

# Maturation trends in red deer females over 39 years in harvested populations

Atle Mysterud<sup>1,\*</sup>, Nigel G. Yoccoz<sup>2</sup> and Rolf Langvatn<sup>3</sup>

<sup>1</sup>Department of Biology, Centre for Ecological and Evolutionary Synthesis (CEES), University of Oslo, PO Box 1066 Blindern, N-0316 Oslo, Norway; <sup>2</sup>Department of Biology, University of Tromsø, N-9037 Tromsø, Norway; <sup>3</sup>Norwegian Institute for Nature Research, Tungasletta 2, N-7085 Trondheim, Norway

## Summary

1. There is increasing awareness that heavy harvesting can lead to rapid evolution towards earlier sexual maturation. With increased harvest pressure, individuals that begin reproduction at light weights have a greater chance of reproducing at least once compared with individuals that begin reproduction at heavier weights and hence later in life. Although well documented in fish, this has not been empirically tested for harvested populations of mammals in terrestrial ecosystems differing in many environmental aspects.

2. Using data from 3856 female red deer (*Cervus elaphus* L.) from three harvested populations, we tested whether red deer maturity changed from 1967 to 2006. In these populations, density has increased markedly over the time period reducing body mass of deer, which has decreased the proportion of females maturing as yearlings. We therefore assessed trends in maturation as yearlings after controlling for body mass. Long-lived iteroparous ungulate females are expected to have a prudent life history not risking their future survival and reproduction under harsh conditions (e.g. at high density). An alternative to the harvest-induced evolution hypothesis is that maturation is driven mainly by phenotypic responses to increased density, and we predicted later maturation even after controlling for the reduction in body mass.

3. There was a marked trend towards later age at maturation in one out of three populations (after controlling for the effect of reduced body mass due to increased density), while there was no marked trend in the two other populations. The harvesting-induced evolution hypothesis was therefore not supported. However, although the decline was predicted from the prudent life-history tactic hypothesis, the estimate for the density effect was positive rather than negative after accounting for the year trend. Although we did not find support for the harvest-induced earlier maturation hypothesis, evidence was not clearly in favour of the alternative hypothesis.

4. Our study contrasts results from trophy-hunting traditions targeting large males, and points to a potential role of the cultural tradition. Harvesting in Scandinavia mainly aims for meat targeting calves and yearlings (and males), which is less likely to yield an evolutionary response in maturation of females. Our results, although being on a plastic trait and not directly on genetic make-up, are indicative that harvesting-induced evolution is weak on age at maturation in these populations under the current management regime.

**Key-words:** calving rates, *Cervus elaphus*, density dependence, harvesting-induced evolution, life-history tactics, seasonality

## Introduction

Until recently, it was advocated that evolution and ecology were operating at so widely different time-scales that ecologists could ignore evolutionary change. It is now becoming more and more apparent that evolution can take place over

tens of generations or fewer (Carroll *et al.* 2007). This may be particularly acute in systems under heavy selection pressure due to anthropogenic changes. In fisheries, selection for earlier maturation has contributed to collapse of stocks (Jørgensen *et al.* 2007; Kuparainen & Merilä 2007). In terrestrial systems, heavy harvesting of trophy rams led to evolution of small-horned prime-aged males at the scale of decades (Coltman *et al.* 2003; Garel *et al.* 2007). A theoretical evaluation

\*Correspondence author. E-mail: atle.mysterud@bio.uio.no

also demonstrates that heavy (even nonselective) harvesting may affect female life history in red deer (*Cervus elaphus* L.), mainly by selecting for smaller weight at first maturity (Proaktor, Coulson & Milner-Gulland 2007), similar to what is going on in fisheries.

Reduced size and age at maturity have been the main indicators that evolution has taken place in fisheries (maturation reaction norms, *sensu* Heino, Dieckmann & Godø 2002, see discussion in Marshall & Browman 2007; Fenberg & Roy 2008). There has been no similar empirical evaluation for large mammals in terrestrial ecosystems subject to harvesting (Harris, Wall & Allendorf 2002; Allendorf *et al.* 2008), despite the fact that most populations of large herbivores are harvested. Recently, concern for such effects in populations of large mammals has arisen (Gordon, Hester & Festa-Bianchet 2004; Bischof, Mysterud & Swenson 2008). For large mammals, age and body mass are also the main two factors determining maturation (Langvatn *et al.* 2004), and mass at first reproduction is the trait used in a theoretical study of harvesting effects in red deer (Proaktor *et al.* 2007).

