

# Temporal quota corrections based on timing of harvest in a small game species

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**Abstract** Theoretical models have shown that the effect of removing a given proportion of the population can be profoundly different if the harvest takes place late in the season compared to early. We explore the effect of these differences using theoretical models based on the concept of demographic value (DV), and empirical data on seasonal patterns of natural mortality risk in two contrasting populations of willow ptarmigan in Norway. Based on the theoretical models we found that changes in the timing of harvest have a much stronger effect in populations with relatively low annual survival compared to populations characterized by longevity typical for species with slow life histories. Also, the timing of harvest is more influential in cases with constant mortality hazards compared to a situation with density dependent natural mortality. Empirical data from our two study populations of willow ptarmigan showed large deviations from the theoretical predictions of models with both constant and density dependent mortality hazards. There were also large differences in both the temporal pattern and magnitude of annual survival between the two ptarmigan populations (54% vs 26% annual survival). Site differences illustrate the importance of knowledge of both the magnitude and temporal pattern of natural mortality hazard to be able to correctly predict the effect of changing the timing of harvest in a population. In the two ptarmigan populations we show how harvest quotas can be adjusted in accordance to the empirical estimates of natural mortality risk, and how this determines the effects of shifting from harvesting early to late in the annual cycle.

**Keywords** Demographic value; Hazard rate; Hunting quota; *Lagopus lagopus*; Seasonal mortality; Willow ptarmigan

## Introduction

Timing of harvest, length of hunting seasons and hunting bag quotas are frequently used regulation mechanisms in management of a wide range of hunted species (Sinclair et al. 2006; Taylor and Dunstone 1996). However, many game-, predator- and pest species worldwide are subject to harvest seasons of considerable length with few quota regulations, and in some cases even with unlimited harvest all year around (e.g. Parkes and Murphy 2003).

Theoretical models exploring how the timing of harvest modifies the population dynamic consequences of harvesting have shown that the effect of removing a given proportion of the population can be profoundly different if the harvest takes place late in the season compared to early. The effect of removing individuals will vary depending on at which point in the annual cycle the harvest occurs and the strength of seasonal density dependence in the population (Boyce et al. 1999; Kokko and Lindstrom 1998; Ratikainen et al. 2008; Xu et al. 2005). A compensatory population response to the decreased number of individuals after hunting is only possible if the remaining individuals in the population respond with increased survival, earlier age at maturity and/or increased reproductive output (Boyce et al. 1999; Burnham and Anderson 1984; Ellison 1991; Roseberry 1979). Typically, such responses are considered to come across due to density dependent changes in vital rates (see Lebreton 2006 for a discussion). Generally, it is shown that a harvest late in the season has a larger impact on the population trajectory, compared to an early season harvest (Kokko and Lindstrom 1998). Hence, harvesting close to the reproductive season in the spring (cf. spring harvest to control greater snow geese *Anser caerulescens atlantica* in

North America, Calvert and Gauthier 2005) will often have much stronger effect on the population dynamics than if the same number of individuals were taken at an earlier stage in the annual population cycle, e.g. at the beginning of autumn (Jonzen and Lundberg 1999; Kokko 2001; Kokko et al. 1998). The exception to this will be when strong density dependence acts in the breeding season, resulting in some adults becoming floaters (surplus birds) (Watson and Moss 2008). In such a case, the timing of harvest might be of less importance (Boyce et al. 1999) as long as it does not interfere with the breeding behavior.

In most harvest models the temporal patterns in natural mortality are modeled assuming a constant hazard over the year, or as a time varying density dependent hazard. However, a steadily growing body of empirical studies shows that the risk of natural mortality typically varies during an annual population cycle (e.g. Aaltonen et al. 2009; Lyons et al. 2009; Riedle et al. 2010; Sandercock et al. 2011), and in many cases deviates substantially from the simplified theoretical modeling assumptions of constant or density dependent natural mortality rates (Fieberg and DelGiudice 2009).

