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In order to estimate the potential importance of each of the demographic traits egg, chick, and apparent winter survival on willow grouse *Lagopus lagopus* population dynamics, a sensitivity/elasticity analysis on a general model for the growth rate of breeding hen willow grouse numbers was performed. The demographic parameters used were taken from a 21-year study of willow grouse population dynamics on a Norwegian island. The growth rate of breeding hen numbers may be sensitive to changes in a parameter either because of the structure of the model or because of a substantial between year variation in the parameter. Therefore, three measures of parameter importance were used: sensitivity, elasticity and an actual elasticity coefficient (AE-coefficient). Sensitivity is an unscaled measure of the impact of a parameter, and thus cannot be used for comparisons between different parameters. Elasticity is a scaled measure of sensitivity allowing direct comparison between effects of different parameters on the growth rate (λ). To interpret the true effect of a demographic parameter on λ, between year variations in the parameter must be accounted for. The actual elasticity coefficient of each parameter is the product of the elasticity coefficient and the coefficient of variation, CV, for the demographic parameter in question. Sensitivity, elasticity and AE-coefficients showed that apparent winter survival of juveniles had the largest potential impact on changes in λ, followed by egg survival, chick survival and adult apparent winter survival. Considering elasticity coefficients alone, apparent winter survival compared to survival from egg laying to four weeks after hatching had 2.3 times the impact on λ. However, between year variation in apparent winter survival was far less than between year variation in survival from egg laying to four weeks after hatching, which leads to them both having a similar impact on λ. Management efforts on willow grouse have largely been devoted to enhancing survival from egg laying to four weeks after hatching which was believed to be the single most important factor determining population size. The results presented suggest that equal attention should be paid to winter survival. One cause of reduced winter survival may be hunting. A model incorporating the area specific survival and chick production resulted in $\lambda = 1$, when chick production was 1.8 chicks per adult and when there was no hunting. The model suggested that grouse could not be hunted in four of the 21 years without reducing the population size on the island and in many years only a modest harvest could be recommended.

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Willow grouse *Lagopus lagopus* population dynamics have interested Norwegian ecologists and hunters for decades and in spite of quite substantial research efforts starting as early as 1928 (B.J.F.F. 1928 reviewed in Myrberget 1988, Steen et al. 1988) the factors determining the changes in population size are poorly understood. Our aim was to evaluate which demographic factors have the strongest effect on the growth rate, λ, of breeding willow grouse hen numbers modelled assuming additivity in all demographic parameters. Based on this population dynamics model, we present a general harvest model for willow grouse and apply it to a data set covering 21 years assuming that hunting mortality is additive to natural mortality.

In mountainous regions of Fennoscandia, populations of small mammals such as lemmings *Lemmus lemmus* and voles *Microtus* spp. fluctuate strongly in size and are often characterised by cyclic population dynamics (Framstad et al. 1993). Predators feeding on small mammals consume willow grouse eggs and chicks as alternative prey. Thus, survival from egg laying to four weeks after hatching is very poor in small-mammal crash years (Steen et al.1988). Microtine density, roughly classified as low, medium and high, predicted 41% of the variation in number of chicks per pair in the autumn (Steen et al. 1988). Early autumn, chick production per pair ranged from 0.65 to 7.28 with a mean of 2.89 (Myrberget 1988). In spite of a 10-fold variation in chick production that correlated with microtine density (Steen et al. 1988), the evidence that breeding population size and breeding population fluctuations of willow grouse follow the microtine cycle is scanty. Total density and number of breeding hens are quite variable, but the effects of microtine density seem to be masked by variation in other factors such as winter survival (Myrberget 1988).

To resolve the effect of different demographic parameters on λ, key factor or sensitivity/elasticity analyses (Caswell 1989) may be used. Key factor analysis has been criticised for being unable to reveal the underlying processes in population dynamics due to an erroneous interpretation of population variance (Royama 1996). Sensitivity analysis evaluates the potential impact of a deviation in a parameter away from the mean parameter value. Sensitivity analyses cannot be used to directly compare the effects of demographic parameters on dynamics when the parameter values are expressed in different units. However, using elasticity analysis it is possible to compare the proportional change in one parameter with the proportional change in another. To get an impression of the degree to which a demographic parameter affects the population growth rate in the real world, elasticity coefficients must be evaluated after correcting, using the observed weighted mean and variance in the demographic parameters from natural populations. Since elasticity co-efficients give the changes in population growth rate dependent on a percentage change in a parameter, we can multiply the elasticity coefficient with the corresponding coefficient of variation (CV) and get an estimate of the actual effect, the Actual-Elasticity-coefficient (AE-coefficient, van Tienderen 1995).