Being a plastic trait, age at maturation can also change due to environmental factors. In large mammals, survival of prime-age females is typically high and stable, while offspring survival is lower and more variable (Gaillard, Festa-Bianchet & Yoccoz 1998). This results from the life-history strategies of these long-lived, iteroparous females (Gaillard & Yoccoz 2003). Fitness is mainly determined by living long to increase number of years with (annual) reproduction. Mothers are therefore expected not risking their own future survival and reproduction under harsh conditions, *i.e.* to have a prudent life history. Many deer populations in Europe and North America have increased markedly in density over the last decades despite being harvested. A prudent life history under high density would cause delayed maturation even after controlling for a density-dependent reduction in body mass, if maturation trends are driven mainly by phenotypic responses to increased density (Albon, Mitchell & Staines 1983; Gaillard *et al.* 2000).

Red deer populations in Norway are heavily harvested (Langvatn & Loison 1999). The total harvest has increased from 3586 in 1967 to 29200 in 2006 (Statistics Norway 2007), which is mainly a result of increased density (Milner *et al.* 2006). Such increasing density of many deer populations contrasts with the many declines observed in fish stocks (Costello, Gaines & Lynham 2008). Red deer females in Norway mature either as 1- or 2-year-olds (Langvatn *et al.* 2004). The increased population density has decreased body mass (Mysterud *et al.* 2001), which has led to a lower proportion of females maturing as yearlings (Langvatn *et al.* 2004). In this study, we test ( $H_1$ ) whether an increasingly higher proportion of red deer females are maturing as yearlings for a given body mass (to control for the density effect operating through body mass) over a 39-year period (1967–2006) in three populations in Norway subject to harvesting. Arguably, this would be indicative of evolution in age at maturation. The alternative hypothesis ( $H_2$ ) is that maturation trends for a given body mass has been delayed as

a result of females having a prudent life-history tactic, maturing at a larger size due to increased population density, *i.e.* due to density effects not operating through body mass directly. This opposite pattern would be expected if phenotypic plasticity is the main driver of maturation trends. The hypothesis  $H_2$  would also predict that density is a better predictor of long-term trends than a linear term for 'year', and that the estimated effect of density should be negative.

## Material and methods

### RED DEER DATA

The data come from three populations (P1, P2 and P3) along the south-west coast of Norway: a detailed description of the forested habitat in steep and hilly terrain is provided elsewhere (Mysterud *et al.* 2001). Using cohort analysis (*cf.* Mysterud *et al.* 2007), the harvest pressure on females seemed fairly similar among populations (years 1991/92–2001) being 12.0% in subpopulation Kvinnherad in P1, 14.3% in subpopulation Stryn in P2 and 12.7% in subpopulation Snillfjord in P3.

Data from 3856 yearlings derive from annual autumn harvest (10 September to 15 November) during the years 1967–2006 (Table S1). Hunting is controlled through licenses issued by local wildlife boards in each municipality. Hunters provided uteri and mandibles together with records of date, locality (municipality) and dressed body mass (~58% of live mass and highly correlated with total mass in cervids). Yearlings are reliably aged based on tooth eruption patterns (Loe *et al.* 2004).

Reproductive history of individual females was estimated post-mortem based on inspection of ovaries (Langvatn 1992). Here we analyse variation in ovulation recorded from the occurrence of a primary *corpus luteum* (PCL) (Langvatn *et al.* 2004). Red deer in Norway ovulate for the first time either as yearlings or as 2-year-olds, and this is closely related to autumn body mass as yearlings (Langvatn *et al.* 2004). The autopsy of ovaries is highly reliable when it comes to determining PCL, as has been assessed from captured individuals with a known reproductive history (Langvatn 1992). Red deer have a single offspring per year (no twinning recorded in Norway).

### DATA ON CLIMATE AND DENSITY

As an index for climate, we used the station-based winter index of the North Atlantic Oscillation (NAO). There has been a close to 10-fold increase in harvest over the years 1967–2006 (Statistics Norway 2007). As an index for density, we use the number of harvested animals per area of red deer habitat as approved by the management authorities (Mysterud *et al.* 2001). This index was for this time period shown to reliably reflect density variations when correlated with density estimates obtained from cohort analysis (Mysterud *et al.* 2007).