Willow ptarmigan *Lagopus lagopus* and red grouse *L.l. scoticus* are important birds for recreational and subsistence hunting throughout their circumpolar range (Johnsgard 1983; Pedersen and Karlsen 2007; Storch 2007; Watson and Moss 2008). In Fennoscandia willow ptarmigan is one of the most popular game birds that each year attracts many small game hunters (Kaltenborn and Andersen 2009). In Norway alone it is estimated that about 60 000 persons hunt for ptarmigan each year, and the annual national bag of willow ptarmigan and rock ptarmigan *L. muta* is 300 000 to 750 000 birds (Statistics Norway; [www.ssb.no/jakt](http://www.ssb.no/jakt)). In Fennoscandia willow ptarmigan are exposed to a rather long hunting season where they can be harvested from August to March, by either flushing, pointing dogs

or traditional methods of winter snaring (Pedersen and Karlsen 2007). In recent years wildlife managers in many areas in Fennoscandia have banned hunting of ptarmigan in winter. This harvest control rule is controversial because snaring and winter hunting have long traditions in northern areas, for instance is winter snaring at high latitudes a part of Saami culture (Pedersen and Karlsen 2007). In some areas in northern Finland as much as 50% of the willow ptarmigan harvest can be from winter snaring (J. Katajamaa pers. comm.). Hence, as closing the harvest season in late autumn is often opposed by hunters, we investigate the effect of reduced quotas for late season harvest discounted by seasonal mortality rates as a management tool instead of total closure. In this study we model the effects of timing of harvest using empirical data on seasonal natural mortality patterns in two contrasting populations of willow ptarmigan. We then illustrate how to adjust the harvest quota according to temporal patterns of natural mortality and timing in the annual cycle when the hunting occurs.

## **Methods**

To conceptualize how timing of harvest affects the expected breeding bird density the following spring, we used models based on the concept of “demographic value”, as defined by Kokko and Lindström (1998). The demographic value (DV) is the expected survival probability for an individual from time  $t=i$  until time  $T=1$  ( $0 \leq i \leq T$ ). When illustrating the empirically derived hazard functions in the later sections, we were interested in the probability for a given bird to survive from onset of the harvesting season in early autumn ( $i=0$ ) until the breeding season in the spring ( $T$ ) (here defined as the last week of June, at the

time of hatching: Munkebye et al. 2003). In total, this time window is 46 weeks long, and for clarity we illustrate the empirically derived functions by using the number of weeks since the start of the harvest season ( $i=0$ ) on the x-axis so that  $T=46$ . In our model, we used the conservative assumption of no compensation for harvest mortality in annual survival (but see Pedersen et al. 2004; Sandercock et al. 2011). All analyses were performed in R 2.12.1 software (R\_Development\_Core\_Team 2010).

#### Constant mortality risk

In the simplest model with constant natural hazard rate  $\mu$  (Fig. 1a) at the appropriate time unit ( $t$ ), the demographic value is calculated as the exponentiated negative cumulative hazard from time  $t=i$  ( $i=0,1,2\dots T$ );  $DV_t = \exp\left[\sum_T^i -\mu_t\right]$  (eq. 1). The length of the remaining season until breeding (time=  $T$ ) is then given as  $T-i$ . An alternative representation for this model with constant hazard rate would be  $DV_t = \exp[-\mu(1-t)]$  (eq. 2), where  $\mu$  is the constant hazard rate, and  $1-t$  is the length of the remaining season (where  $t$  is given as fractions of the total season).

#### Density dependent mortality risk

To model direct density dependence in the mortality rates (Fig. 1b), we assumed for simplicity that the natural hazard rate decreases as the season progress because densities are reduced (Kokko & Lindström 1998). In this model, the time dependent natural hazard rate was modeled as follows:  $\mu_t = \mu_0 * n_t$  (eq. 3), where  $\mu_t$  is the hazard rate at time  $t$ ,  $\mu_0$  is the initial hazard rate (i.e. at the start of the time period/season), and  $n_t$  is the population

size at time  $t$ . Here, we scaled the population density so that  $n_0$  is 1 (i.e.  $n_t$  is the relative population size at time  $t$ ).  $DV_t$  can then be calculated from eq. 1, by summing the cumulative hazard from time  $t$  to  $T$ . Alternatively,  $DV_t$  can be estimated by following the notation in eq. 2, and integrate over the remaining time interval  $T-t$ .