Knowing the elasticity coefficients of the population dynamics, it should be possible to identify which demographic parameters management efforts should focus on. The results from the elasticity analysis show that winter mortality is as important as survival from egg laying to four weeks after hatching in determining the growth in hen numbers. This means that hunting may be an important factor in determining population growth of willow grouse especially in years with low production. We therefore examine the harvest potential of willow grouse populations using data from a Norwegian island population.

Data background

The data originate from a 21-year study conducted on Tranøy, a 127 ha island situated in northern Norway, by the late Svein Myrberget and students (Myrberget 1988). Tranøy lies about 1 km from the nearest island and 1 km from the mainland. There was a dairy farm on the island from 1960 to 1965; apart from that there was no human activity on the island until 1976 when sheep were introduced. The general population trend of willow grouse as estimated by total counts of all birds on the island was declining (Fig. 1). Dogs were used to find nests which were monitored until hatching; later broods were flushed and juveniles and adults were counted at the appropriate times (for a more detailed description see Myrberget 1988).
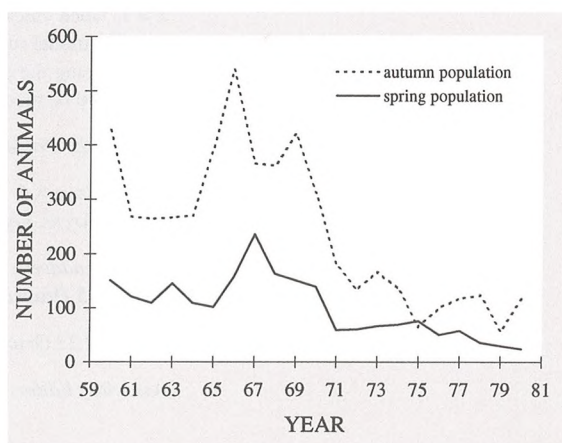

Figure 1. Population trend of the willow grouse population at Tranøy, 1960-1980. The broken line indicates the autumn population density; the solid line indicates the total spring breeding population.

Raw data used in the analysis (Table 1) were read off the graphs of Myrberget (1988). The quality of the data is evident from the mean, maximum and minimum as well as sample sizes across years for the numbers of clutches and the numbers of birds on which survival estimates are based. Winter survival rates as presented by Myrberget do not represent the true survival, but a combination of natural mortality, hunting mortality, migration and immigration (see below for discussion). We therefore use 'apparent winter survival' instead of 'winter survival' throughout the paper when referring to this data set.

Although the expected number of willow grouse arrived in 1971 and started establishing territories, half of the adult birds had left the island by mid June. Because Myrberget (1988) does not clearly state how summer survival and other demographic traits were treated for 1971, we excluded all data from 1971 from our main analysis. Note, however, that apparent winter survival can still be calculated since the birds arrived at the island in the spring.

As the data were gathered over many years, it might be possible to find time-dependent trends in the demographic parameter estimates. This was checked for by autoregression analysis with first order autoregressive error terms on the arcsine, transformed survival rates and untransformed clutch size. Only egg survival (from laying to hatching) showed a significant negative trend from 1960 to 1980. This was due to one year of extremely low egg survival, 1979, and was not a time-dependent trend in the egg survival rates. As there is no real trend in any of the apparent survival or reproductive parameter estimates, no parameters are detrended. Myrberget (1985, 1988) checked for density dependence in the demographic parameters for the Tranøy data and found that only clutch size was negatively correlated with willow grouse density.

