Pelletier et al. 2007). However, in the case of our study, we found no relationship between
381 early winter mass and either absolute or relative winter mass loss. Individuals with low pre-
382 winter condition were not pregnant, while the positive effect on recruitment that we observed
383 among pregnant females in response to our manipulation of winter forage availability
384 suggested a nutritional constraint to reproductive success in both populations, but particularly
385 in Telemark. This was supported by field estimates suggesting a low availability of natural
386 winter forage (Milner et al. 2012) and depletion of preferred forage resources during winter
387 (van Beest et al. 2010c) in that study area. Although observed body mass losses among
388 individuals not using supplementary feed were not extreme (in the order of 10-15%), they
389 occurred over a period of 8-10 weeks. Body mass was likely to continue to decline until the
390 start of the new growing season in early May (Schwartz et al. 1987), giving considerably
391 greater seasonal mass losses and likely increasing the difference in condition between those
392 using and not using supplementary feed.

393 While supplementary feeding is widely practised to improve body weights, trophy sizes
394 and winter population densities (Peek et al. 2002; Putman and Staines 2004; Milner et al.
395 2012), evidence that supplementation increases reproductive rates is equivocal (Putman and
396 Staines 2004; but see Ozoga and Verme 1982; Rodriguez-Hidalgo et al. 2010). However,
397 lactation, offspring growth rates and offspring survival do seem to be improved by winter
398 feeding (Smith et al. 1997; Kozak et al. 1995). In line with this, we found poor nutritional
399 conditions during winter had a carry-over effect, influencing summer calf survival. A number
400 of other studies have shown reduced offspring survival following harsh winters or conditions
401 of food limitation (Skogland 1984; Tveraa et al. 2003; Hamel et al. 2010). This presumably
402 results from low maternal provisioning, either because mothers are unable to provide more,
403 or because females with reduced body reserves at the end of winter may favour allocation of
404 energy in spring to replenishing their own reserves over lactation, hence ensuring their own

405 survival during the following winter (Gaillard et al. 2000; Bårdsen et al. 2008) and passing
406 the cost of reproduction onto their offspring (Martin and Festa-Bianchet 2010).

407 Moose are known to allocate resources to reproduction based on condition at
408 conception (Sæther and Haagenrud 1983; Sand 1996a; Testa and Adams 1998), but our study
409 suggests a further adjustment of reproductive investment in response to winter resource
410 availability. Furthermore, as moose can twin, they have greater flexibility in their
411 reproductive strategy than most other large ungulates, and indeed it is possible that more of
412 our pregnant females may have been carrying twins but subsequently lost one before birth,
413 which we could not detect. With the data available from our study we could not determine
414 whether reproductive allocation adjustment during gestation was a bet-hedging strategy to
415 maximise reproduction without compromising survival or whether females were simply
416 unable to invest more resources in their offspring. However, compared with other ungulate
417 species, moose invest unusually little during gestation, with offspring birth masses only half
418 of that expected for their body size (Gaillard 2007). This may allow moose to postpone the
419 decision to skip breeding from conception, when future winter conditions are unknown, to
420 gestation when winter conditions are apparent. Further research is required to fully
421 understand moose reproductive allocation in relation to winter severity and resource
422 availability.

423 From our study it appears that the main cause of the low observed autumn recruitment
424 rates in both populations was reproductive failure between mid-gestation and weaning. As
425 this was related to winter mass loss, wildlife managers wishing to address the problem should
426 focus on improving winter nutritional conditions by reducing wintering densities and/or
427 enhancing forage availability.