### STATISTICAL ANALYSES

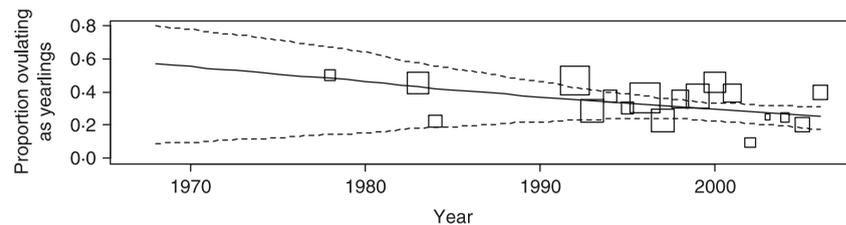
We used a generalized linear mixed model (implemented in the library 'lme4' in R version 2.6.0; R Development Core Team 2007) with a binomial distribution and logit link to analyse variation in the probability of ovulation among yearling red deer in the harvest. We were primarily interested in whether, for a given body mass, the proportion of ovulating has changed or remained stable ('year' scaled to start at year 1967). Previous analysis documented that the effect

**Table 1.** Results from mixed-effects logistic regression models of probability of ovulation of yearling red deer in three populations (P1, P2, and P3) from 1967 to 2006 harvested in Norway. Baseline level for population is P1

Parameter	Estimate	SE	<i>z</i>	<i>P</i>
Fixed effects				
Intercept	-12.9490	4.8236		
Spline(julian date, d.f. = 1)	3.1871	4.1566		
Spline(julian date, d.f. = 2)	15.9377	1.7127		
Spline(julian date, d.f. = 3)	7.5372	2.7418		
Spline[ln(body mass), d.f. = 1]	-5.4768	6.2486		
Spline[ln(body mass), d.f. = 2]	6.1359	3.6091		
Spline[ln(body mass), d.f. = 3]	4.7084	4.3662		
Year (scaled to 1967)	0.4376	0.3198	1.368	0.171
St (density index)	-0.5759	0.6715	-0.858	0.391
Population (P2 vs. P1)	-2.2601	1.0542	-2.144	0.032
Population (P3 vs. P1)	-0.0966	0.8410	-0.115	0.909
Distance from the coast	0.3523	0.2150	1.638	0.101
NAO	-0.0182	0.0415	-0.438	0.662
Year × Population (P2 vs. P1)	-1.2439	0.3877	-3.208	0.001
Year × Population (P3 vs. P1)	-0.6366	0.3431	-1.855	0.064
Density × Population (P2 vs. P1)	2.0636	0.9393	2.197	0.028
Density × Population (P3 vs. P1)	0.4478	0.8122	0.551	0.581
Random term	Variance	SD		
Municipality; <i>n</i> = 58	0.0244	0.1561		

SE = standard error (for fixed terms); SD = standard deviation (for random term). Output is from the best model based on AIC (Table S2).

**Fig. 1.** The probability of ovulating in yearling female red deer for animals with above mean body mass and last half of rut over a 28-year time period (1978–2006) in population P2, Norway. Note that the analysis has used a continuous relationship for body mass and date of harvest. Squares area is directly proportional to square root of sample size.



of body mass and julian date (as deer are harvested over the entire rutting period) on ovulation in yearlings are nonlinear (Langvatn *et al.* 2004), and we used flexible cubic splines for these nonlinear relationships using library ‘splines’ in R. We also controlled for distance to coast, which is a major correlate of habitat and local climate. Model selection was performed using both Akaike information criterion (AIC) and Bayesian information criterion (BIC), the latter being more conservative for large sample sizes. The baseline model contained date (spline, d.f. = 3), body mass (spline, d.f. = 3), distance to the coast, the winter NAO index, and municipality as a random term to account for unbalanced sampling. We then added the terms year, density and their interactions with population. We did this in a global model as well as in population-specific models. We assessed goodness-of-fit of a simpler global model (without the random term) using the sum of squares test (Le Cessie & Van Houwelingen 1991) using the library ‘Design’ in R (Harrell 2001).

## Results

After controlling for a phenotypic trait (body mass) and date of harvest, we found no evidence for earlier maturation during the period 1967 to 2006 as predicted from  $H_1$  (Table 1, Table S2, Fig. 1). Only population P2 showed evidence for a

trend, and this was negative (Table 1). The population-specific models supported this (Table S3). For P1, the baseline model judged from BIC included neither year nor density, while the AIC suggested inclusion of a positive year trend. When restricting analysis to the municipality ‘Kvinnherad’ in P1 with most data, both AIC and BIC pointed to the baseline model and the year effect was negative when estimated, suggesting that the weak positive estimate for year in P1 arose at least partly due to imbalanced sampling among municipalities. In total, this suggested no marked trend in maturation for a given body mass in P1 (Table S3). For P2, the best model judged from both AIC and BIC included the year term, and the estimate was significantly negative (Fig. 1). However, although clearly contrary to  $H_1$ , there was no solid evidence for  $H_2$  either, as the model with density performed less well (Table S3), and since the estimate for density was positive after accounting for the year trend (Table 1). For P3, the best model included density; however, the estimate was far from significant, leaving only weak evidence in favour of  $H_2$ . The NAO index did not affect these long-term trends. There was no evidence for lack of fit using goodness-of-fit statistic in the overall model ( $Z = 1.391$ ,  $P = 0.164$ ).

