Combined effects of long-term feeding, population density and vegetation green-up on reindeer demography

M. BALLESTEROS,† B.-J. BÅRDSEN, P. FAUCHALD, K. LANGELAND, A. STIEN, AND T. TVERAA

Norwegian Institute for Nature Research (NINA), Arctic Ecology Department, Fram Centre, 9296 Tromsø, Norway

Abstract.   Large herbivores living in seasonal environments are generally food-limited through density dependence and climatic factors. This may result in starvation and increased mortality in winter and reduced fecundity the following summer. Variability in winter conditions has the potential to create persistent fitness differences at the cohort- and the individual-level in iteroparous species. Using a 9-year dataset from two herds of individually marked free-ranging reindeer we assessed whether population growth rates, somatic allocation (female body mass) and reproductive allocation (reproductive success and calf body mass) were affected by supplementary feeding, population density and the timing of the onset of spring (i.e., vegetation onset). The supplementary fed population had a higher population growth rate, the females were more likely to reproduce and their calves were heavier than in the control population. Female body mass was negatively related to timing of vegetation green-up in both herds. Since both populations increased in the last decade we found support to our prediction that density-dependence negatively affected our study herds. Indeed, density negatively affected growth rates, female body mass, reproductive success and calf body mass in both populations and, as expected, this effect was more marked in the control herd. We suggest that food supplemented females may, at least partially, be able to compensate for the energetic costs of negative density-dependence following late vegetation green-up while control females may not. Our findings reveal that late winter conditions have an important limiting role in the study area and that density-dependent food limitation in late winter/early summer acts as a main factor affecting our reindeer population.

Key words: carrying capacity; Enhanced Vegetation Index (EVI); Fennoscandia; quasi-experimental manipulation; *Rangifer tarandus tarandus*; ungulate.

† **E-mail:** manuel.ballesteros@nina.no

INTRODUCTION

Population dynamics and life-history traits of large herbivores can be greatly influenced by stochastic environmental variation, density-dependence and vegetation productivity (Gaillard et al. 1998, 2000). Moreover, the influence of these extrinsic factors on reproduction and survival operate mainly through effects on body mass (Jorgenson et al. 1993, Sæther 1997, Gaillard et al. 2003). Body mass is therefore an important phenotypic characteristic with a strong influence on individual fitness (e.g., Sæther 1997, Gaillard et al. 2000).

In temperate environments large herbivores experience large contrasts in climate and food availability between seasons (e.g., Fauchald et al. 2004a, Bårdsen et al. 2008). Body mass has been

found to be affected by both snow cover and food accessibility in winter (Schmidt and Hoi 2002, Solberg et al. 2004) and food quality and quantity in spring/summer (Pettorelli et al. 2005a). Increased competition for food due to increased density can considerably affect body mass further modulating reproduction and neonatal survival (Forchhammer et al. 2001, Pettorelli et al. 2007, Bårdsen et al. 2011). Furthermore, it has been suggested that the negative effects of harsh climatic conditions are exacerbated by population density (Coulson et al. 2001, Bonenfant et al. 2009) and that poor early life development conditions can have long-term consequences on a cohort's life history (Lindström 1999, Lummaa and Clutton-Brock 2002, Solberg et al. 2004).

In reindeer, *Rangifer tarandus tarandus*, Tveraa et al. (2003) have demonstrated that body mass at the end of the winter is of critical importance to survival and reproduction. Besides the fact that late winter conditions can directly affect body mass development and survival, harsh winters can affect reindeer indirectly through modifications of their reproductive allocation the following summer (e.g., Bårdsen et al. 2008). During summer, females with an offspring have to balance the amount of resources spent on their own gain in mass and investment in reproduction, which may affect their survival probability the following winter. The effects of reproductive decisions are observed on the following autumn body mass due to the lost opportunity for individuals with calves to gain mass in summer (Bårdsen et al. 2010). Thus, body mass plays a central role for reindeer life histories and population dynamics. The effects of density and environmental fluctuations on reindeer are mostly food mediated, and supplementary feeding has been used to improve late winter condition (Bårdsen et al. 2008, 2009). In fact, supplementary feeding of ungulates is a common management practice used to buffer the effect of environmental stochasticity on body mass by protecting animals from winter starvation while maintaining high population densities (Fauchald et al. 2004a, Putman and Staines 2004).

Most long-term studies on wild large herbivores are observational and experimental manipulations are largely lacking (Gaillard et al. 1998). Indeed, long-term studies (of marked individuals) combining an experimental manipulation are needed to unravel the relationship between population parameters and variables such as density and environmental factors (Festa-Bianchet et al. 1998, Gaillard et al. 1998). Here we report the long-term population level effects of food supplementation, population density and vegetation green-up on winter body mass and reproductive success of two reindeer populations in northern Norway using data from 2002–2010. In the present study, feeding conditions were manipulated as one population received supplementary feeding during late winter/early summer (treatment) while the other was grazing only on natural pastures (control). We expected supplementary feeding to affect population dynamics by increasing the ecological carrying capacity and the intrinsic population growth rate of the treatment population. Furthermore, we predicted supplementary feeding to result in elevated body masses, improved fecundity and a reduced effect of reindeer density and environmental variation on average calf and female body masses as well as female fecundity. Onset of spring was chosen as our measure of environmental conditions as it has been shown to be a main climate associated predictor in other studies of northern large herbivore populations (Pettorelli et al. 2005a, b, Helle and Kojola 2008, Post and Forchhammer 2008). Accordingly, we predicted that supplementary feeding would reduce the effect of the timing of the onset of spring. Finally, since late gestation and early postnatal life are critical periods for developmental growth, we expected calves to be more affected by environmental variation than adults.

METHODS

Reindeer herding in Norway

The semi-domestic reindeer husbandry in Norway is organized in a system of owners, siidas and districts. Each siida represents a group of owners, and one or several siidas form a district that utilizes an appointed territory defined by law and agreements, both in space and time. To avoid mixing of herds, summer siida pastures in most districts of Finnmark, Northern Norway, are well defined by a system of fences and natural barriers. In addition, the animals are marked with owner specific ear-cuts.