428

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440

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Table 1 Classification of pregnancy and birth status classes based on serum progesterone levels, GPS data and field observations. The proportion (and number) of female moose in Telemark (2007 and 2008) and Hedmark (2009 and 2010) in each class (n = 61) are given

Class	Description	Progest. nmol/L	GPS birth signal	≥ 1 calf obsv. spr	≥ 1 calf obsv. aut	Telemark	Hedmark
Not preg	Not pregnant	< 4	No	No	No	0.19 (5)	0.06 (2)
Prenatal mort	Pregnancy failed or uncertain	≥ 4	No	No	No	0.26 (7)	0.14 (5)
Perinatal mort	Gave birth but no calf observed	≥ 4	Yes	No	No	0.07 (2)	0.06 (2)
Summer mort	Calf born but lost in summer	≥ 4	Yes	Yes	No	0.15 (4)	0.09 (3)
Autumn calf	Calf born & reared to autumn	≥ 4	Yes	Yes	Yes	0.33 (9)	0.65 (22)

Table 2 Pregnancy (n=66), calving (n=64) and autumn recruitment (n=61) rates across all collared adult female moose (sample sizes in parentheses)

	Telemark		Hedmark	
	2007	2008	2009	2010
Pregnancy rate (January)	0.80 (15)	0.86 (14)	0.89 (18)	1.00 (19)
Calving rate (June)	0.40 (15)	0.64 (14)	0.65 (17)	0.83 (18)
Recruitment rate (Autumn)	0.23 (13)	0.43 (14)	0.69 (16)	0.61 (18)

Figure Legends

Fig. 1 Recent trends in a) moose wintering density, b) autumn recruitment rate and c) calf carcass weights in each study population d) within Norway (● Telemark, ○ Hedmark). Winter density was estimated based on harvest size and net population growth rate (Milner et al. 2012). Autumn recruitment rate was the number of calves observed per adult female by hunters for Siljan + part of Skien municipalities (Telemark), and for Stor-Elvdal municipality in Hedmark (National Cervid Register 2011). Average calf carcass weights were from Siljan municipality, Telemark (National Cervid Register 2011) and from Stor-Elvdal Landowners' Association (unpubl. data) in Hedmark

Fig. 2 January and March serum progesterone levels (mean \pm SE) of adult female moose in relation to pregnancy and calving status (see Table 1 for classes). Sample sizes are shown inside bars

Fig. 3 January and March live mass of adult female moose in relation to pregnancy and calving status (see Table 1 for classes). Sample sizes are given along the x-axis. Boxes show the first to third quartile range with median (thick horizontal line). Dotted lines give the minimum and maximum values except for the class Autumn calf in which they show 1.5 x interquartile range, together with outliers (open dots)

Fig. 4 The effect of relative winter mass change on a) probability of successful calving in spring and b) probability of summer calf survival. Solid dots show observed points and solid lines show predicted probabilities, dotted lines show \pm 1 SE

Fig. 5 Relative winter mass change in relation to use of supplementary forage, where relative winter mass change was log (March mass / January mass) and the percentage of time spent within 100m of feeding stations was used as an index of use of supplementary forage. Solid line shows fitted GAM model, dotted lines show \pm 1 SE

Fig. 6 Number of moose calves raised till autumn in relation to relative winter mass change among all females (n=48). Sample sizes are given along the x-axis. Boxes show the first to third quartile range with median (thick horizontal line). Dotted lines give the minimum and maximum values except for the class 0 calves in which they show 1.5 x interquartile range, together with outliers (open dots).