#### Empirically derived seasonal mortality risk

We also estimated demographic values based on the empirical seasonal hazard-function from radio collared willow ptarmigan in two study populations of central Norway with contrasting annual natural mortality patterns: an inland population from Meråker (Sandercock et al. 2011), and a coastal island population from Smøla (Bevanger et al. 2011). The hazard function for natural mortality was estimated with a smoothing spline function (gss package, Chong 2011). We reduced the default value for the smoothing parameter from 1.2 to 0.5 at the risk of overfitting (see Sandercock et al. 2011 for a complete description of the hazard rate calculations). In Meråker data were stratified into harvest mortality and other mortalities to account for competing risks (Heisey and Patterson 2006; Sandercock et al. 2011), and considered only the natural mortality hazards. The dataset from Smøla did not contain harvest mortality, so competing risks were not considered in the analysis.

In principle, once the natural hazard rate at time  $t$  is estimated (here with the function `hzdrate.sshzd` in package `gss`) eq.1 can again be applied to estimate  $DV_t$ . However, more conveniently,  $DV_t$  for the empirically derived seasonal hazard functions can be directly estimated with the `survexp.sshzd`-function in R-package `gss` (Chong 2011), by setting the

start-argument in the command line to  $t$  and the time-argument to  $T$ . In fact, the function gives an estimate of expected survival from  $t$  (the start-argument in the function) to  $T$  (the time-argument in the function), which is exactly the definition of  $DV_t$ . If a parametric model is used to describe the seasonal patterns in the hazard, an analytical model can be set up to estimate  $DV_t$  equivalent to eq. 2.

## Results and Discussion

The theoretical models clearly showed that the timing of removing a given number of individuals from the population influence the next years breeding population size (Fig. 2; see also Kokko and Lindstrom 1998). Increasing demographic values, as time approaches the reproduction season in spring, is a general trait for both the density dependent and the constant natural mortality models (Fig. 2). However, there were large differences depending on the life history strategies in annual survival. Generally, populations with life histories described by high annual survival (e.g.  $S=0.95$  in Fig. 1 and Fig. 2) will have smaller temporal changes in demographic values during a year. Populations with low annual survival will have relatively larger temporal changes in demographic values. For example, in populations with a 25% annual survival ( $S=0.25$ ) the demographic value increases 4-5 times from start to end. Therefore, changes in the timing of harvest will have a much stronger effect in populations with relatively low annual survival as found in many short-lived species (e.g. many small game species like quail, grouse and passerines), than in populations characterized by longevity (e.g. large ungulates and large carnivores). The same principle also could be valid within populations subject to age-selective harvesting — if different age-classes have large



differences in mortality schedules, the timing of harvest will be most influential on those with the lowest survival (most often juveniles; Gaillard et al. 1998).

Populations with constant natural mortality hazards over the annual cycle showed a slower temporal increase in demographic values than those with density dependent hazards (Fig. 2a vs b), and the differences in demographic values increased with decreasing annual survival. As such, the timing of harvest seems to be more influential for the next years breeding population in cases with constant hazards compared to if the natural mortality is density dependent.

The empirical data on natural mortality hazard patterns from our two study populations of willow ptarmigan showed seasonal peaks and large deviations from the theoretical models with constant or density dependent natural hazard rates (Fig. 3). Interestingly, we found large differences in both the temporal pattern and magnitude of annual survival between the two ptarmigan populations. The inland population (Meråker) had an annual survival of 0.54 and a natural mortality hazard with two enlarged mortality peaks, one in autumn and one in spring (Fig. 3, see also Sandercock et al. 2011). Both mortality peaks were caused by increased predation risk during the periods of nesting and autumn movements by gyrfalcons (*Falco rusticolus*) in the mountain areas (Sandercock et al. 2011). In contrast to this, the coastal ptarmigan population (Smøla) only had an annual survival of 0.26 and showed an increased natural mortality peak during mid winter. Also in this population the natural mortality was mainly caused by raptor predation from gyrfalcons, goshawks (*Accipiter gentilis*) and golden eagle (*Aquila chrysaetos*), migrating into and spending the winter months at this coastal area, resulting in higher mortality in the willow

ptarmigan population during this time of the year. The large differences in temporal dynamics of natural mortality and magnitude of annual survival between the two populations resulted in clear differences of demographic values. In particular at the first half of the season there are large differences in demographic values for individuals from the coastal population compared to the inland population.