## Discussion

A number of different factors may explain the absence of evidence that red deer are maturing earlier for a given age and body mass over a 39-year time period as expected from harvesting-induced evolutionary hypothesis ( $H_1$ ). To the contrary, there was a trend of maturing at larger size and later age over time in one of the three populations (Fig. 1). Our alternative hypothesis of a conservative life-history tactic of females ( $H_2$ ) predicted such a pattern. Red deer in Scotland (Albon, *et al.* 1983) and some other species of large herbivores (Gaillard *et al.* 2000) matured at larger size in areas at high density. Since the local density index is highly correlated with the time trend, it is difficult to tease their effects apart (i.e. the year effect may include part of the density effect since density has been increasing over the past 40 years). However, the density estimate was positive rather than negative after adjusting for the year trend, and this pattern seemed evident also when inspecting the data. We can therefore reject  $H_1$ , but evidence was not strongly supporting  $H_2$  either. The exact pattern of selective harvest has not been quantified for these populations, but it is mainly quotas controlling harvest so that further selectivity is reduced. It is also highly unlikely selective harvest could bias sampling for this trait, since we analyse the probability for ovulation relative to body mass, such that size-selective harvesting cannot bias estimates.

It is not straightforward to make inference regarding evolution from plastic traits and reaction norms, rather than directly from genetic make-up (Marshall & Browman 2007). Clearly, although 39 years is a long time, it corresponds only to about seven generations for a large mammal such as red deer (Gaillard *et al.* 2005). It may easily be argued that this is simply too short in an evolutionary perspective. Although the level of heritability of the same trait in different organisms may play a yet unknown role, the generation length is the same as for cod (*Gadus morhua* L.) in marine systems (Pogson *et al.* 2001), where evidence for evolution has arisen (Olsen *et al.* 2004). One can also argue that the decline over time due to yet unknown factors would have been even stronger without evolution, which we cannot fully exclude. However, a more parsimonious interpretation of the trends is that with the current harvesting regime in Scandinavia, the results are indicative that harvesting-induced evolution is not strong towards early maturation, at least in females. A selection for early maturation has in fisheries arisen due to a strong phenotypic-based harvest regime for large-sized individuals, which in many ways are similar to rather extreme trophy-hunting traditions of male ungulates (Coltman *et al.* 2003; Garel *et al.* 2007). However, there are clearly large cultural differences in harvesting both males and females (Milner *et al.* 2006), which will largely affect the selection pressure.

Theoretical modelling suggests that the key factor for these adaptive responses is the increase in mortality due to harvesting before reproduction (Proaktor *et al.* 2007). The benefits of reproducing early increase with increased harvest pressure (Proaktor *et al.* 2007). In Scandinavia, harvesting

is mainly for meat, and there is a reluctance to shoot females with offspring (as shown for moose *Alces alces* L.; Nilssen & Solberg 2006). Breeding early may therefore lower the probability of being shot. Whether this will occur depends on the strength of the trade-off between reproduction and survival of both the mother and the offspring (Proaktor *et al.* 2007). Large mothers give birth to large calves (Loison *et al.* 2004), and during harsh winters offspring body mass in autumn is a key to overwinter survival (Loison, Langvatn & Solberg 1999), so there is clearly a cost to early reproduction if you start reproducing at a light weight. The current red deer population are expanding after a bottleneck in the 1800–1900 likely arising from a combination of overharvesting, predation and severe climate (Ahlén 1965). One might therefore speculate that the red deer populations in Norway have stabilized on a point balancing harvest and natural mortality before this study was initiated in 1967.