In winter, the siida-herds are separated by continuous herding on a defined share of common pastures. If siida-herds get mixed, the animals are gathered and the herds separated.

Study area and reindeer data

The present study was conducted on two different semi-domestic reindeer populations in Finnmark (Fig. 1). The two herds are members of the same summer siida and from May to October (post-rut), they share an oceanic summer pasture area of ~400 km^2 strictly defined by fences and natural barriers (Fig. 1). This area is dominated by rugged terrain rising from sea-level to the highest peaks at ~1000 m above sea levels (a.s.l). During autumn, they gradually migrate to the continental winter pastures further inland, with rolling terrain, wood clad valleys at ~300 m a.s.l and bare hilltops at ~500 m a.s.l. In December, the animals are gathered and the two populations are separated by herding on the common winter pastures. During winter, both herds share the same pastures (i.e., the same habitat conditions) until they start migrating towards the summer pastures in April.

Since 2000 the population subjected to experimental manipulation has been kept within an enclosure from mid/late April until late May/early June (depending on snow and pasture conditions). In the enclosure each individual of the population was supplementary fed with 800 g per day of reindeer pellets (Poron Herkku Raisio, Finland; calorific value: 9.9 MJ/kg). The control population was not subjected to any foraging manipulation since animals were using natural pastures only (Fig. 1). To secure enough natural pasture during calving, the enclosure (~5 km perimeter) was moved annually within a larger area close to the border of the summer pasture until spring green-up started. Calves from the treatment population were marked in late May/early June and released on the summer pastures where they mixed with the control population. The control herd reached the calving ground inside the summer pasture area in early May, distant from approximately 15 km of the supplemented herd, and offspring were marked during a collective gathering in early July.

Calf predation was monitored closely in the two herds during summers 2002 and 2003 (Fauchald et al. 2004*b*). In the treatment popula-

tion the mortality inside the enclosure during May was 3%. Free ranging in the summer pastures, the manipulated population suffered a loss of 1.5% from June-September while the control population suffered a loss of 3% from July-September. Based on these records and the fact that predators are actively removed by humans in the study area, predation was considered to be low and herders' management and harvesting strategies appeared as the main top-down processes affecting population growth rates within both populations.

A sample of 476 adult females (older than 2 years; treatment: $N = 355$, control: $N = 121$) were included in the study between winter 2002 and winter 2010. Each study animal was individually marked with an ear tag and/or a collar for identification. Presence of a calf was registered at the owners' calf markings by observing if females had a calf on foot in late May early June in the supplementary fed population and in July in the control population. In winter (December), female and calf body mass were registered to the nearest 0.2 kg using an electronic balance (Avery Berkel, Birmingham, UK). However, no calf body mass was recorded in winter 2002. We used the data available from official counts made in the spring each year as an index of reindeer density, i.e., the number of males, females and calves, counted in the spring divided by the size of the summer pasture area (km^2). Official counts of harvested animals on the 31st of March have been used to estimate the ratio between the number of harvested animals and the total number of reindeer for each year.

Vegetation data: spring green-up

Timing of the onset of spring has been shown to affect the performance of ungulates inhabiting highly seasonal environments: earlier green-up, which is related to higher quantity and/or quality of food resources, positively affecting body masses (Pettorelli et al. 2005*a*). Furthermore, spring green-up is an important predictor of environmental conditions in our study area (Bårdsen and Tveraa 2012). Although other climate indices and environmental factors encountered during other seasons might also affect our population, there were not considered in this study.

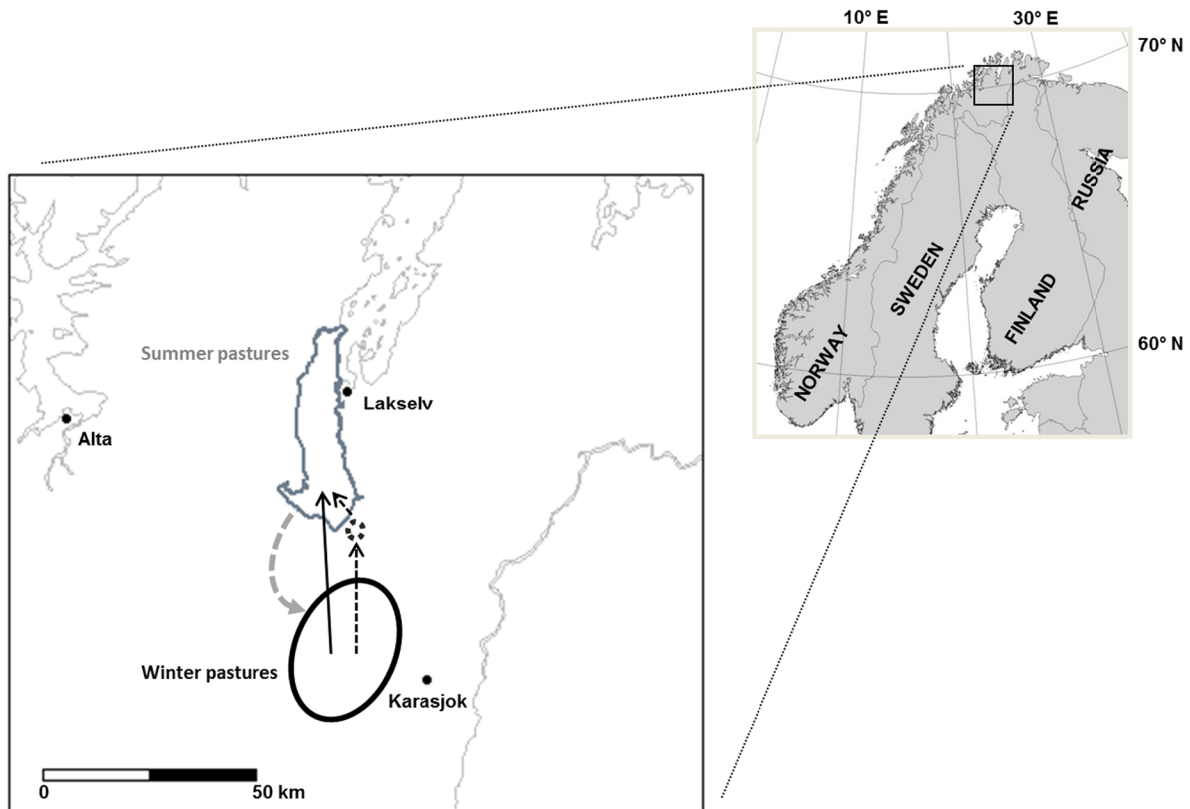We used a double logistic model to describe