Fig. 1

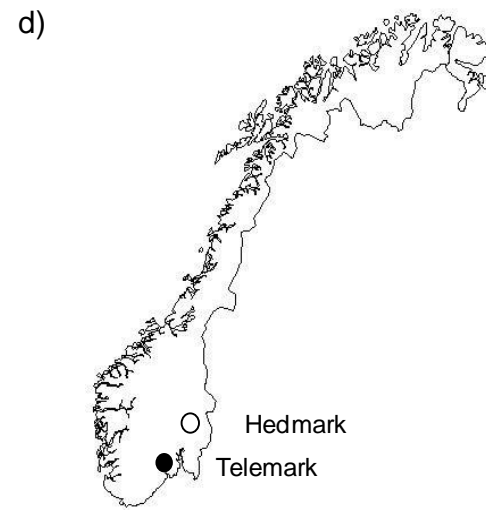
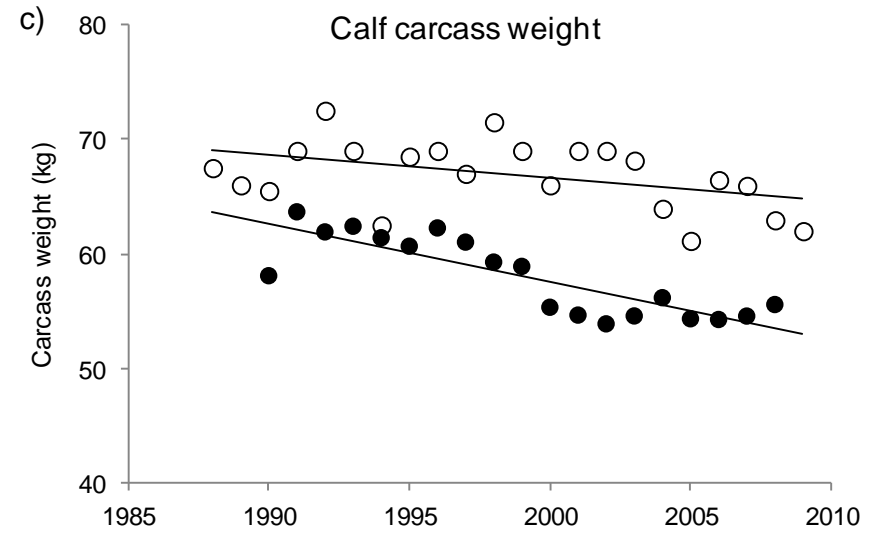
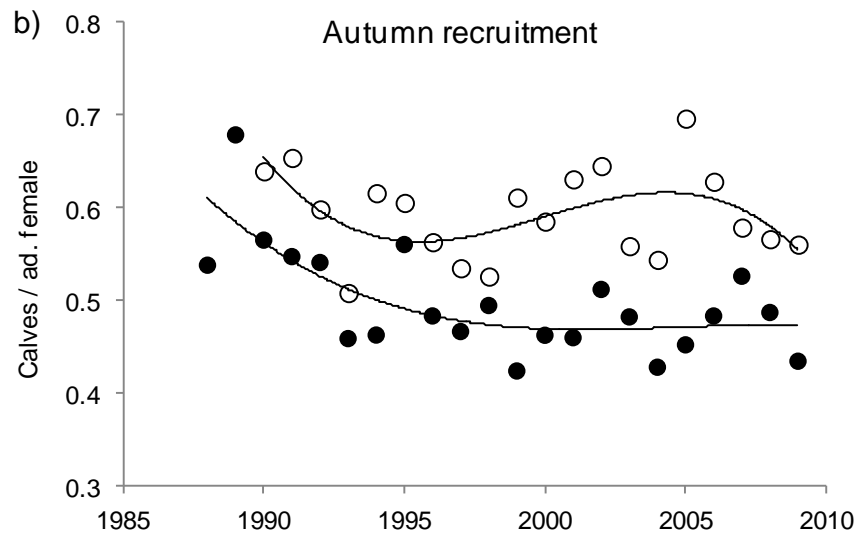
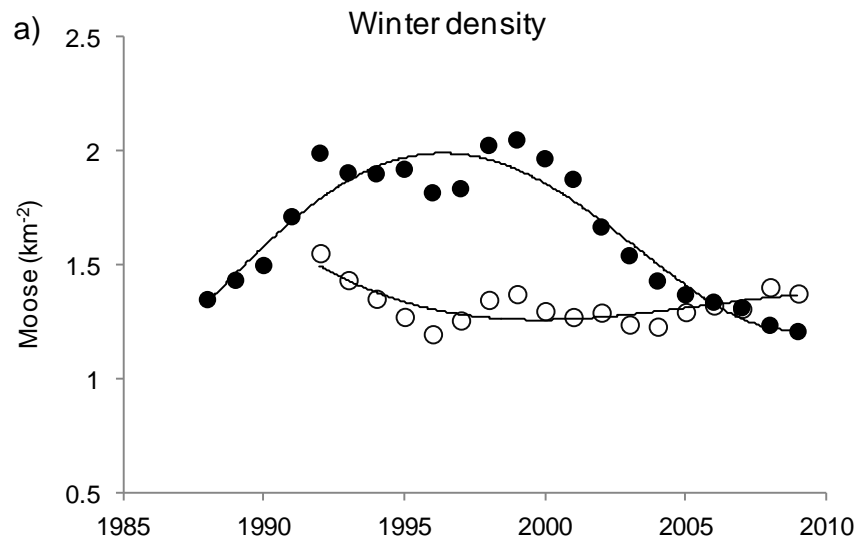