From a theoretical viewpoint, the management recommendation for long-lived, iteroparous species would be to target subadult and old females, rather than young adults and prime-age females, if the aim is to avoid evolutionary effects (Proaktor *et al.* 2007). To a large extent, this is the way harvesting occurs in Scandinavia (Langvatn & Loison 1999); the main aim for harvest regulated by the quotas is calves and yearlings, i.e. subadults (in addition to males). In 2006, calves accounted for 23.3% of harvest, yearlings 31.4%, adult males 23.9%, while adult females accounted for 21.4% of the harvest (Statistics Norway 2007, for trends cfr. Milner *et al.* 2006). Aiming for old females is difficult in practice and is likely not carried out to a large extent. Reduced senses (Ericsson & Wallin 2001) and reduced probability of having a calf (Langvatn *et al.* 2004) may nevertheless increase the probability to be shot. However, we have come to a point where harvesting aims are changing due to very high densities in many areas (Gordon *et al.* 2004), moving more towards population control and thus an increased harvesting pressure on adult females. The interpretation of this study is thus not that we can ignore thinking about evolution in these systems. Clearly, the lack of responses today may not last with a new strategy for harvesting unless a cautious approach is taken.

## Acknowledgements

We acknowledge the financial support of the Research Council of Norway to A.M. (YFF), and useful comments to a previous draft by Jean-Michel Gaillard, David Koons and one anonymous referee.

## References

- Ahlén, I. (1965) Studies on the red deer, *Cervus elaphus* L., in Scandinavia. *Swedish Wildlife Research*, **3**, 177–376.
- Albon, S.D., Mitchell, B. & Staines, B.W. (1983) Fertility and body weight in female red deer: a density-dependent relationship. *Journal of Animal Ecology*, **52**, 969–980.
- Allendorf, F.W., England, P.R., Luikart, G., Ritchie, P.A. & Ryman, N. (2008) Genetic effects of harvest on wild animal populations. *Trends in Ecology & Evolution*, **23**, 327–337.
- Bischof, R., Mysterud, A. & Swenson, J.E. (2008) Should hunting mortality mimic the patterns of natural mortality? *Biology Letters*, **4**, 307–310.
- Carroll, S.P., Hendry, A.P., Reznick, D.N. & Fox, C. W. (2007) Evolution on ecological time-scales. *Functional Ecology*, **21**, 387–393.