Table 1. Values of the demographic parameters used in the analysis: Clutch size (Clutch), survival of eggs from egg laying to hatching (egg survival, Egg_S), proportion of eggs that hatched (Hatch), proportion of chicks that survived from hatching to four weeks (chick survival, $Chick_S$), proportion of juveniles surviving the winter (juveniles apparent winter survival, Juv_S), proportion of adults surviving the winter (adult apparent winter survival, Ad_S), adult survival from arrival at Tranøy until mid May (adult summer survival, SS), mean value of juvenile (Juv_S) and adult (Ad_S) apparent winter survival (Pooled winter survival), survival of an egg from egg laying to four weeks after hatching (PROD). The abbreviations are the same as the ones used in the formulas. Standard deviation in the clutch size is based on the total variance and is not weighted as in the other parameters.

Year	Clutch	Egg survival	Hatch	Chick survival	Juvenile winter survival	Adult survival	Adult summer survival	Pooled winter survival	Survival from egg laying to four weeks after hatching
1960	11.37	0.92	0.99	0.39			0.99		0.35
1961	9.89	0.92	0.90	0.32	0.32	0.51	1.00	0.41	0.27
1962	10.00	0.81	0.93	0.45	0.39	0.71	0.99	0.55	0.34
1963	9.79	0.49	0.99	0.43	0.39	0.40	0.99	0.39	0.21
1964	10.00	0.89	0.94	0.46	0.28	0.49	0.92	0.38	0.38
1965	10.21	0.91	0.94	0.75	0.33	0.57	0.99	0.45	0.64
1966	10.00	0.81	0.97	0.69	0.33	0.72	0.99	0.53	0.55
1967	8.00	0.40	0.88	0.56	0.18	0.57	0.99	0.38	0.20
1968	8.95	0.70	0.96	0.58	0.20	0.68	0.99	0.44	0.39
1969	9.89	0.81	0.95	0.58	0.18	0.60	0.99	0.39	0.45
1970	9.89	0.71	0.96	0.63	0.38	0.47	0.98	0.42	0.42
1972	9.89	0.67	0.96	0.53	0.48	0.49	0.97	0.48	0.34
1973	10.74	0.74	0.94	0.53	0.25	0.65	0.98	0.45	0.36
1974	10.00	0.72	1.00	0.49	0.50	0.49	0.99	0.50	0.35
1975	8.74	0.69	0.94	0.20	0.42	0.55	0.91	0.48	0.13
1976	10.21	0.66	0.91	0.31	0.39	0.64	0.98	0.52	0.18
1977	11.89	0.74	0.88	0.51	0.20	0.37	0.98	0.29	0.33
1978	11.89	0.79	0.94	0.57	0.17	0.52	0.94	0.34	0.42
1979	9.68	0.18	0.95	0.31	0.41	0.67	1.00	0.54	0.05
1980	12.21	0.84	0.96	0.61					0.49
Weighted mean	9.80	0.70	0.95	0.54	0.27	0.52	0.97	0.39	0.36
Weighted SD	1.05	0.18	0.03	0.14	0.11	0.10	0.03	0.07	0.14
Min	8.00	0.18	0.88	0.20	0.17	0.37	0.91	0.29	0.05
Max	12.21	0.92	1.00	0.75	0.50	0.72	1.00	0.55	0.64

In the data set, apparent winter survival is divided into the age-classes juveniles and adults. There is no division between first, second and third-year reproductive parameters. We therefore use the two apparent winter survival age-classes (first-year juveniles and adults) and one reproductive class in the model. Parameter descriptions used in the model are presented below with their model notation given in brackets.

Clutch size

Clutch size (Clutch) expresses the mean observed clutch size in a given year (mean number of clutches = 20.5, min = 5, max = 49). Renests are excluded.

Egg survival

Egg survival (Egg_S) expresses the proportion of the eggs laid that did not disappear during incubation (mean number of clutches = 27.8, min = 10, max = 76), multiplied by 1.5 (a correction factor based on data from 1974-78 in Myrberget et al. (1982). The factor corrects for losses during laying and incubation, as well as compensation for losses by renesting. All figures given in Myrberget et al. (1988) have been corrected with this factor, and we have chosen not to back transform the data. The excluded year, 1971, was a microtine crash year and low egg survival could be expected. However, the year turned out quite normal with an egg survival of 0.85.

Hatching success

Hatching success expresses the proportion of the eggs in the nest at the time of hatching that resulted in a live chick (mean number of eggs = 154.5, min = 7, max = 418).