Fig. 1. Study area and position of summer (grey area) and winter (black area) pastures for the control and the supplementary fed populations. Thick dotted grey line indicates the common migration route between summer and winter pastures. Thin solid black line (control herd) and thin dotted black lines (supplemented herd) represent the migration route between winter and summer pastures with females from the supplemented herd only giving birth on their way to the summer pastures (black dotted circle).

the Enhanced Vegetation Index (EVI) values from the Moderate Resolution Imaging Spectroradiometer (MODIS) to determine spring onset (see Beck et al. 2006). The EVI was developed to optimize the vegetation signal with improved sensitivity in high biomass regions and improved vegetation monitoring compared to the Normalized Difference Vegetation Index (NDVI, Huete et al. 2002). By taking into account the blue reflectance, the EVI improves vegetation monitoring sensitivity through a reduction in atmosphere influences and a de-coupling of the canopy background (e.g., soil wetness) in, for example, open canopies like tundra and wetlands (Huete et al. 2002). The spatial scale of resolution was ~250 m and we estimated the average of EVI values for each year, from 2002–

2010, using 16-day composites. From these EVI values we computed one EVI index: the onset of vegetation greenness or spring green-up (measured as the number of days since the 1st of January) determined by the spring inflection point value of the double logistic model describing EVI (see Beck et al. 2006).

Statistical analyses

To estimate the intrinsic growth rate (r) and the ecological carrying capacity (K) we used the Ricker-model, which is a discrete generation model suitable for the understanding of population dynamics (Forsyth and Caley 2006). We followed Morris and Doak (2002), using $\log(\lambda_t)$ as the response and population density (D_t) as the only potential predictor in the Ricker model:

$\log(\lambda_t) = r(1 - D_t/K)$, with $\log(\lambda_t) = \log(D_{t+1}) - \log(D_t)$. The model was fitted using nonlinear least-square regressions to the time series data for the control and the manipulated herds separately using the nls function (Pinheiro and Bates 2000). To control for harvesting strategies in the two herds we used the ratio between the number of slaughtered animals and the total number of reindeer, log transformed, in the growth rate analysis.

We used linear models (LM) to analyze the effect of supplementary feeding, population density and spring onset on growth rates and body mass of both the females and their calf. Population, spring onset, density and calf sex were used as potential predictors. In all models, we started by fitting a global model containing all predictors and biologically meaningful inter-actions. From this model, we formed a set of a priori candidate models with reduced number of parameters where all covariates and interactions were removed sequentially (see Appendix: Tables A1, A2 and A3). From this pool of models we selected the most parsimonious model with the lowest Akaike's information criterion (AIC or AICc in the growth rate analysis only) value (Burnham and Anderson 2002; Appendix: Tables A1, A2 and A3). When the difference between two models was ≤2, we retained the simplest model according to the principle of parsimony (Burnham and Anderson 2002).

In order to analyze the effect of the previous explanatory variables on reproductive success, i.e., data on calf presence (1) or absence (0) for each individual female, we used generalized linear models (GLM) with logit link-function and a binomial distribution (i.e., logistic regression model). Similarly to the analyses of body mass we used the same model selection procedure as for the linear models above (see Appendix: Table A4 for details). All statistical analyses were performed in R 2.14.1 (R Development Core Team 2011), and the null hypothesis was rejected at an α-level of 0.05.

RESULTS

Reindeer density increased from 2002 to 2010, notably in the food supplemented group ($R^2 = 0.86$, $F_{2,13} = 39.95$, $P < 0.01$, Fig. 2A). The average body mass of females and calves decreased
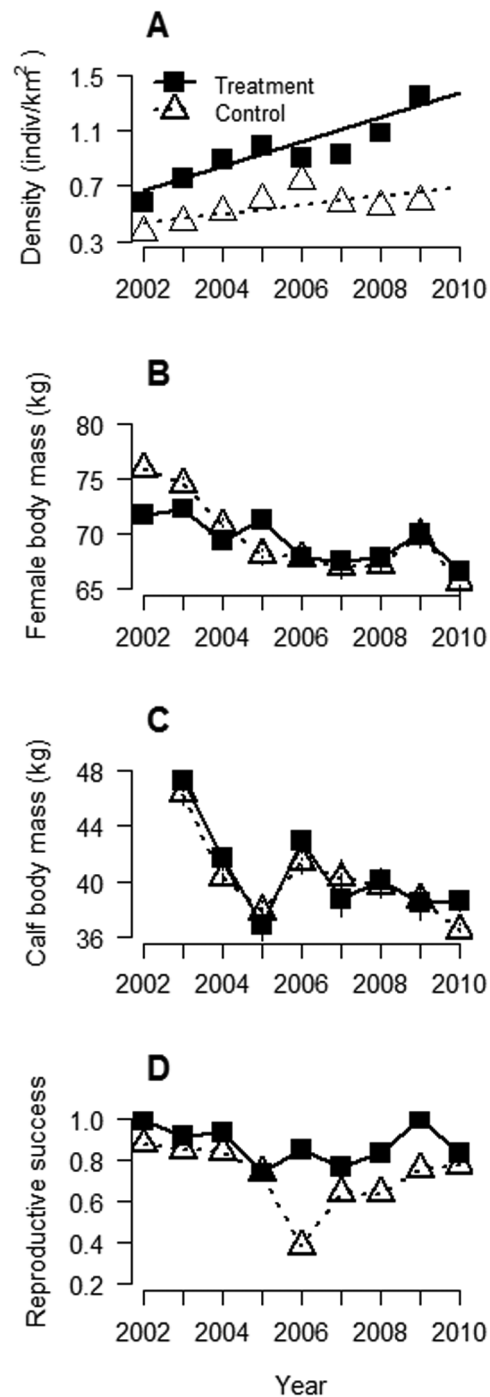

Fig. 2. Reindeer population density (A), female average body mass (B), calf average body mass (C) and the proportion of females reproducing (D), in the two populations (treatment in the form of supplementary feeding: black line and filled squares; and control: dotted line and open triangles).

throughout the period for both herds (Fig. 2B, C). Finally, reproductive success was higher in the supplemented group compared to the control group (Fig. 2D).

