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Minimum viable population size of capercaillie *Tetrao urogallus*: results from a stochastic model

Volker Grimm & Ilse Storch

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In order to estimate minimum area requirements for viable isolated populations of capercaillie *Tetrao urogallus* in Central Europe, we developed a stochastic population model. Model parameters were largely based on the results of a field study in the Bavarian Alps. Environmental fluctuations (amount of rainfall in June and July) are taken into account in the early survival of chicks. For the default parameter set, the model predicts a minimum capacity needed for viability, i.e. for the extinction risk not to exceed 1% in 100 years, of about 470 individuals. In the Bavarian Alps, this corresponds to area requirements of an isolated viable population in an order of magnitude of 250 km^2. These results are, however, sensitive to small changes in model parameters such as female survival, clutch survival and chick survival. We conclude that minimum viable population size and minimum area requirements may vary considerably across the range of the capercaillie. Therefore, we plan to apply our model to different parameter sets from different regions in order to explore the range of conditions under which capercaillie populations may be viable.

Key words: capacity, capercaillie, environmental noise, extinction, minimum viable population, model, sensitivity

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Even if the mean rate of population growth is positive, populations are in danger of becoming extinct if they are too small to buffer environmental and demographic fluctuations. But how small is 'too small'? Answering this question is important to guide management decisions in fragmented landscapes. Therefore, a major task of conservation biology is to determine "minimum viable populations and their area requirements" (Shaffer 1981: 100). Shaffer defined viability as an extinction risk that does not exceed a certain threshold within a certain time interval; typically 1 or 5% in 100 years are used. Then, a minimum viable population (MVP) in a given habitat is defined as the smallest isolated population which is viable. Although rough assessments of MVP may be inferred from biogeographic patterns (Shaffer 1981), the main tool to determine MVP quantitatively are stochastic population models (Shaffer 1981).

For capercaillie *Tetrao urogallus* in central Europe, Storch (1995) proposed a preliminary estimate of an MVP of 500 birds based on biogeographic patterns. The first model-based assessment of MVP for capercaillie has recently been presented by Marshall & Edwards-Jones (1998); the aim of their study was to evaluate the suitability of potential sites for reintroducing capercaillie in Scotland. Based on the generic population simulation model VORTEX (Lacy, Hughes & Miller 1995) they conclude that under certain conditions, a population of 60 individuals in a habitat with a capacity (i.e. ceiling population size) of 150 individuals would be viable.

Reliable estimates of MVP and minimum area re-

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quirements are urgently needed in capercaillie conservation (Storch 2000). Related to the discrepancy between the existing estimates and their management implications, we developed a stochastic model of capercaillie population dynamics and parameterised it with field data from the Bavarian Alps, Germany (Storch 1993a,b, 1994, 1995, and I. Storch, unpubl. data). Our objective was to provide a prototype of a population model specifically developed for capercaillie, that allows rough estimates of MVP requirements and contributes to a better understanding of the conditions for persistence of isolated capercaillie populations.

Methods

The model

The simulation model considers both males and females. One time-step in the model corresponds to one year in reality. A time-step starts in May with egg-laying. Individuals less than one year old are referred to as chicks. Within each time-step, the following seven processes occur one after the other (see Table 1 for parameter values and the following section for parameter choice):

1) Egg-laying: clutch size is determined from a discrete probability distribution (ClutchSize). One-year-old hens have smaller clutches than older hens (ClutchSize1yr);
2) Nest losses: entire clutches may be lost during incubation (ClutchSurv);
3) Hatching: a small proportion of eggs may fail to hatch (HatchRate);
4) Early chick survival: young chicks may die related to wet weather (Moss 1985, Klaus, Andreev, Bergmann, Müller, Porkert & Wiesner 1989). Each year, a survival rate is drawn from a discrete probability distribution that reflects rainfall in early summer (see Table 1). Early chick survival is the process in which environmental noise (Burgman, Ferson & Akakaya 1993) comes into play in the model (EarlyChickSurv);
5) Mortality: all other sources of mortality are subsumed under survival rates over the whole year (AdultSurv, OneAdultSurv) or, for the chicks, over summer and winter (SummerChickSurv and WinterChickSurv). In the model, survival rates (including HatchRate and ClutchSurv) are interpreted as survival probabilities (Burgman et al. 1993), thus mimicking demographic noise;
6) Ageing: at the end of the simulation year, the age of all individuals is incremented by one year. Individuals which grow older than MaxAge are removed;
7) Density dependence: population growth is never unlimited because resources (e.g. space) are limited or because emigration and mortality (due for instance to predation or parasites) may increase at high densities. If mechanisms of density dependence are considered in a model, an equilibrium population size will exist which is usually referred to as 'carrying capacity' (e.g. Wissel 1989). For capercaillie, however, the mechanisms of density dependence are not well understood. Therefore, we assumed a ceiling population size K: if the number of adults exceeds K, adults of randomly determined age and sex are removed from the population until the population size is equal to K (Burgman et al. 1993). We will refer to K as to the 'maximum capacity of the habitat' or, for short, the 'capacity'. K is the maximum conceivable population size in a given habitat, which may be reached after an unusually long period of 'good years'. Since nothing is known about inbreeding depression in capercaillie, the model ignores genetic effects.