Chick survival

Chick survival ($Chick_S$) expresses the observed proportion of chicks surviving from hatching until the age of 3-4 weeks (number of broods examined unknown). The survival values for 1960-73 are based on the average number per brood from hatching until the age of four weeks. For 1974-80 the survival is given for known broods only (mean number of chicks = 146, min = 6, max = 418).

Survival from egg laying to four weeks after hatching

We define survival from egg laying to four weeks after hatching as ($Egg_S \times Hatch \times Chick_S$). Chick production (PROD) is defined as: $0.5 \times Clutch \times$ (survival from egg laying until four weeks after hatching).

Juvenile apparent winter survival

Juvenile apparent winter survival (Juv_S) expresses the number of yearlings breeding the following year divided by the total number of juveniles present in late July the preceding year. Juveniles can be distinguished from adults in the spring as first-year breeders have more black pigment on the two outermost wing feathers than on the rest of the wing feathers (Bergerud et al. 1963). True adult winter survival is probably underestimated due to lack of detectability and hunting mortality (mean number of juveniles in the autumn = 151, min = 18 , max = 400).

Adult summer survival

Adult summer survival (S_S) simply expresses one minus the proportion of the total number of breeding birds found dead in May, June and July (mean number of adults at the beginning of May = 101, min = 24, max = 236).

Apparent adult winter survival

Apparent adult winter survival is the proportion of the adults in late July present the next spring (Ad_S). The number of adults present in the next spring equals the number of second year breeders present the following spring. Errors are the same as for juvenile apparent winter survival (mean number of adults entering the winter = 103, min = 30, max = 234).

Pooled apparent winter survival

Pooled apparent winter survival is defined as $Ad_S \times Juv_S /2$.

Determining mean and between year coefficients of variation

The Total Variance (TV) in the raw data set (see Table 1) contains two types of variance: Sampling Variance (SV) and Between Year Variance (BYV) (TV = BYV + SV). The biologically interesting variance is the BYV and not the SV. True BYV can be expressed as: BYV = TV - SV, assuming independence between the two variance components. In the figures of Myrberget (1988) no confidence intervals are given for the within year survival estimates that equal the SV. To correct for the lack of confidence intervals (and SV) in a given year, and the consequent overestimation of BYV (by not accounting for SV) we assumed a binomial SV (p(1-p)/N) within each year. Each year was assumed to have independent sampling variances. We could therefore add the SV over all years (weighted by sample size) to obtain a total SV for all years. For clutch size and egg survival, numbers of nests were used as sample size; otherwise the total number of

individuals each year were used as sample size. By subtracting the SV from the TV calculated from Table 1, we were left with the BYV in the demographic parameter in question. For clutch size we used the crude total variance. Since clutch size is not given as a probability we cannot assume binomial variance, and we have no way of assessing sampling variance. We believe this is a minor problem since counting eggs in a nest is not a difficult task and the sampling variance should be small. Coefficient of variation, CV, is calculated as the between year standard deviation divided by the weighted mean value.

Model and analysis

We chose to model the growth rate, λ, as the change in the number of breeding female willow grouse (N_t) from one spring to the next spring (N_{t+1}). This is modelled by:

$$N_{t+1} = N_t \times \lambda \qquad 1$$

where λ is defined as:

$$\lambda = (Ad_S \times S_S) + (S_S \times (Clutch \times 0.5) \times Egg_S \times Hatch \times Chick_S \times Juv_S) \qquad 2$$

In the model we assume an even sex ratio at hatching, identical survival rates between the sexes with no interaction/dependency between any of the mortality factors.

Sensitivity of λ with respect to any parameter, x_i, is defined as $d\lambda/dx_i$, i.e. the derivative of λ with respect to parameter x_i evaluated for the weighted mean values of the parameters (Caswell 1989). The elasticity coefficient is defined as $dLn\lambda/dLn(x_i)$ (Caswell 1989), and elasticity for the demographic parameter, i, is equal to:

$$E_i = dLn\lambda/dLn(x_i) = (1/\lambda)(d\lambda/d x_i) x_i \qquad 3$$

Elasticity coefficients give the effect on λ of a unit increase or decrease in the demographic parameter. Therefore, we can compare the effects of different demographic parameters directly. Elasticity coefficients only measure the theoretical effect, imposed by the model structure, of a change in a demographic factor and do not evaluate to which degree a given demographic parameter influences the λ in real life. To examine the effect of a given demographic parameter we must incorporate the natural variation in the parameter (van Tienderen 1995). Between year coefficient of variation (CV) in the demographic parameters is a scaled measure of the between year variation. By multiplying the elasticity coefficients and their corresponding CV's we get an actual elasticity coefficient, the AE-coefficient:

$$AE_i = E_i \times CV_i \qquad 4$$

A high AE-coefficient means that the elasticity coefficient is also high, that the potential influence on λ is high and there is large variation in the demographic trait. Demographic traits with the highest AE-coefficients have the largest influence on the growth rate, λ, and are probably the most important factor in determining the changes in population size. A high elasticity coefficient combined with a low variance will necessarily have less impact on λ.

Sensitivity, elasticity and AE-coefficients were calculated for all demographic parameters. To compare the role of survival from egg laying to four weeks after hatching and apparent winter survival we performed the same analysis.

Results

Sensitivity

Sensitivities evaluated for the weighted mean values of the demographic parameters from Myrberget (1988, Table 1) showed that juvenile apparent winter survival, during the period from late July to the following spring, is the most important factor (Table 2) in determining changes in λ; pooled apparent winter survival is also more important in determining changes in λ than survival from egg laying to four weeks after hatching (PROD).

Elasticity, E_i

The elasticity coefficient evaluated for the weighted mean values gave the same elasticity for all reproductive parameters except for adult survival and adult summer survival (Table 3). This means that a 10% change in

Table 2. Ranked sensitivity index for all the demographic parameters mentioned in Table 1. Survival from egg laying to four weeks after hatching is the product of egg survival (Egg$_S$), hatching success (Hatch) and chick survival (Chick$_S$) and is analysed as one value. All notations as in Table 1.

Demographic parameter	Sensitivity index
Juvenile apparent winter survival	1.709
Adult apparent winter survival	0.969
Adult summer survival	0.992
Chick survival	0.836
Egg survival	0.646
Hatch	0.479
Clutch	0.093
Survival from egg laying to four weeks after hatching	1.259
Pooled winter survival	2.677

Table 3. Demographic factors ranked according to their actual elasticity coefficients (elasticity $\times$ CV). The AE-coefficient is a relative measure of the importance of the different demographic factors on λ. All notations as in Table 2.

Source	Elasticity	CV	AE-coefficient	Ranking from sensitivity
Juvenile apparent winter survival	0.472	0.403	0.190	1
Egg survival	0.472	0.262	0.123	5
Chick survival	0.472	0.254	0.120	4
Adult survival	0.528	0.197	0.104	2
Clutch	0.472	0.107	0.051	7
Adult summer survival	1.000	0.026	0.026	3
Hatch	0.472	0.035	0.016	6
Survival from egg laying to four weeks after hatching	0.477	0.386	0.184	
Pooled winter survival	1.098	0.184	0.202	

Clutch, Egg_S, Hatch, $Chick_S$ and Juv_S has the same impact on λ. Adult apparent winter survival, Ad_S, had a slightly larger impact than Clutch, Egg_S, Hatch, $Chick_S$ and Juv_S. Adult summer survival, S_S, had twice the impact of the same change in any of the other parameters. Pooled apparent winter survival had an elasticity equalling 1.1. Thus a 10% reduction in winter survival caused, for instance by hunting leads to an 11% reduction in the number of breeding hens relative to what should have been expected from the chick production and pooled winter survival. Changes in pooled apparent winter survival will have an impact 2.3 times greater than the impact of the same change in survival from egg laying to four weeks after hatching.

Actual elasticity coefficient, AE

AE-coefficients given in Table 3 show that juvenile survival (Juv_S) is the most important parameter. Both Egg_S and $Chick_S$ have almost identical influence on changes in λ. Summer adult survival illustrates the use of AE-coefficients well. The sensitivity and elasticity analyses show that adult apparent summer survival could have a large impact on the changes in λ, but since there is hardly any between year variance in adult summer survival this contributes little to changes in λ. Comparisons between the AE-coefficients for survival from egg laying to four weeks after hatching (0.18) and pooled apparent winter survival (0.2) show that the two factors have an almost identical impact on λ.