Growth rates

The supplementary fed population showed a more positive growth rate compared to the control population (main effect of treatment: 0.33, $P < 0.01$, Table 1A), but the growth rates in both populations were negatively affected by density (main effect of density: -0.77, $P < 0.01$, Table 1A). Neither spring onset nor any of the interactions involving manipulation affected growth rates. Intrinsic growth rate and carrying capacity were higher in the supplemented population compared to the control one ($r = 0.62$ vs. 0.39 and $K = 1.77$ vs. 1.68, Table 2) and as reindeer density increased, the annual growth rate of both populations declined (Fig. 3A). Harvesting rates did not differ between the two populations (ANOVA: $F = 2.36$, $P = 0.14$) and variation in harvest rates did not have a significant effect on the population growth rates in the populations (main effect of harvest: 0.13, $P = 0.32$, Table 1A).

Female body mass

Reindeer belonging to the supplementary fed population were not heavier compared to animals in the control population (main effect of treatment: -0.61 kg, $P = 0.18$, Table 1B). Density had a negative effect on female body mass (main effect of density: -7.29 kg, $P < 0.01$, Table 1B). Moreover, the interaction between the manipulation and density was positive and significant meaning that the supplementary fed population was less affected by negative density-dependence compared to the control one (Treatment $\times$ Density interaction: 4.90 kg, $P = 0.01$, Table 1B and Fig. 3B). Spring onset had a negative effect on female body mass (main effect of spring onset: -0.16 kg, $P < 0.01$, Table 1B) and as the interaction between manipulation and spring onset was not significant (Treatment $\times$ Spring onset interaction: 0.10 kg, $P = 0.09$, Table 1B) the effect of spring onset was similar across the two populations. Nevertheless, the treatment population was less affected by the negative effect of late spring green-ups on female body mass (Table 1B, Fig. 4).

Calf body mass

Calves in the supplementary fed population had a higher body mass than calves belonging to the control group (main effect of treatment: 1.56 kg, $P = 0.02$, Table 1C). Males were significantly larger than females (Calf sex: 2.37 kg, $P < 0.01$, Table 1C). Calf body mass was negatively affected by density in both populations (main effect of density: -12.79 kg, $P < 0.01$, Table 1C and Fig. 3C). The effect of spring onset on calf body mass was not significant. There was no evidence for an influence of supplementary feeding on the effect of spring onset and density on calf body mass.

Reproductive success

The supplementary fed population had a higher reproductive success than the control one (probability of 0.91 vs. 0.85 of having a calf for treated vs. control females keeping all other predictors at their average values, $P < 0.01$; Table 3 and Fig. 3D). Reproductive success was negatively related to reindeer density (main effect of density: -0.27, $P < 0.01$, Table 3). As expected, reproductive success in the supplementary fed population was less affected by negative density-dependence than the control herd (Treatment $\times$ Density interaction: 0.29, $P < 0.01$, Table 3). The estimated effect of spring onset on reproductive success was also negative but non-significant (Table 3).

DISCUSSION

The present quasi-experimental study allowed us to assess the effects of supplementary feeding, onset of spring and density on reindeer fitness-related traits. Our results support the hypothesis that late winter conditions are of critical importance for reindeer and that supplementary winter feeding acts as a buffer against negative environmental conditions and high population density since: (1) supplementary feeding had a positive effect on both population growth rates and carrying capacity, calf body mass and reproductive success; (2) variation in onset of spring had a stronger effect on population growth rates, body masses and reproductive success in the control population than in the supplementary fed population; and (3) the negative effect of density on adult and calf body

Table 1. Parameter estimates from linear models relating (A) growth rate, (B) winter female body mass and (C) winter calf body mass to experimental manipulation (control vs. treatment in the form of supplementary feeding), spring onset, density, harvest and calf sex.

Parameter	Estimate	SE	t	P	R^2	F	df	P
A) Growth rate (λ)					0.62	4.4	4, 11	0.02
(Intercept)	−0.09	0.07	−1.37	0.20				
Manipulation (Treatment)	0.33	0.09	3.56	<0.01				
Spring onset	$6.8 \cdot 10^{-3}$	$4.6 \cdot 10^{-3}$	1.48	0.17				
Density	−0.77	0.20	−3.82	<0.01				
Harvest	0.13	0.12	1.03	0.32				
B) Female body mass (kg)					0.06	12.17	5, 867	0.01
(Intercept)	70.50	0.38	184.55	<0.01				
Manipulation (Treatment)	−0.61	0.46	−1.34	0.18				
Spring onset	−0.16	0.05	−3.27	<0.01				
Density	−7.29	1.78	−4.10	<0.01				
Manip. (Treat.) × Spring onset	0.10	0.06	1.68	0.09				
Manip. (Treat.) × Density	4.90	1.99	2.46	0.01				
C) Calf body mass (kg)					0.22	12.49	6, 239	0.01
(Intercept)	39.63	0.63	62.98	<0.01				
Manipulation (Treatment)	1.56	0.67	2.34	0.02				
Spring onset	$1.8 \cdot 10^{-3}$	0.07	−0.03	0.98				
Density	−12.79	3.22	−3.97	<0.01				
Calf sex (male)	2.37	0.57	4.13	<0.01				
Manip. (Treat.) × Spring onset	−0.11	0.09	−1.28	0.20				
Manip. (Treat.) × Density	4.58	3.85	1.19	0.24				

Note: Spring onset, density and harvest were centered, i.e., subtracting the average, to make the intercept biologically meaningful (it represents the predicted value for the animals belonging to the control group with a value for the average of these three predictors).

mass as well as female reproductive success tended to be more pronounced in the control population.