Fig. 2

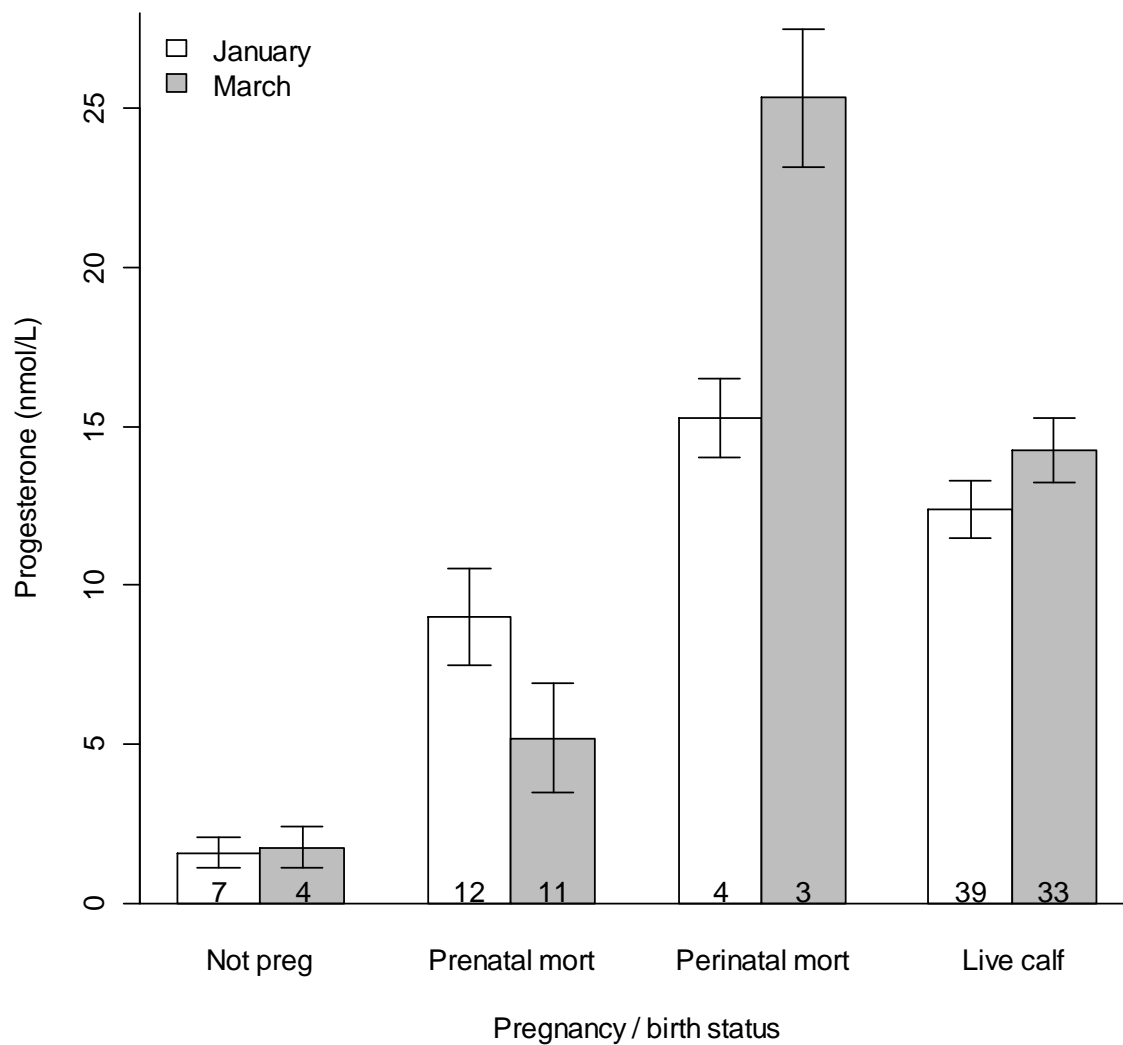