- Coltman, D.W., O'Donoghue, P., Jorgenson, J.T., Hogg, J.T., Strobeck, C. & Festa-Bianchet, M. (2003) Undesirable evolutionary consequences of trophy harvesting. *Nature*, **426**, 655–658.
- Costello, C., Gaines, S.D. & Lynham, J. (2008) Can catch shares prevent fisheries collapse? *Science*, **321**, 1678–1681.
- Ericsson, G. & Wallin, K. (2001) Age-specific moose (*Alces alces*) mortality in a predator-free environment: evidence for senescence in females. *Ecoscience*, **8**, 157–163.
- Fenberg, P.B. & Roy, K. (2008) Ecological and evolutionary consequences of size-selective harvesting: how much do we know? *Molecular Ecology*, **17**, 209–220.
- Gaillard, J.-M. & Yoccoz, N.G. (2003) Temporal variation in survival of mammals: a case of environmental canalization? *Ecology*, **84**, 3294–3306.
- Gaillard, J.-M., Festa-Bianchet, M. & Yoccoz, N.G. (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology & Evolution*, **13**, 58–63.
- Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toigo, C. (2000) Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, **31**, 367–393.
- Gaillard, J.-M., Yoccoz, N.G., Lebreton, J.-D., Bonenfant, C., Devillard, S., Loison, A., Pontier, D. & Allainé, D. (2005) Generation time: a reliable metric to measure life-history variation among mammalian populations. *American Naturalist*, **166**, 119–123.
- Garel, M., Cugnasse, J.-M., Maillard, D., Gaillard, J.-M., Hewison, A.J.M. & Dubray, D. (2007) Selective harvesting and habitat loss produce long-term life history changes in a mouflon population. *Ecological Applications*, **17**, 1607–1618.
- Gordon, I.J., Hester, A.J. & Festa-Bianchet, M. (2004) The management of wild large herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology*, **41**, 1021–1031.
- Harrell, F.E. (2001) *Regression Modelling Strategies with Applications to Linear Models, Logistic Regression, and Survival Analysis*. Springer, New York.
- Harris, R.B., Wall, W.A. & Allendorf, F.W. (2002) Genetic consequences of hunting: what do we know and what should we do? *Wildlife Society Bulletin*, **30**, 634–644.
- Heino, M., Dieckmann, U. & Godø, O.R. (2002) Measuring probabilistic reaction norms for age and size at maturation. *Evolution*, **56**, 669–678.
- Jørgensen, C., Enberg, K., Dunlop, E.S., Arlinghaus, R., Boukal, D.S., Brander, K., Ernande, B., Gårdmark, A., Johnston, F., Matsumura, S., Pardoe, H., Raab, K., Silva, A., Vainikka, A., Dieckmann, U., Heino, M. & Rijnsdorp, A. D. (2007) Managing evolving fish stocks. *Science*, **318**, 1247–1248.
- Kuparainen, A. & Merilä, J. (2007) Detecting and managing fisheries-induced evolution. *Trends in Ecology & Evolution*, **22**, 652–659.
- Langvatn, R. (1992) Analysis of ovaries in studies of reproduction in red deer (*Cervus elaphus* L.): Application and limitations. *Rangifer*, **12**, 67–91.
- Langvatn, R. & Loison, A. (1999) Consequences of harvesting on age structure, sex ratio and population dynamics of red deer *Cervus elaphus* in central Norway. *Wildlife Biology*, **5**, 213–223.
- Langvatn, R., Mysterud, A., Stenseth, N.C. & Yoccoz, N.G. (2004) Timing and synchrony of ovulation in red deer constrained by short northern summers. *American Naturalist*, **163**, 763–772.
- Le Cessie, S. & Van Houwelingen, J.C. (1991) A goodness-of-fit test for binary regression models, based on smoothing methods. *Biometrics*, **47**, 1267–1282.
- Loe, L.E., Meisingset, E.L., Mysterud, A., Langvatn, R. & Stenseth, N.C. (2004) Phenotypic and environmental correlates of tooth eruption in red deer (*Cervus elaphus*). *Journal of Zoology*, **262**, 83–89.
- Loison, A., Langvatn, R. & Solberg, E.J. (1999) Body mass and winter mortality in red deer calves: disentangling sex and climate effects. *Ecography*, **22**, 20–30.
- Loison, A., Solberg, E.J., Yoccoz, N.G. & Langvatn, R. (2004) Sex differences in the interplay of cohort and mother quality on the body mass of red deer calves. *Ecology*, **85**, 1992–2002.
- Marshall, C.T. & Browman, H.I. (2007) Disentangling the causes of maturation trends in exploited fish populations. *Marine Ecology Progress Series*, **335**, 249–251.
- Milner, J.M., Bonenfant, C., Mysterud, A., Gaillard, J.-M., Csányi, S. & Stenseth, N.C. (2006) Temporal and spatial development of red deer harvesting in Europe - biological and cultural factors. *Journal of Applied Ecology*, **43**, 721–734.
- Mysterud, A., Yoccoz, N.G., Stenseth, N.C. & Langvatn, R. (2001) The effects of age, sex and density on body weight of Norwegian red deer: evidence of density-dependent senescence. *Proceedings of the Royal Society B: Biological Sciences*, **268**, 911–919.
- Mysterud, A., Meisingset, E.L., Veiberg, V., Langvatn, R., Solberg, E.J., Loe, L.E. & Stenseth, N.C. (2007) Monitoring population size of red deer: an evaluation of two types of census data from Norway. *Wildlife Biology*, **13**, 285–298.
- Nilsen, E.B. & Solberg, E.J. (2006) Patterns of hunting mortality in Norwegian moose (*Alces alces*) populations. *European Journal of Wildlife Research*, **52**, 153–163.
- Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Ernande, B. & Dieckmann, U. (2004) Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature*, **428**, 932–935.
- Pogson, G.H., Taggart, C.T., Mesa, K.A. & Boutillier, R.G. (2001) Isolation by distance in the atlantic cod, *Gadus morhua*, at large and small geographic scales. *Evolution*, **55**, 131–146.
- Proaktor, G., Coulson, T. & Milner-Gulland, E.J. (2007) Evolutionary responses to harvesting in ungulates. *Journal of Animal Ecology*, **76**, 669–678.
- R Development Core Team (2007) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Statistics Norway (2007) *Official Hunting Statistics of Norway*. Statistics Norway, Oslo and Kongsvinger, Norway.

Received 28 April 2008; accepted 4 December 2008

Handling Editor: Tim Benton

## Supporting information

Additional supporting information may be found in the online version of this article:

**Table S1.** An overview of the sample size of yearling females by year with known ovulation status from three populations in Norway.

**Table S2.** Model selection for all three populations, including all years or restricting to data from 1990 onwards.

**Table S3.** Model selection for each of the three populations separate, including all years or restricting to data from 1990 onwards.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.