Effects of supplementary feeding

Supplementary feeding in late winter/early spring did not significantly affect female body mass the subsequent autumn. The latter result could be due to quantitative and/or qualitative (i.e., duration) insufficiencies of the treatment during this period of high energy requirement. Although it would have been informative to conduct the supplementary feeding at other

Table 2. Intrinsic growth rate (r) and ecological carrying capacity (K) estimates for the (A) control (natural pastures) and (B) supplementary fed population using the Ricker model.

Parameters	Estimate	SE	t	P
(A) Control				
R	0.39	0.21	1.84	0.12
K	1.68	0.32	5.22	<0.01
Residual		0.143		
(B) Manipulation				
R	0.62	0.15	4.20	<0.01
K	1.77	0.17	10.32	<0.01
Residual		0.100		

critical time periods (e.g., throughout autumn), the herding practices (i.e., gathering schedules of the animals) did not allow it. Our results are nonetheless in line with previous findings showing no difference in body condition (i.e., body fat) between supplementary fed and free-ranging elk in winter (Bailey 1999). Similarly, in reindeer, positive effects of winter supplementary feeding were reported on spring but not summer or autumn body masses (Bårdsen et al. 2009).

We observed positive effects of supplementary feeding on growth rate, calf body mass and reproductive success. Following the risk sensitive reproductive strategy hypothesized in reindeer (e.g., Bårdsen et al. 2008), we showed that insuring food predictability during late winter and early spring (i.e., prior to breeding) increases, on a long-term basis, the willingness of females to allocate resources into reproduction. Indeed, the experimentally improved food conditions during winter at the peak of nutritional demand in late gestation (Clutton-Brock et al. 1989) might allow females to increase their reproductive allocation in the fetus. As a result, this may lead to heavier newborns as birth mass is related to winter nutrition in many herbivores (Skogland 1983). Namely, Keech et al. (2000) have

Fig. 4. Relationship between average female body mass and spring onset (treatment group in the form of supplementary feeding: black line and filled squares; and control: dotted line and open triangles).
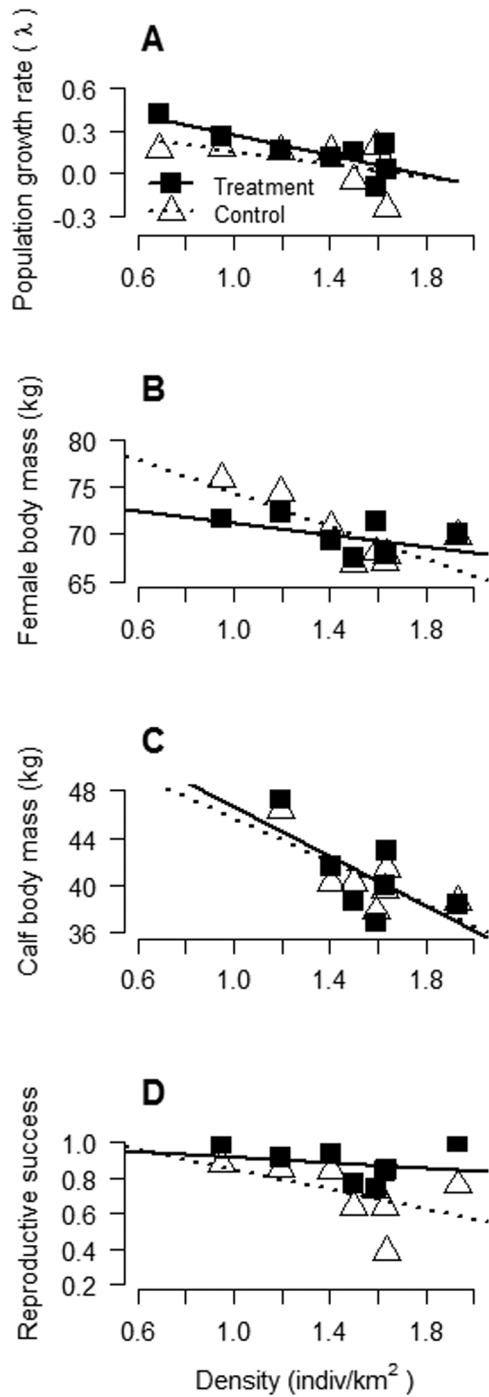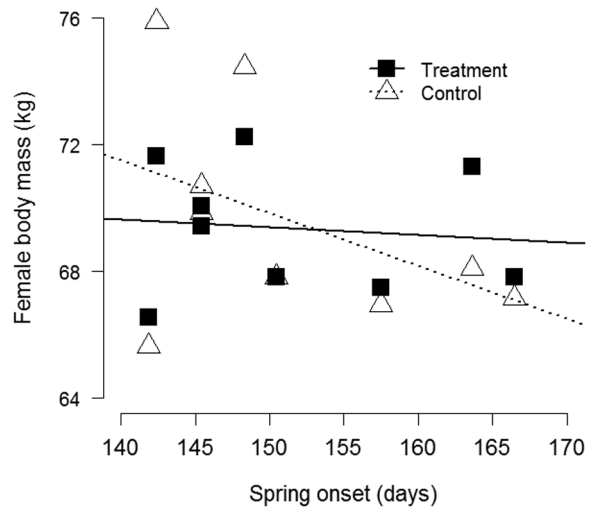

Fig. 3. Annual population growth rate (A), female average body mass (B), calf average body mass (C) and the proportion of females with a calf (D) as a function of density in the two populations (treatment group in the form of supplementary feeding: black line and filled squares; and control: dotted line and open triangles).

shown that birth mass of moose calves was positively correlated to body fat reserves of their mothers in late winter. Individuals born under favorable conditions can in turn reproduce earlier, reach a higher body mass and have a higher reproductive success compared to individuals born under less favorable conditions (Gaillard et al. 2000, Bonenfant et al. 2009). Consequently, calves of mothers receiving supplementary feeding should benefit from greater

Table 3. Generalized linear model relating reproductive success to experimental manipulation (control vs. treatment in the form of supplementary feeding), spring onset and density.