Fig. 3

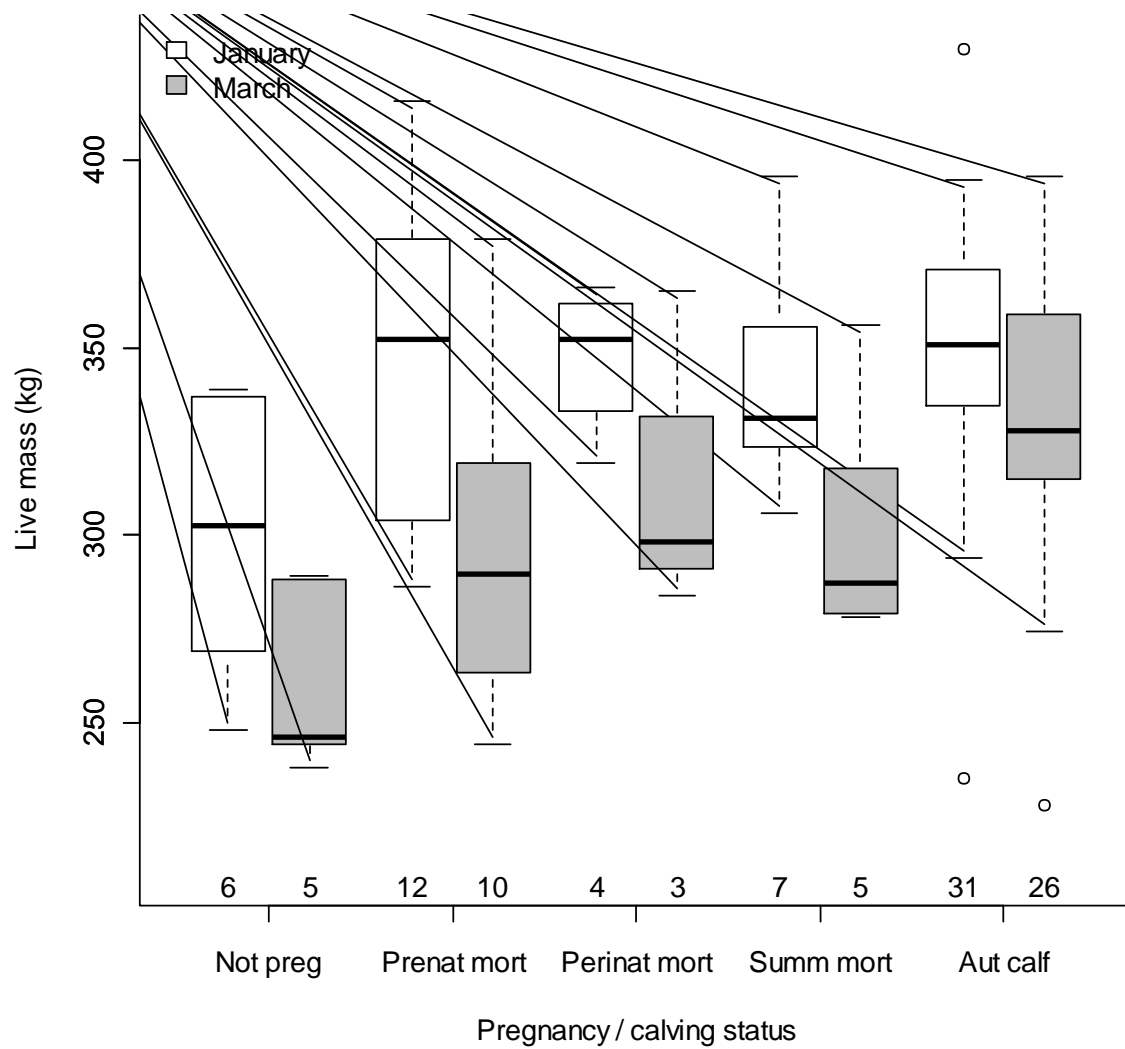