Because of the numerous random events in the model, no single model run is representative. We thus ran - for a given set of model parameters - the model at least 1,000 times. At the beginning of each simulation, the population consisted of K/2 adults of randomly determined sex and age. Each single simulation was run until either the population died out or until the time horizon specified was reached. Using the so-called "$\ln(1-P_0)$-plot" (Wissel, Stephan & Zaschke 1994, Stelter, Reich, Grimm & Wissel 1997), the mean time to extinction was determined from the distribution of extinction times.

Model parameters

The parameters of the model were largely estimated based on the results of a telemetry study in the Teisenberg area in the Bavarian Alps, Germany (Storch 1993a,b, 1994; I. Storch, unpubl. data). As demographic data from Teisenberg were based on small samples, parameter estimates should be considered as preliminary. Additional information was taken from the literature.

In the model, capercaillie lived for a maximum of 10 years (MaxAge), the highest age documented for a tagged bird at Teisenberg (I. Storch, unpubl. data). For clutch survival (ClutchSurv) (Storch 1994), hatching rate (HatchRate) (Storch 1994) and adult survival (AdultSurv) (Storch 1993b), mean values from Teisenberg were rounded off to the closest 5% and adopted.

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For clutch size, a probability distribution was modelled using Teisenberg data (Storch 1994, I. Storch, unpubl. data). Yearling capercaillie hens are generally believed to lay smaller clutches than older hens (Klaus et al. 1989, Lindström, Ranta, Lindén & Lindén 1997); one yearling from Teisenberg laid five eggs. In the model, clutches of 4-6 eggs were assumed for yearling females (ClutchSize1yr).

Early chick survival (EarlyChickSurv), i.e. during the first two weeks after hatching, is largely weather dependent (Moss 1985, Klaus et al. 1989). Female chicks generally survive better than male chicks. This is most pronounced in years with wet weather during early summer (Klaus et al. 1989). On Teisenberg, an area with very wet summers (rainfall from June to July averaged 401 mm during 1961-1996), early chick survival averaged 38% (Storch 1994). To assess the variability of early chick survival, we used rainfall data from the Anger-Stoissberg weather station collected during 1961-1996 (courtesy of M. Hirschberg, Munich University). However, even in years with above-average rainfall (1990: 558 mm; 1991: 469 mm; 1993: 538 mm), not all broods are equally exposed to rain, and some chicks of radio-tagged hens survived (I. Storch, unpubl. data). This may be because even in wet years rainfall is unevenly distributed over time, and hatching dates on Teisenberg are spread over a period of five weeks (early June - mid July; Storch 1994). Thus, even in extremely wet years some chicks may escape weather-related mortality.

Based on these considerations, a probability distribution was constructed for early chick survival. The amount of rain in June and July was divided into 100-mm classes ranging within 100-600 mm. A maximum and minimum survival rate were attributed to the extreme rainfall classes. For the other classes, survival rate was assumed to decrease linearly with rainfall (see Table 1).

On Teisenberg, 20% of the chicks which hatched survived until autumn (Storch 1994). Summer chick survival (SummerChickSurv) was modelled accordingly; female chicks were assumed to survive better than males (Wegge 1980). Thereafter, as in adults (Storch 1993b), males survived better than females, and survival rates were assumed to improve with increasing age of the birds (WinterChickSurv; OneAdultSurv; AdultSurv).

Assessing minimum viability

For a given capacity of the habitat, K, the risk of extinction after 100 years was determined using a protocol developed by Hildenbrandt, Bender, Grimm & Henle (1995): each time a certain population size, N, occurred during simulation the remaining time to extinction, T_E, was registered. Then, after a sufficient number of simulation years (10^5-10^6) the probability of extinction after 100 years when starting with N individuals, $P_{0,N}(100)$, was calculated as the number of cases in which T_E was less than or equal to 100 years divided by the number of all the cases registered.