Parameters	Estimate	SE	z	P
(Intercept)	0.75	0.02	33.40	<0.01
Manipulation (Treatment)	0.15	0.03	5.85	<0.01
Spring onset	$-4.2 \ 10^{-3}$	$2.7 \ 10^{-3}$	−1.56	0.12
Density	−0.27	0.10	−2.82	<0.01
Manip. (Treat.) × Spring onset	$-5.5 \ 10^{-3}$	$3.3 \ 10^{-3}$	−1.67	0.10
Manip. (Treat.) × Density	0.29	0.11	2.69	<0.01

Note: Spring onset and density were centered, i.e., subtracting the average, to make the intercept biologically meaningful. Residual deviance = 115.44, df = 972. Null deviance = 126.99, df = 977.

maternal care via for example higher milk quantity and quality (richer fat content), as shown in mule deer (Tollefson et al. 2011) and elk (Cook et al. 2004), allowing them to maximize their growth (e.g., in red deer: Clutton-Brock et al. 1982; elk: Smith et al. 1997) and overwinter survival (e.g., in three species of mountain ungulates: Pettorelli et al. 2007).

Density-dependence

Density-dependent processes were the main factors negatively affecting population growth rate, adult and calf body mass as well as reproductive success. Our results are in accordance with previous findings where density-dependent food-limitation has been suggested as the main mechanism regulating reindeer populations in Fennoscandia (Skogland 1985, Tveraa et al. 2007). The combination of high densities and harsh winter conditions results in episodes of starvation affecting female and calf body condition and/or adult and neonatal survival (e.g., Solberg et al. 2001, Tveraa et al. 2003). Indeed, density-dependence may negatively affect female body mass via an increased food competition in summer and autumn preventing reindeer from acquiring the amount of fat reserves needed for the following winter (see also Bårdsen et al. 2010, Simard et al. 2010, Bårdsen and Tveraa 2012). Moreover, autumn body mass is known to act as an insurance against winter starvation (e.g., Fauchald et al. 2004a). Accordingly, high density may not only impair female body mass but also reproduction.

The food supplemented population tended to compensate, at least partially, the negative effect of density on reproductive success. However, we found a negative effect of density on reproductive success in the control population, which mirrors previous results from other populations (e.g., red deer: Coulson et al. 2000; white-tailed deer: Simard et al. 2010) where increasing density reduced female fecundity. Density-dependence experienced by individuals in early life may have long-term effects on life-histories and on population dynamics in general, through delayed effects on reproduction and reproductive strategies (Pettorelli et al. 2001, Gaillard et al. 2003, Rodriguez-Hidalgo et al. 2010). In fact, females with an offspring have to partition the amount of resources spent investing in their calf, which

compromises their survival the next winter, and investing in their own mass gain, which will enhance their survival probability (Bårdsen et al. 2011). As a result, we can expect a higher proportion of adult females with no calf at the onset of winter, in the control population in particular, allowing them to spare the energetic costs associated with lactation (Clutton-Brock et al. 1989) and to enter winter with higher body fat reserves compared to years with maternal commitments. Calf body mass was more affected by high density compared to adult female body mass. Indeed, juveniles are generally expected to be more vulnerable than adults to high population density, presumably affecting vegetation quantity and quality (Gaillard et al. 2000, Bonenfant et al. 2009), since offspring have to pay a direct cost of density-dependence through body mass loss early in life and an indirect cost through a decrease in maternal reproductive allocation in utero (Forchhammer et al. 2001).

Effects of spring onset

Foraging conditions in spring and early summer are important for variation in demographic traits and population dynamics of northern large herbivores (Herfindal et al. 2006). Indeed, this period of particularly high energy requirement (late gestation and lactation) corresponds to the peak of nutritional demand for female ungulates and will influence future maternal care and body condition (Clutton-Brock et al. 1989, Pettorelli et al. 2006). Here we report that control females increased their summer body mass in years with early onset of spring, whereas supplementary fed females did not respond to spring green-ups. Moreover, the fact that reproductive success was not significantly related to spring onset in both populations indicates that females did not adopt an optimal reproductive strategy to increase reproductive allocation when food was available earlier in the season for certain years. These results mirror findings from previous studies stating that female reindeer have adopted a risk sensitive reproductive allocation strategy (e.g., Bårdsen et al. 2008).

Calf body mass is usually related to weather parameters which are known to influence ungulates through their effects on plant phenology and forage quality (e.g., Langvatn et al. 1996). However, our results show that calf body mass

during winter was not affected by the onset of spring in any of the populations, which contrasts with previous findings on roe deer (Pettorelli et al. 2006) and reindeer (Pettorelli et al. 2005*a*) where plant productivity in the spring had a marked effect on winter body mass for the youngest ones. A possible explanation could be that spring green-up was influenced by density, via habitat deterioration, hiding a potential positive effect of the onset of spring (see also Côté et al. 2004). Furthermore, as reported by Pettorelli et al. (2006) in roe deer, similar responses to spring green-up and density were found for both male and female calves in both herds (lower rank model, not presented) indicating no difference between the sexes.

In conclusion, our results suggest that supplementary feeding acts as a buffer against stochastic variation in environmental conditions since the control population experienced more constraints compared to the fed population. Moreover, we have shown that food supplementation has an effect on the population level since feeding: (1) tends to enhance the carrying capacity of populations; and (2) enhances both direct and indirect effects at the individual-level. Feeding directly affects body mass (calves) and reproductive success, and indirectly affects how density-dependence and vegetation green-up impacts individuals. Body mass of the fed animals was, however, negatively affected by increasing densities. This suggests that supplementary feeding in winter/spring does not compensate for density-dependent effects operating during summer. Therefore, one can expect that continued population growth in response to improved access to food, through e.g., man induced actions like supplementary feeding, will eventually increase vulnerability to density-independent climatic effects the following winter. This finding has important implications both for reindeer owners and for the future management of this socio-economic system.

ACKNOWLEDGMENTS

LITERATURE CITED

Bailey, J. R. 1999. A working model to assist in determining initiation of supplemental feeding of elk and a carrying capacity model for the National Elk Refuge, Jackson, Wyoming. Thesis. University of Wyoming, Laramie, Wyoming, USA.

Bårdsen, B.-J., P. Fauchald, T. Tveraa, K. Langeland, and M. Nieminen. 2009. Experimental evidence of cost of lactation in a low risk environment for a long-lived mammal. Oikos 118:837–852.