Sensitivity and elasticity analyses demand that there is no covariance between the different parameters in the model nor any density dependence in the parameters. To check this we correlated all demographic parameters. The only significant correlation ($P < 0.05$) was between clutch size and egg survival ($r = -0.45$, $P = 0.048$) and juvenile apparent winter survival and the proportion of eggs that

hatched ($r = 0.5$, $P = 0.044$). After a Bonferoni correction the P-value for acceptance was 0.002, so none of the correlations should be regarded as significant. As stated earlier, the only density-dependent factor found earlier was clutch size (Myrberget 1985, 1988).

Managing a willow grouse population.

Managing a game population with a 10-fold stochastic variation in chick production and a randomly varying adult mortality is fraught with problems (Lande et al. 1995). For willow grouse in Norway the harvest must either vary with intensity or, optimally, use a threshold harvest strategy (Lande et al. 1995). In the following section we develop a general management model to investigate how high a harvest a willow grouse population can sustain. We demonstrate a density and chick production dependent (PROD) variable management strategy and apply it to the Tranøy willow grouse population.

Management models for wildlife populations should only include input parameters available to the managers/hunters before the hunting season. Since chick production of willow grouse is dominated by the impact of predation and random factors such as weather conditions, the final decision as to how many willow grouse can be harvested, can only be made after chick production is known. We focus on two properties, i.e. the proportion of the population harvested and the consequences of this to the population. To estimate the harvest parameter, H_{mort}, we need four figures, i.e. the apparent winter survival of juveniles and adults, chick production and the number of breeding hens. Chick production (PROD) is expressed as: PROD = ((Clutch $\times$ 0.5) $\times$ Egg_S $\times$ Hatch $\times$ $Chick_S$). Traditionally, production is expressed as 'Chicks per pair' in autumn, which equals two times PROD.

To find the harvestable proportion of the population,

hunting mortality, H_{mort}, is included in equation 2 above as natural survival multiplied with $(1-H_{mort})$. Total compensation of natural survival through hunting is equivalent to assuming perfect density-dependent survival (Ellison 1991). Partial or total compensation of survival to hunting mortality has been observed in some tetraonids, but density dependence has not been shown in willow grouse (Myrberget 1985, Ellison 1991), even though breeding densities during 1971-1980 were only half the pre-1971 densities. A given level of compensation (partial or total) can be obtained either by reducing the effect of hunting (lowering H_{mort}) or increasing winter survival. Including H_{mort} in equation 2 gives a growth rate, λ, expressed as:

$$\lambda = Ad_S \times (1-H_{mort}) \\ + PROD \times Juv_S \times (1-H_{mort}) \qquad 4$$

If $\lambda = 1$ the following equation can be used to calculate H_{mort}:

$$H_{mort} = 1-1/(Ad_S + PROD \times Juv_S) \qquad 5$$

The two apparent winter survival parameters are given in Table 1, and chick production can be estimated in late August when the number of chick and adults in flushed broods can be counted. On Tranøy almost every displaying cock will get a hen. Thus, the number of displaying cocks yields a good estimate of the number of breeding hens. Numbers can be estimated using line transect techniques (Buckland et al. 1993). At Tranøy the breeding population has been followed closely by searching for
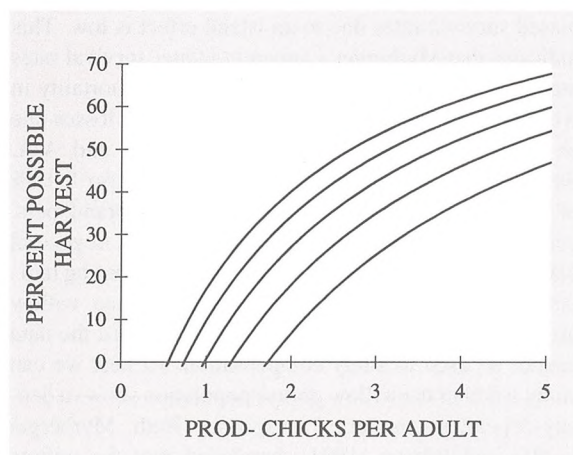