To determine the minimum capacity K needed for viability, first the critical mean time to extinction was determined according to the relationship between mean time to extinction, T_m, and the probability of extinction by time t, $P_0(t)$:

$$P_0(t) \approx t / T_m \Leftrightarrow T_m \approx t / P_0(t) \qquad (1).$$

This approximation holds for small values of $P_0(t)$ and for population sizes which are within the range of 'normal' fluctuations of population size, i.e. for which the extinction risk within one year is approximately $1/T_m$ (Stephan 1992, Wissel et al. 1994). We used an extinction threshold and a time horizon of 1% in 100 years.

According to equation 1, the critical mean times to extinctions which correspond to 1% in 100 years (this paper) and 5% in 50 years (Marshall & Edwards-Jones 1998) were 100/0.01 = 10,000 years and 50/0.05 = 1,000 years, respectively. A plot of T_m versus the capacity K then delivered the critical size of K needed for viability.

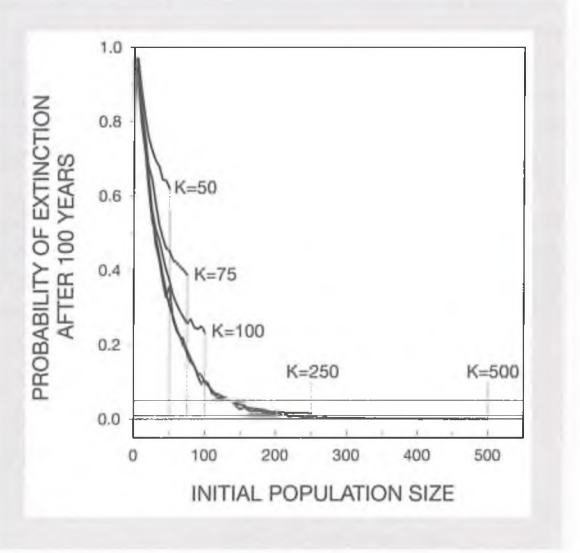


Figure 1. Probability of extinction after 100 years in relation to initial population size at time t = 0 for five different capacities (K) of the habitat. The parallels to the x-axis indicate an extinction risk of 5 and 1%, respectively (for the model parameters used see Table 1).

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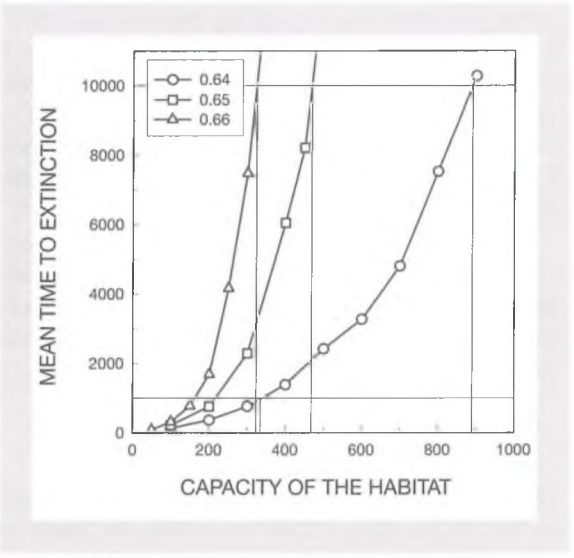


Figure 2. Mean time to extinction, T_m, (in years) versus capacity of the habitat for three values of the adult female survival rate AdultSurvFemale. The line at T_m = 10,000 indicates the threshold mean time to extinction needed to fulfil our criterion of viability (extinction risk not larger than 1% in 100 years); the line at T_m = 1,000 indicates the threshold for the criterion used by Marshall & Edwards-Jones (1998) (5% in 50 years). AdultSurvFemale = 0.65 corresponds to the default parameter set of Table 1. The minimum capacities needed for the viability of the three cases are 890, 470 and 323 for AdultSurvFemale = 0.64, 0.65, and 0.66, respectively. The minimum capacity for the default parameters and the criterion of 5% in 50 years is about 215.

Table 1. Model parameters.