Bårdsen, B.-J., P. Fauchald, T. Tveraa, K. Langeland, N. G. Yoccoz, and R. A. Ims. 2008. Experimental evidence of a risk sensitive life history allocation in a long-lived mammal. Ecology 89:829–837.

Bårdsen, B.-J., J.-A. Henden, P. Fauchald, T. Tveraa, and A. Stien. 2011. Plastic reproductive allocation as a buffer against environmental stochasticity—linking life history and population dynamics to climate. Oikos 120:245–257.

Bårdsen, B.-J., and T. Tveraa. 2012. Density-dependence vs. density-independence—linking reproductive allocation to population abundance and vegetation greenness. Journal of Animal Ecology 81:364–376.

Bårdsen, B.-J., T. Tveraa, P. Fauchald, and K. Langeland. 2010. Observational evidence of a risk sensitive reproductive allocation in a long-lived mammal. Oecologia 116:627–639.

Beck, P. S. A., C. Atzberger, K. A. Høgda, B. Johansen, and A. K. Skidmore. 2006. Improved monitoring of vegetation dynamics at very high latitudes: a new method using MODIS NDVI. Remote Sensing of Environment 100:321–334.

Bonenfant, C., J. M. Gaillard, T. Coulson, M. Festa-Bianchet, A. Loison, M. Garel, L. E. Loe, P. Blanchard, N. Pettorelli, N. Owen-Smith, J. Du Toit, and P. Duncan. 2009. Empirical evidence of density-dependence in populations of large herbivores. Advances in Ecological Research 41:313–357.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, New York, USA.

Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1989. Fitness costs of gestation and lactation in wild mammals. Nature 337:260–262.

Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red deer: behavior and ecology of two sexes. University of Chicago Press, Chicago, Illinois, USA.

Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs 165:1–61.

Côté, S. D., T. P. Rooney, J.-P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer

overabundance. Annual Review of Ecology, Evolution, and Systematics 35:113–147.

Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. Science 292:528–531.

Coulson, T., E. J. Milner-Gulland, and T. Clutton-Brock. 2000. The relative roles of density and climatic variation on population dynamics and fecundity rates in three contrasting ungulate species. Proceedings of the Royal Society B 267:1771–1779.

Fauchald, P., T. Tveraa, C. Henaug, and N. G. Yoccoz. 2004a. Adaptive regulation of body reserves in reindeer, *Rangifer tarandus*: a feeding experiment. Oikos 107:583–591.

Fauchald, P., T. Tveraa, N. G. Yoccoz, and R. A. Ims. 2004b. En økologisk bærekraftig reindrift. Hva begrenser naturlig produksjon og høsting?. NINA Fagrapport 76, Tromsø, Norway.

Festa-Bianchet, M., J.-M. Gaillard, and J. T. Jorgenson. 1998. Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. American Naturalist 152:367–379.

Forchhammer, M. C., T. H. Clutton-Brock, J. Lindström, and S. D. Albon. 2001. Climate and population density induce long-term cohort variation in a northern ungulate. Journal of Animal Ecology 70:721–729.

Forsyth, D. M., and P. Caley. 2006. Testing the irruptive paradigm of large-herbivore dynamics. Ecology 87:297–303.

Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58–63.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology, Evolution, and Systematics 31:367–393.

Gaillard, J.-M., A. Loison, C. Toigo, D. Delorme, and G. Van Laere. 2003. Cohort effects and deer population dynamics. Ecoscience 10:412–420.

Helle, T., and I. Kojola. 2008. Demographics in an alpine reindeer herd: effects of density and winter weather. Ecography 31:221–230.

Herfindal, I., B.-E. Sæther, E. J. Solberg, R. Andersen, and K. A. Høgda. 2006. Population characteristics predict responses in moose body mass to temporal variation in the environment. Journal of Animal Ecology 75:1110–1118.

Huete, A., K. Didan, T. Miura, E. P. Rodriguez, X. Gao, and L. G. Ferreira. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. Remote Sensing of Environment 83:195–213.

Jorgenson, J. T., M. Festa-Bianchet, M. Lucherini, and W. D. Wishart. 1993. Effects of body size, population density, and maternal characteristics on age at first reproduction in bighorn ewes. Canadian Journal of Zoology 71:2509–2517.

Keech, M. A., R. T. Bowyer, J. M. Ver Hoef, R. D. Boertje, B. W. Dale, and T. R. Stephenson. 2000. Life-history consequences of maternal condition in Alaskan moose. Journal of Wildlife Management 64:450–462.

Langvatn, R., S. D. Albon, T. Burkey, and T. H. Clutton-Brock. 1996. Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. Journal of Animal Ecology 65:653–670.

Lindström, J. 1999. Early development and fitness in birds and mammals. Trends in Ecology and Evolution 14:343–348.

Lummaa, V., and T. Clutton-Brock. 2002. Early development, survival and reproduction in humans. Trends in Ecology and Evolution 17:141–147.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland, Massachusetts, USA.

Pettorelli, N., J. M. Gaillard, P. Duncan, J. P. Ouellet, and G. Van Laere. 2001. Population density and small-scale variation in habitat quality affect phenotypic quality in roe deer. Oecologia 128:400–405.

Pettorelli, N., J. M. Gaillard, A. Mysterud, P. Duncan, N. C. Stenseth, D. Delorme, G. Van Laere, C. Toigo, and F. Klein. 2006. Using a proxy of plant productivity (NDVI) to find key periods for animal performance: the case of roe deer. Oikos 112:565–572.

Pettorelli, N., A. Mysterud, N. G. Yoccoz, R. Langvatn, and N. C. Stenseth. 2005b. Importance of climatological downscaling and plant phenology for red deer in heterogeneous landscapes. Proceedings of the Royal Society of London B 272:2357–2364.

Pettorelli, N., F. Pelletier, A. von Hardenberg, M. Festa-Bianchet, and S. D. Côte. 2007. Early onset of vegetation growth vs. rapid green-up: impacts on juvenile mountain ungulates. Ecology 88:381–390.