Figure 2. Theoretical harvest percentage of the autumn population demanding zero growth rate in number of breeding hens dependent on chick production. The line furthest to the right is where adult apparent winter survival is 0.51 and juvenile survival apparent winter survival is 0.26 (from Table 1). From right to left each line represents the harvest percentage assuming that survival is underestimated by 5, 10, 15 and 20%, respectively
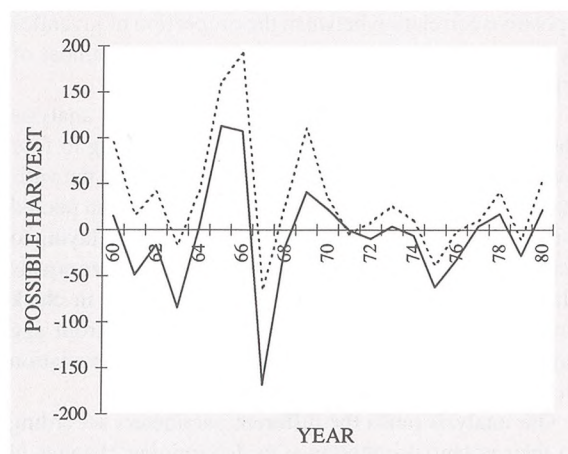

Figure 3. Number of willow grouse harvestable at Tranøy assuming mean adult apparent winter survival (0.51) and juvenile apparent winter survival (0.26), the yearly observed spring densities and year specific chick production (solid line). The dotted line represents the harvest if Myrberget (1988) underestimated apparent winter survival by 10% or willow grouse show a 100% compensation in natural survival rates for 10% increased mortality due to hunting. Negative values indicate that no harvest is possible and that the population declines regardless of hunting

nests, and the number of breeding pairs is known through total counts.

We calculated the possible harvest percentage of willow grouse in the autumn (Fig. 2) as a function of different chick production levels, with $\lambda = 1$. The different curves in Figure 2 represent scenarios where the survival estimates from Tranøy underestimated the true survival by 5, 10, 15 and 20%. Consequently, the four different curves also describe possible hunting yields at different levels of 100% compensation (see above).

When using the model with the Tranøy willow grouse population data, the yearly yield expressed as a function of the number of hens (see Fig. 1), chick production (PROD) and the pooled apparent winter survival estimates (see Table 1), is given in Figure 3. The striking result is that during 1960-1980 the population could not be hunted in four of the 21 years. This was also the case when assuming 100% compensation of 10% losses due to hunting or 10% underestimation of winter survival rates.

Discussion

In his review, Myrberget (1988) concluded that the most important factor regulating breeding population size in willow grouse is annual chick production (PROD). This conclusion was based on two observations: 1) that there was a positive highly significant correlation between the numbers of adults and juveniles in autumn and the number of breeders the following year, and 2) that there was

a positive correlation between the proportion of juveniles in the autumn census and the increase in the number of breeding hens.

In contrast to Myrberget's conclusions, our analysis shows that variation in survival from egg laying to four weeks after hatching has slightly less impact on the variation in breeding population size growth rate than pooled winter survival (see Table 3). Survival from egg laying to four weeks after hatching multiplied by clutch size equals chick production. The between year variation in chick production is caused by variation in survival from egg laying to four weeks after hatching and not by variation in clutch size.

Our analysis ranks the different parameters according to their potential importance in determining changes in the number of breeding willow grouse hens. First-year willow grouse apparent winter survival is about 1.5 times more important than both egg and chick survival, which have similar impacts on breeding hen population growth rate. The fourth most important parameter is adult apparent winter survival. Juvenile apparent winter survival is the most important factor in determining changes in the breeding population, λ, as sensitivity (unscaled measure of the effect on λ), elasticity (scaled measure of the effect on λ) and AE-coefficient (relative importance measured by adjusting the elasticity coefficient with the actual variability in the parameter) all give the same results. Further research aimed at determining the most important factors affecting population size changes should therefore be devoted to finding the causes of the variation in first-year apparent winter survival.

Judging from the sensitivity analysis, adult apparent winter survival is quite important in determining λ. In the elasticity analysis it is the second most important parameter after adult summer survival. When accounting for between year variation in adult winter survival, the AE-coefficient, it drops to fourth place. This is due to little between year variation in adult winter survival. Egg survival is the fifth most important parameter judging from the sensitivity analysis, but after accounting for the large variation in egg survival between years it moves to second place. These two cases illustrate an important point: elasticity and sensitivity analyses can only indicate the possible impact of one parameter and we can only judge which factor can change growth rate in a natural population after accounting for the between year variance in the demographic parameters, AE-coefficient (van Tienderen 1995).