Comparing the quota correction factors derived from the empirical data in the two ptarmigan study populations (Fig. 4) shows that when changing the harvest from the first week of the season to the last week of the season, the quota reduction has to be almost twice as high in a coastal compared to an inland population. For example, in Norway today the hunting season on willow ptarmigan ends by week 29 (February 28th) in most of the country, and if we choose to move all the harvesting to the end of the season we have to reduce the quota from the start of the season by 21% and 53%, for the inland and coastal population respectively. Here the timing of harvest based on the concept of demographic values, illustrate two important points. First, to quantify the effect of timing of harvest, information about the seasonal mortality risks in the harvested population is needed. When survival prospects are low the appropriate quota reduction by shifting from early to late season harvest increases. Secondly, we also see the importance of knowledge of the temporal pattern of natural mortality hazard when changing the timing of harvest in a population.

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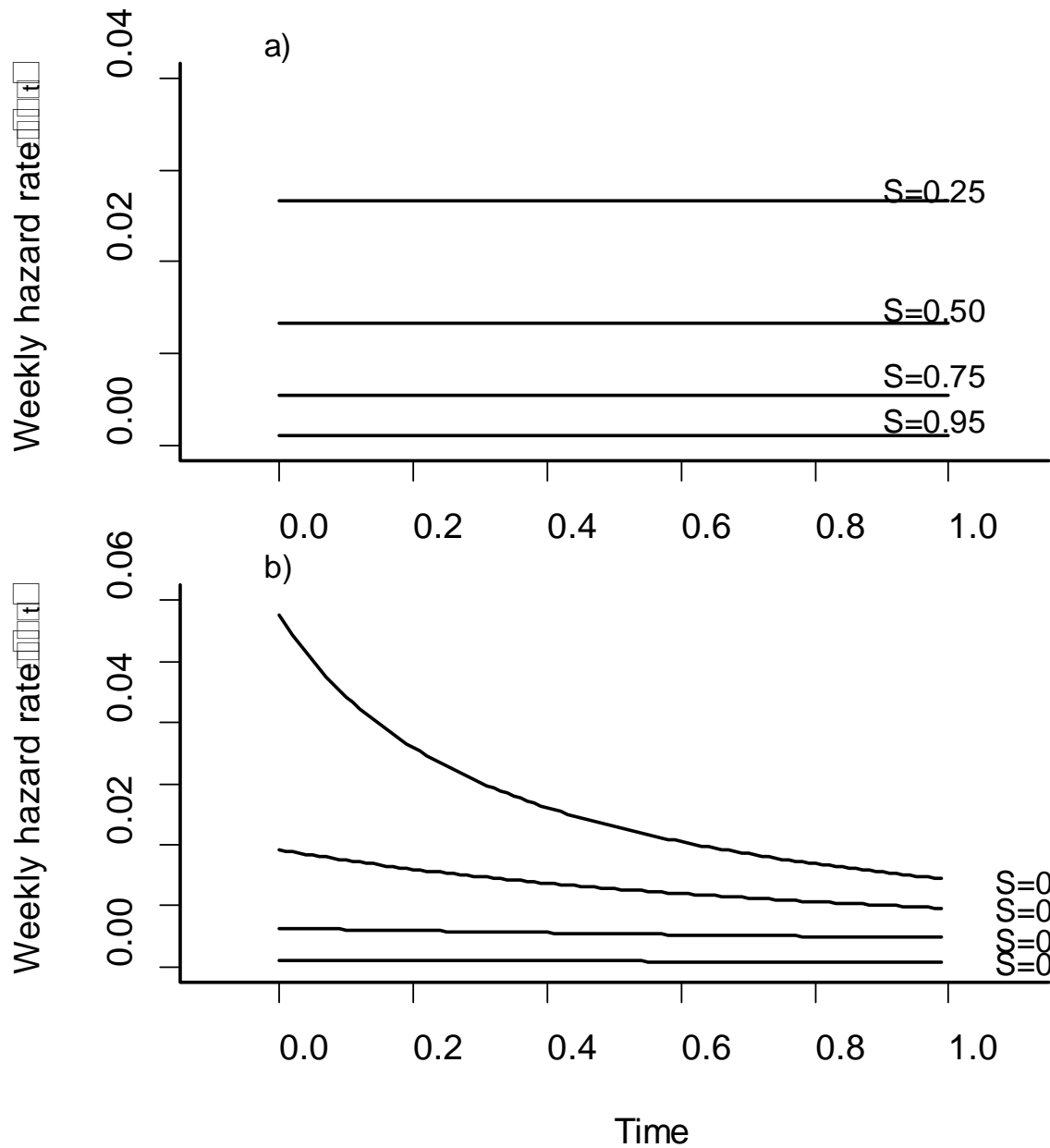
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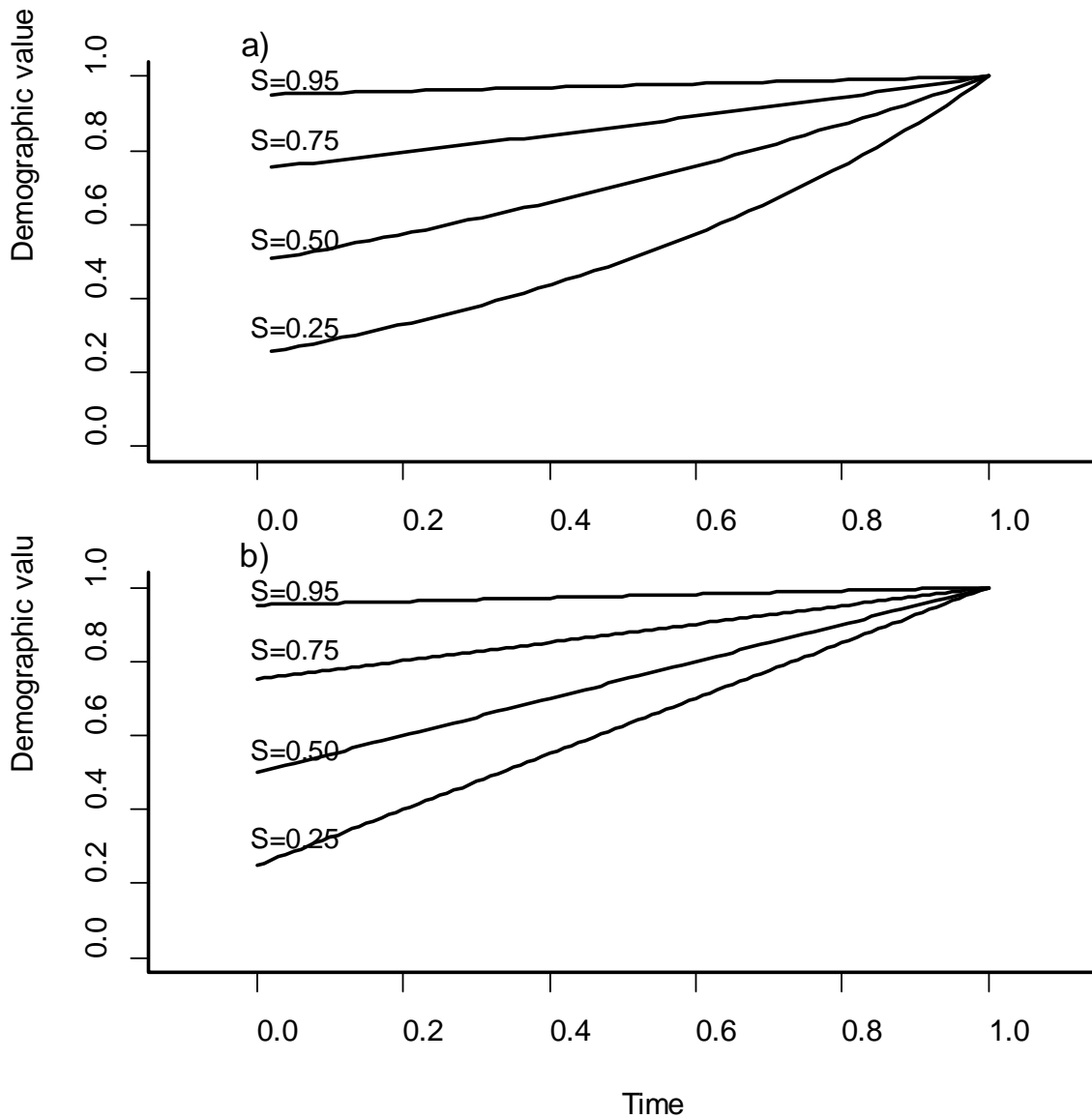
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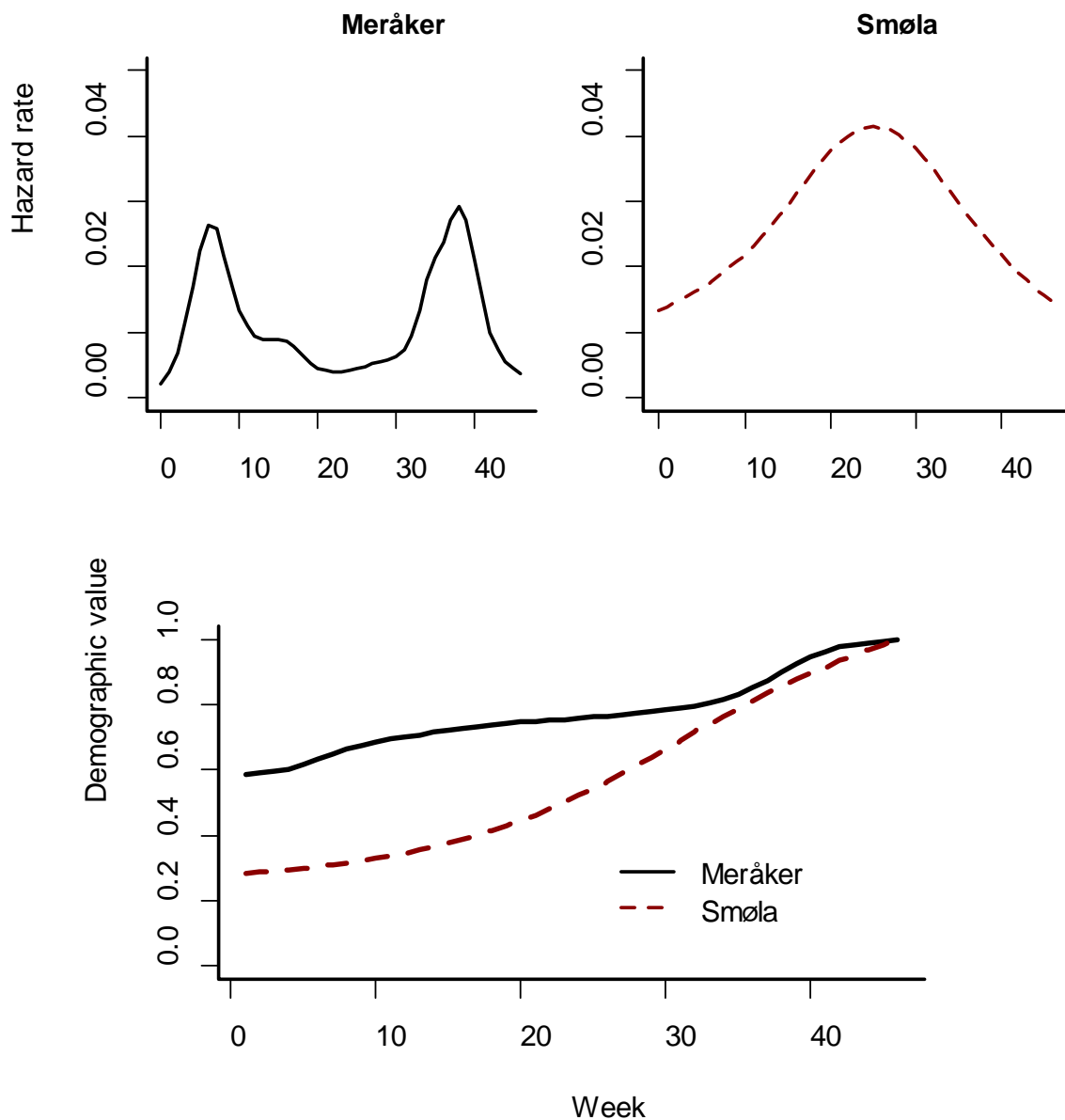