Fig. 4

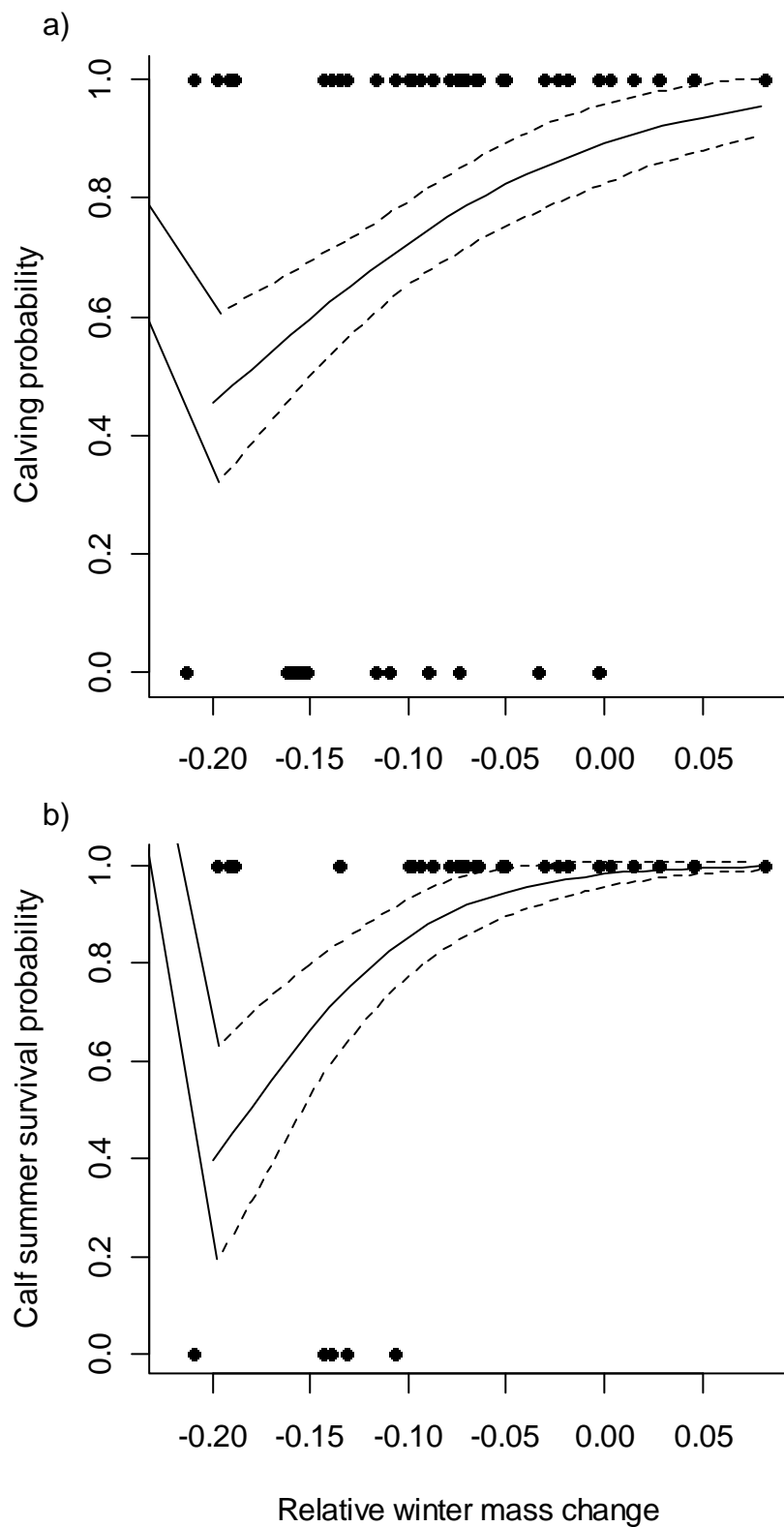


Fig. 5