Parameter	Default value
MaxAge [years]	10
ClutchSurv	0.65
HatchRate	0.95
SummerChickSurvMale	0.5
SummerChickSurvFemale	0.6
WinterChickSurvMale	0.75
WinterChickSurvFemale	0.55
OneAdultSurvMale	0.8
OneAdultSurvFemale	0.6
AdultSurvMale	0.85
AdultSurvFemale	0.65
K [individuals]	100
ClutchSize1yr*	.3/4, .4/5, .3/6
ClutchSize*	.05/5, .2/6, .5/7, .2/8, .05/9
EarlyChickSurvMale**	0/.9, .139/.71, .389/.52, .305/.33, .167/.15
EarlyChickSurvFemale**	0/.9, .139/.78, .389/.67, .305/.56, .167/.45

* probability/clutch size
** probability/survival rate

Results

In order to determine the minimum viable population size for a given habitat, the probability of extinction after t = 100 years versus initial population size at time t = 0 for five different capacities K is given (Fig. 1). Only for a capacity of K = 500 did the extinction risk fall below the threshold of 1%. In this case, the minimum viable population size was about 240 individuals. For K = 250, the extinction risk fell below the 5%, but not the 1% mark. For all smaller capacities, population size never reached the minimum viable population size. However, it should be noted that even for a capacity of K = 100, a current population size of 50 led to an extinction risk of about 35%, i.e. there is a 65% chance that the population will still exist after 100 years. The mean time to extinction, T_m was plotted versus K to assess the minimum capacity K needed for viability (Fig. 2). For the default parameter set of Table 1, the minimum capacity for viability was about 470. The sensitivity of this result was tested by running the model with a single parameter slightly changed at a time. Figure 2 shows the results for the parameter which is known to strongly affect the extinction risk (Verboom, Metz & Meelis 1993): female survival rate, AdultSurvFemale. Besides this first scenario, the following scenarios are compiled in Table 2: 2) variation of nest losses (ClutchSurv); 3) changing the probability distribution

Table 2. Minimum capacity, K, needed for viability (extinction risk less than or equal to 1% in 100 years) for different variations of the model parameters. All parameters except those explicitly mentioned here are as in Table 1.

Scenario	Parameter changed	Value	Minimum capacity
1	AdultSurvFemale	0.65	470 *
		0.64	890
		0.66	323
2	ClutchSurv	0.64	785
		0.66	338
3	Probabilities of EarlChickSurv (♀ and ♂)**	0, 0.1737, 0.35, 0.274, 0.20 (flattened distribution)	505
		0, 0.125, 0.404, 0.32, 0.15 (more peaked distribution)	460
4	Range of EarlyChickSurvFemale**	0.9, 0.77, 0.65, 0.52, 0.4 (broadened range)	>>1000 ***
		0.9, 0.8, 0.7, 0.6, 0.5 (narrowed range)	122
5	Distribution of clutch size of one-year-old hens (ClutchSize1yr)	.2/4, .3/5, .3/6, .2/7	265

* Reference value obtained with the parameter set of Table 1.
** See text for explanation.
*** Presumably several thousands (T_m for K = 900 was less than 400 years).

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of early chick survival: 'more peaked' (taking 10% off the two extreme classes and adding these to the two central classes) and 'more flattened' (adding 10% from the two central classes to the two extreme classes); 4) changing the range of survival rates attributed to the rain fall classes: 'narrowing' ([0.5, 0.9]) and 'broadening' ([0.4, 0.9]); and 5) modifying the distribution of clutch sizes of one-year-old hens leading to a higher mean clutch size of 5.5 (instead of 5.0 in Table 1).

The minimum capacities following from these five scenarios vary between 122 and 890, except for the 'broadened' range of scenario 4) where capacities even larger than 1,000 did not allow viability.

Discussion

'Minimum viable population' (MVP) means two different things: first, for a given habitat which is large enough, the threshold population size needed for viability, for example 240 individuals in a habitat with a capacity of 500 (see Fig. 1); and second, the minimum capacity of a habitat needed for viability, e.g. 470 (see Fig. 2). These two aspects of MVP are often confused, although evidently 'population size' has to be distinguished from 'capacity'. In contrast to Shaffer's original definition of MVP (see Introduction) we consider the latter aspect, which refers to area requirements, as more relevant: how large a habitat ought to be to allow viability. Therefore, in the following we focus on the minimum capacities needed for viability.