Do apparent winter survival estimates reflect normal survival rates?

The true apparent winter survival rate will inevitably be underestimated by the procedure used by Myrberget

(1988) since migration counts as mortality and hunting mortality is hidden in the survival estimates. Hunting is not allowed on Tranøy, but as the willow grouse often leave the island in the autumn they may be hunted on their wintering grounds. Since individuals were not marked, migration could not be detected either. Assuming equal immigration and emigration, underestimation due to emigration would not systematically bias the survival estimates. The way apparent winter survival parameters are calculated assumes that recapture/resighting is 100%. In reality recapture/resighting probability is lower and this will negatively bias the survival estimates. If recapture/resighting probability varies substantially between years the bias in apparent winter survival rates is totally unpredictable and use of the variation in these parameters is questionable. However, recapture/resighting was probably high due to the considerable effort invested each year and the effect of this bias is probably low. Another factor possibly affecting systematically the estimated apparent winter survival could be social pressure preventing new cocks from establishing a territory. However, this would require density-dependent apparent winter survival which was not observed (Myrberget 1985, Ellison 1991). The apparent winter survival estimates given in Table 1 and used in the analysis must therefore be considered as minimum estimates.

Willow grouse mortality rates from a radio-telemetry study in Sweden suggest that juvenile winter survival varies between 10% and 40% and adult winter survival is approximately 50% (T. Willebrand and A.A. Smith, pers. comm.). Even though the Swedish survival rates originate from an inland population, the survival rates of the two studies are similar, which means that the possibility of biased survival rates due to an island effect is low. This indicates that Myrberget's apparent winter survival rates are not extremely biased. Studies of natural mortality in willow grouse show that this is dominated by losses due to predation (Hudson 1992, T. Willebrand and A.A. Smith, pers. comm.), while hunting accounts for 8-10% of yearly mortality (Jørgensen 1994, T. Willebrand, pers. comm.). Ellison (1991) argued that tetraonids in general partially or totally compensate for moderate hunting mortality by increased individual survival. Since willow grouse at Tranøy were not individually marked the data cannot be used to study compensation. At best we can study whether the willow grouse population shows a density-dependent numerical response. Both Myrberget (1985) and Ellison (1991) concluded that the willow grouse at Tranøy showed no density dependence in apparent winter survival rates.

Managing a willow grouse population

Studies on density dependence in winter survival or com-

pensation have failed to reveal any consistent trend. Myrberget (1985) and Ellison (1991) failed to find any density dependence in survival in willow grouse, and Pedersen (1988) experimentally showed the existence of surplus cocks and hens following a good chick production year. Since there is no clear basis for assuming density dependence or compensation as a general feature in willow grouse, populations should be managed as if hunting was additive to natural mortality. Such an approach will also be the most conservative.

In willow grouse management the aim is often to harvest the largest possible share without damaging the population. This is an easy task if the population size is sufficiently large or if its dynamics are not affected by stochastic demographic or environmental variation. As we have shown, the demographic parameters of willow grouse population dynamics may vary almost randomly and population sizes are not always very large. Our analysis shows that production and apparent winter survival have almost identical impacts on the dynamics. Since 56% of the variation in production can be explained by small mammals and weather conditions (Steen et al. 1988) and as this accounts for about half of the variation in subsequent breeding population size (see our results above) we can only predict approximately 25% of the variation in breeding population size from microtines and weather conditions. Managing a population for which we have such poor predictive powers must be done with some care and we propose that harvest levels are kept well below the possible maximum yield.

The randomly varying demographic parameters of willow grouse population dynamics suggest that a threshold harvest strategy should be used (Lande et al. 1995). However, since we can estimate population size and chick production before the harvest season we feel that using a threshold management approach based simply on the number of animals does not utilise all available information and we therefore suggest that the model outlined above is used. With this model, it will only take a minimum of effort to ensure that the population is not overexploited and that all possible information is utilised. This will in turn increase the potential harvest since the model does not have to account for much stochasticity.

The problem with both management approaches is that they demand regulation of the harvest intensity shortly before the hunting season. On larger estates this can be done by limiting the number of hunting licenses sold. On privately owned or rented properties it requires personal restraint by the hunter.

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