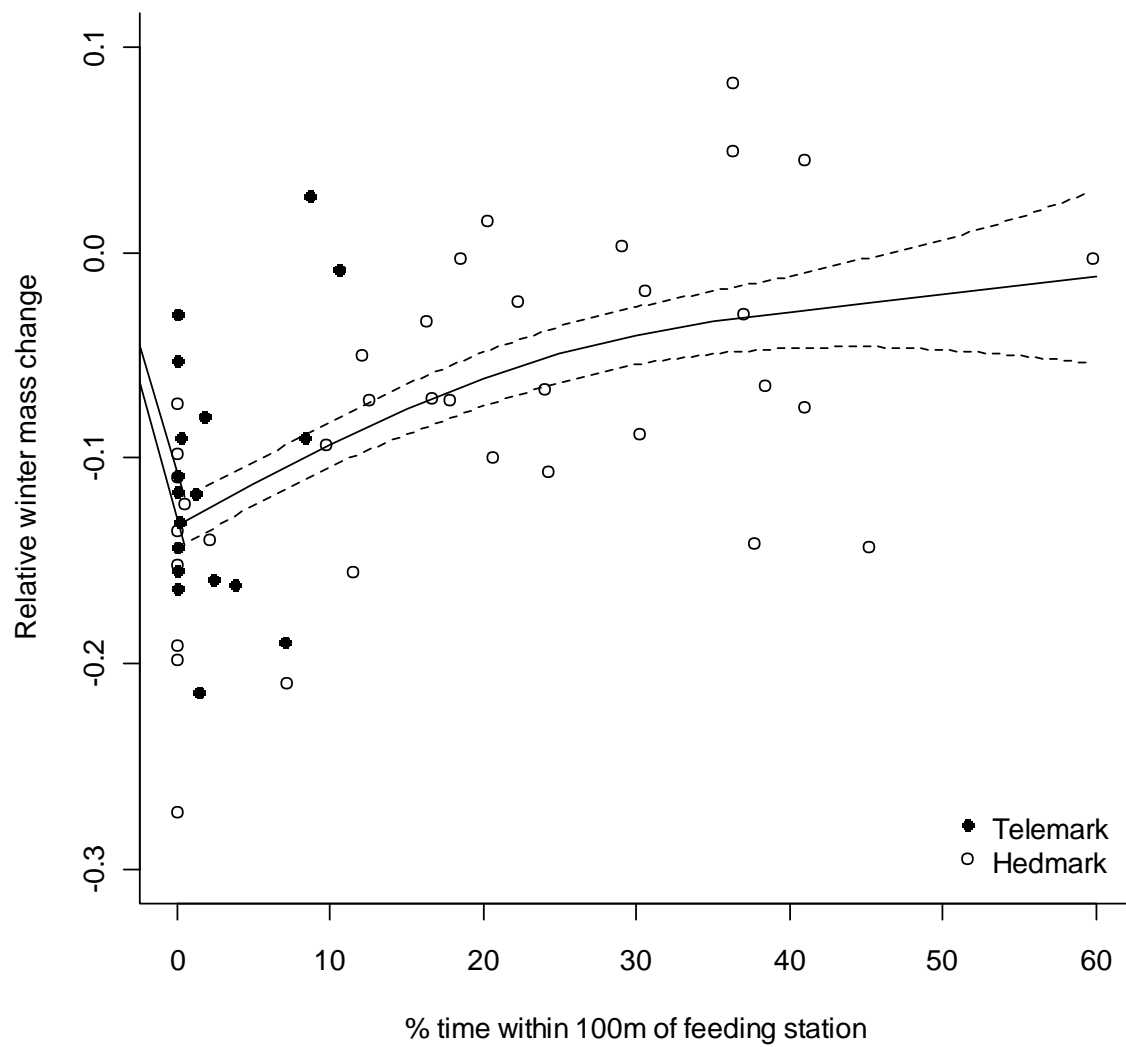


Fig. 6