Pettorelli, N., R. B. Weladji, Ø. Holand, A. Mysterud, H. Breie, and N. C. Stenseth. 2005a. The relative role of winter and spring conditions: linking climate and landscape-scale plant phenology to alpine reindeer body mass. Biology Letters 1:24–26.

Pinheiro, J. C., and D. M. Bates. 2000. Mixed-effects models in S and S-PLUS. Springer-Verlag, New York, New York, USA.

Post, E., and M. C. Forchhammer. 2008. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. Philosophical Transactions of the Royal Society B 363:2367–2373.

Putman, R. J., and B. W. Staines. 2004. Supplementary

winter feeding of wild red deer *Cervus elaphus* in Europe and North America: justifications, feeding practice and effectiveness. Mammal Review 34:285–306.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rodriguez-Hidalgo, P., C. Gortazar, F. S. Tortosa, C. Rodriguez-Vigal, Y. Fierro, and J. Vicente. 2010. Effects of density, climate, and supplementary forage on body mass and pregnancy rates of female red deer in Spain. Oecologia 164:389–398.

Sæther, B.-E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. Trends in Ecology and Evolution 12:143–149.

Schmidt, K. T., and H. Hoi. 2002. Supplemental feeding reduces natural selection in juvenile red deer. Ecography 25:265–272.

Simard, M. A., T. Coulson, A. Gingras, and S. D. Côte. 2010. Influence of density and climate on population dynamics of a large herbivore under harsh environmental conditions. Journal of Wildlife Management 74:1671–1685.

Skogland, T. 1983. The effects of density dependent resource limitation on size of wild reindeer. Oecologia 60:156–168.

Skogland, T. 1985. The effects of density-dependent resource limitations on the demography of wild reindeer. Journal of Animal Ecology 54:359–374.

Smith, B. L., R. L. Robbins, and S. H. Anderson. 1997. Early development of supplementally fed, free-ranging elk. Journal of Wildlife Management 61(1):26–38.

Solberg, E. J., P. Jordhøy, O. Strand, R. Aanes, A. Loison, B.-E. Sæther, and J. D.C. Linnell. 2001. Effects of density-dependence and climate on the dynamics of a Svalbard reindeer population. Ecography 24:441–451.

Solberg, E. J., A. Loison, J. M. Gaillard, and M. Heim. 2004. Lasting effects of conditions at birth on moose body mass. Ecography 27:677–687.

Tollefson, T. N., L. A. Shipley, W. L. Myers, and N. Dasgupta. 2011. Forage quality's influence on mule deer fawns. Journal of Wildlife Management 75:919–928.

Tveraa, T., P. Fauchald, C. Henaug, and N. G. Yoccoz. 2003. An examination of a compensatory relationship between food limitation and predation in semi-domestic reindeer. Oecologia 137:370–376.

Tveraa, T., P. Fauchald, N. G. Yoccoz, R. A. Ims, R. Aanes, and K. A. Høgda. 2007. What regulate and limit reindeer populations in Norway? Oikos 116:706–715.

Supplemental Material

Appendix

Table A1. The set of candidate models used in the analyses of growth rate (Table 1A). The best model presents the lowest Akaike's information criterion for small sample size (AICc), a ΔAICc equal to zero and the highest AICc weight (wAICc). The predictors included in the models are marked with an "X".

| | Model | | | | |
Parameter	1	2	3	4	5
Manipulation (Treatment)	X	X	X	X	X
Spring onset	X	X	X	X	X
Density	X	X	X	X	X
Harvest	X	X	X	X	X
Manipulation (Treat.) × Spring onset	X	X	X	X	
Manipulation (Treat.) × Density	X	X	X		
Harvest × Density	X	X			
Spring onset × Density	X				
df	10	9	8	7	6
AICc	25.98	14.40	3.25	−4.04	−9.46
ΔAICc	35.44	23.87	12.72	5.42	**0.00**
wAICc	0.00	0.00	0.00	0.06	**0.94**

Table A2. The set of candidate models used in the analyses of female body mass (Table 1B). The best model presents the lowest Akaike's information criterion (AIC) value, a ΔAIC equal to zero and the highest AIC weight (wAIC). The predictors included in the models are marked with an "X".

	Model		
Parameter	1	2	3
Manipulation (Treatment)	X	X	X
Spring onset	X	X	X
Density	X	X	X
Manipulation (Treat.) × Spring onset	X	X	X
Manipulation (Treat.) × Density	X	X	X
Spring onset × Density	X	X	
Manipulation (Treat.) × Spring onset × Density	X		
df	9	8	7
AIC	5625.61	5623.67	**5621.67**
ΔAIC	3.93	2.00	**0.00**
wAIC	0.09	0.25	**0.66**

Table A3. The set of candidate models used in the analyses of calf body mass (Table 1C). The best model presents the lowest Akaike's information criterion (AIC) value, a ΔAIC equal to zero and the highest AIC weight (wAIC). The predictors included in the models are marked with an "X".

	Model		
Parameter	1	2	3
Manipulation (Treatment)	X	X	X
Spring onset	X	X	X
Density	X	X	X
Calf sex (male)	X	X	X
Manipulation (Treat.) × Spring onset	X	X	X
Manipulation (Treat.) × Density	X	X	X
Spring onset × Density	X	X	
Manipulation (Treat.) × Spring onset × Density	X		
df	10	9	8
AIC	1443.52	1442.93	**1441.20**
ΔAIC	2.32	1.73	**0.00**
wAIC	0.18	0.24	**0.58**

Table A4. The set of candidate models used in the analyses of reproductive success (Table 2). The best model presents the lowest Akaike's information criterion (AIC) value, a ΔAIC equal to zero and the highest AIC weight (wAIC). The predictors included in the models are marked with an "X".

	Model		
Parameter	1	2	3
Manipulation (Treatment)	X	X	X
Spring onset	X	X	X
Density	X	X	X
Manipulation (Treat.) × Spring onset	X	X	X
Manipulation (Treat.) × Density	X	X	X
Spring onset × Density	X	X	
Manipulation (Treat.) × Spring onset × Density	X		
df	9	8	7
AIC	701.01	700.17	**699.66**
ΔAIC	1.35	0.51	**0.00**
wAIC	0.22	0.34	**0.44**