**Fig. 1** Annual patterns in weekly mortality rates for theoretical mortality patterns of **a)** constant mortality hazards and **b)** direct density dependent mortality hazards. S-values illustrates different life history strategies of annual survival from 25% ( $S=0.25$ ) to 95% ( $S=0.95$ ).

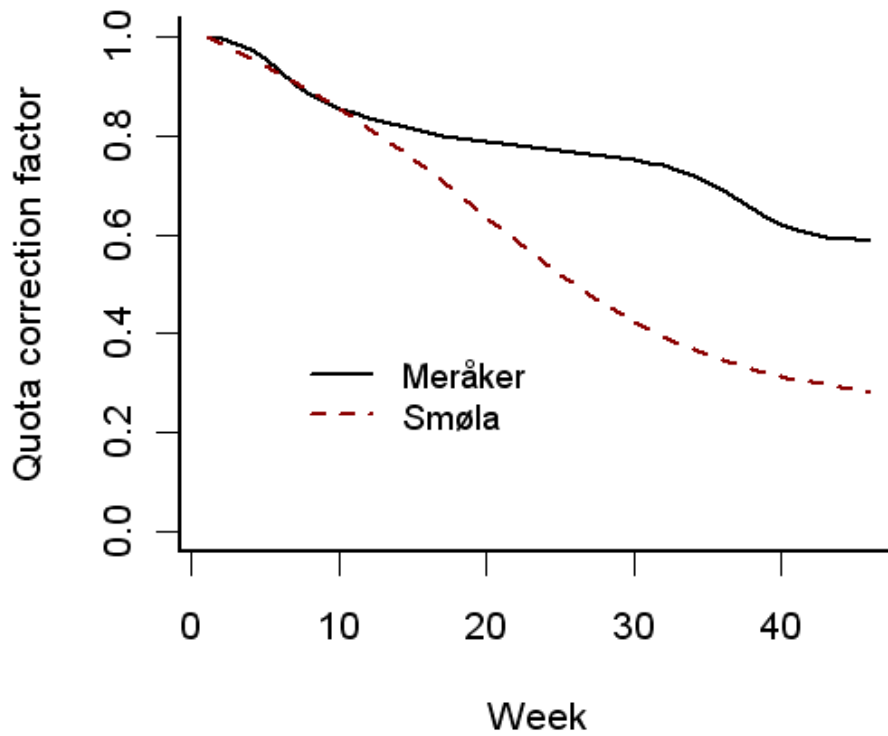




**Fig. 2** Annual variation in demographic value for theoretical mortality patterns of a) constant mortality hazards and b) direct density dependent mortality hazards. S-values illustrates different life history strategies of annual survival from 25% ( $S=0.25$ ) to 95% ( $S=0.95$ ). Adapted from Kokko and Lindström (1998).



**Fig. 3** Empirical data on annual patterns of natural mortality hazards and demographic value, from willow ptarmigan in an inland population (Meråker;  $S=0.54$ , solid line) and a coastal population (Smøla;  $S=0.26$ , dotted line). (Week 1 = mid August; week 46 = breeding; see methods section).



**Fig. 4** Seasonal variation in quota correction factors based on demographic values for two contrasting willow ptarmigan populations; an inland population (Meråker; solid line) and a coastal population (Smøla; dotted line). The effect of removing individuals from the population is constant if reduction in quotas for late season harvest is discounted by the demographic value. (Week 1 = mid August; week 46 = breeding; see methods section).