Marshall & Edwards-Jones (1998) determine a minimum capacity of 150 individuals, whereas we end up with a minimum capacity of about 470 based on the default parameter set. These two values cannot be compared directly because they are based on different definitions of viability. Our Figure 2, however, allows us to determine the minimum capacity needed for viability for any definition of viability. For example, imposing the critical mean time to extinction which corresponds to Marshall & Edwards-Jones' (1998) definition of viability, i.e., 1,000 years, leads to a minimum capacity of about 215 individuals. Thus, the estimate of the minimum capacity needed for viability based on VORTEX (150) is more optimistic than our estimate. This may be due to differences in demographic parameters of capercaillie in Scotland and in the Bavarian Alps, which certainly exist, but may also be affected by differences in model structure.

Moreover, Marshall & Edwards-Jones' (1998) parameter values for environmental fluctuations, which are known to largely determine the extinction risk (Wissel et al. 1994), are not based on real-world data, but on the default values of VORTEX. Likewise, they used VORTEX default processes of inbreeding depression (Marshall & Edwards-Jones 1998). It remains unclear if the usage of some of the more or less arbitrary default parameters and processes of VORTEX increase or decrease the difference between our (this paper) and Marshall & Edwards-Jones' (1998) estimates.

The minimum capacity needed for viability as predicted by our model, 470, seems to support earlier estimates of an MVP of 500 (Storch 1995). Yet this conclusion would be premature, because any model's results depend on a set of assumptions. Two aspects of these assumptions are particularly important: uncertainty in model parameters and uncertainty in model structure (Beissinger & Westphal 1998).

As to the first aspect: Our results confirm what is known in general from population viability analyses. Even relatively small changes in the parameters which have a strong impact on the intrinsic rate of increase lead to considerable changes in the predicted extinction risk and, in turn, minimum capacity (see Table 2), i.e. female survival rate, clutch survival and the recruitment of female chicks. Of similar importance is the extent of environmental fluctuations, i.e. year-to-year variations in early chick survival. The lesson to be learned from Table 2 is that linking capercaillie or any other species to one particular minimum viable population size or minimum capacity needed for viability is insignificant because demographic and environmental parameters will be different in different parts of the range. Therefore, questions of viable populations and minimum area requirements of capercaillie cannot be solved with results from a particular parameter set alone. Consequently, we plan to parameterise our model for a host of parameter sets from different parts of the range. In addition, we will equip our simulation programme with a user-friendly interface and will make it generally available.

Besides the uncertainty of model parameters, the model structure may be inappropriate. Our model is extremely simple and corresponds to a stochastic version of Leslie-matrix models (e.g. Burgman et al. 1993). Therefore we may have missed additional processes which may have a strong impact on extinction risk. For example, it is known that the particular mechanism of density dependence may sharply affect the extinction risk (Beissinger & Westphal 1998). However, at present the database for a more detailed model seems slim because most research on capercaillie has focused on other problems than those relevant to modelling the dynamics of small populations. Still, our model can be

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used for relative assessments of viability (Beissinger & Westphal 1998) but for more quantitative assessments and for verifications of the model using secondary predictions (*sensu* Beissinger & Westphal 1998), more research is needed which focuses on demography and on patterns which might be used for model construction, parameterisation and verification ('pattern-oriented modelling', Grimm 1994, Grimm, Frank, Jeltsch, Brandl, Uchmański & Wissel 1996).

Despite all uncertainties, our results suggest that (isolated) populations of capercaillie living in habitats which can support less than 100 individuals are not viable, i.e. have an extinction risk larger than 1% in 100 years. Habitats that lead to similar demographic parameters as those in the Bavarian Alps should be able to support at least about 500 individuals for a capercaillie population to be viable. Population densities of capercaillie vary considerably between different parts of its range. In some areas of Russia, 20 birds may be counted per km² (Klaus et al. 1989), whereas in the Bavarian Alps, two birds per km² (averaged over areas of about 50 km²) must be considered a high density (I. Storch & A. Zeitler, unpubl. data). Thus, under the present Bavarian circumstances, an area of about 250 km² is needed to sustain a population of about 500 capercaillie.

This paper exclusively addressed isolated populations. If local populations are linked via dispersing juveniles, metapopulation theory predicts that the whole network may be viable even if none of the local populations is viable. We assume that this is the case for capercaillie in the Bavarian Alps where small populations living on forested mountains ranges of 50-100 km² in size are separated by farmland valleys (Storch 1993b, 1997, Storch & Segelbacher 2000). The ultimate goal of the model presented here is to use it as a building block for a spatially-structured model. With such a model, we will be able to study the relative effects of habitat capacity and fragmentation.

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