BioOne COMPLETE

Population viability analysis of the Japanese rock ptarmigan Lagopus muta japonica in Japan

Authors: Suzuki, Ayaka, Kobayashi, Atsushi, Nakamura, Hiroshi, and Takasu, Fugo

Source: Wildlife Biology, 19(4) : 339-346

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/13-021

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Wildl. Biol. 19: 339-346 (2013)
DOI: 10.2981/13-021
© Wildlife Biology, NKV
www.wildlifebiology.com

Original article

Population viability analysis of the Japanese rock ptarmigan *Lagopus muta japonica* in Japan

Ayaka Suzuki, Atsushi Kobayashi, Hiroshi Nakamura & Fugo Takasu

The Japanese rock ptarmigan *Lagopus muta japonica* breeds only in limited alpine areas at high elevations (> 2,500 m a.s.l.) in Japan. The estimated population size is about 2,000 birds and their breeding distribution is subdivided into several local areas, in each of which they may be at risk of local extinction. We estimated age-specific demographic parameters of the core population breeding on Mt. Norikura in Gifu and Nagano prefecture in Japan. We also estimated population viability using deterministic and stochastic population models. Age-specific fertility (the number of female offspring that survived to the next breeding season per female) was 0.417 ± 0.086, 0.490 ± 0.080, 0.513 ± 0.153, 0.435 ± 0.078, 0.562 ± 0.139, 0.580 ± 0.122 (mean ± SE) for ages 1-6+, respectively. The annual survival rate was 0.739 ± 0.047, 0.624 ± 0.064, 0.513 ± 0.087, 0.732 ± 0.151, 0.447 ± 0.220, 0.486 ± 0.089. The population growth rate, evaluated by use of a deterministic projection-matrix model, predicted a stable population, $\lambda = 1.105 \pm 0.063$, 95% CI = 0.985-1.231 and $\lambda = 1.114 \pm 0.062$, 0.996-1.239, using two different assumptions for the final age of reproduction by ptarmigan. We evaluated the risk of extinction as the proportion of λs that was < 1, and this was $\leq$ 4.4%. To complement the deterministic model, we developed an individual-based stochastic population model in which each of the individuals produced a variable number of offspring and survived one year with certain probabilities that were drawn from estimated distributions of age-specific clutch size and survival rates. Averaged population growth rate under the stochastic model was $\lambda = 1.1$, and the risk of extinction defined as the proportion of trials in which population size ≤ 1 within 30 years was $\leq$ 8.9%, even when the starting population was small (15 birds). These results suggest that the local population at Mt. Norikura is stable in size and suffers a relatively low risk of extinction. We suggest that this population can serve as a potential source for surrounding small local populations that may be sink populations.

Key words: individual-based model, Lagopus mutus japonica, matrix projection model, population viability analysis, risk of extinction, rock ptarmigan

Ayaka Suzuki & Fugo Takasu, Department of Information and Computer Sciences, Nara Women's University, Kita-Uoya Nishimachi, Nara 630-8506, Japan - e-mail addresses: suzuki-ayaka0820@ics.nara-wu.ac.jp (Ayaka Suzuki); takasu@ics.nara-wu.ac.jp (Fugo Takasu)
Atsushi Kobayashi, Department of Biology, Toho University, Miyama 2-2-1, Funabashi 274-8510, Japan - e-mail: a.kobayashi0820@gmail.com
Hiroshi Nakamura, Department of Education, Shinshu University, Nishi Nagano, Nagano 380-8544, Japan - e-mail: hnakamu@shinshu-u.ac.jp

Corresponding author: Fugo Takasu

Received 29 January 2013, accepted 3 August 2013

Associate Editor: R.J. Gutiérrez

The Japanese rock ptarmigan *Lagopus muta japonica* breeds in alpine zones in central Honshu Island, Japan. Its breeding range is limited to several high mountains (> 2,500 m a.s.l.). This population is the most southerly distributed rock ptarmigan in the world and is completely isolated from continental populations. Haneda et al. (1985) estimated the population to be 3,000 in the 1980s. These populations are relict of ice age distributions of ptarmigan and form a meta-population of local populations inhabiting isolated mountains (Nakamura 2007). Several populations on separate

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

mountains have either declined or become extirpated since the 1930s (Nakamura 2007). Causes of these declines are poorly understood but loss of, and damage to, habitat caused by Japanese deer *Cervus nippon* and Japanese macaque *Macaca fuscata* and an increase of predation pressure by red fox *Vulpes vulpes japonica* and jungle crow *Corvus macrorhynchos* may be responsible for the population declines (H. Nakamura, unpubl. data).

Because of the decline in many local populations, we studied the population viability of ptarmigan in one core population with the goal to enhance conservation of ptarmigan in Japan. Most population viability analyses of ptarmigan have employed deterministic models (e.g. Sandercock et al. 2005a,b, Wilson & Martin 2011). However, Novoa et al. (2011) used stochastic population models in which demographic stochasticity was explicitly considered. In this approach, a population was extinct once the population size became zero, unless the population was recolonised by immigrants. These approaches provided different insights to the species' population dynamics and evaluation of risk of extinction. Therefore, we developed both deterministic and stochastic population models to project age-structured population dynamics of a population of Japanese rock ptarmigan. Our objective was to assess population viability of a core rock ptarmigan population in Japan and its risk of extinction.

Material and methods

Study areas

Our study area was Mt. Norikura (3,026 m, 36°06'N, 137°32'E) in the Northern Alps of Japan. This alpine zone (> 2,500 m a.s.l.) was isolated from other alpine zones on adjacent mountains by forested slopes and valleys. The area of ptarmigan breeding range was 14.4 km^2 with creeping pine *Pinus pumila* and evergreen dwarf bushes such as black crowberry *Empetrum nigrum var. japonicum*, cowberry *Vaccinium vitis-idaea* and yellow-flowered rhododendron *Rhododendron aureum* as the major cover type. Creeping pine was important for nesting sites (Sawa et al. 2011), and dwarf bushes were important feeding sites for females and broods (Kobayashi & Nakamura 2011).

Field surveys

During April-November 2006-2011, we regularly traversed the study area and visually searched for ptarmigan using 8 x binoculars and normal vision and also listened for vocalising birds. We conducted one to four surveys each month. When we detected an unmarked individual, we slowly approached and captured the bird using a noose pole (Zwickel & Bendell 1967); we then ringed the bird with a numbered aluminum band and a unique colour combination (see below). We also recorded the bird's age, sex (based on feather colour) and location, using a GPS. When we detected a marked bird, we recorded its sex, age and its unique colour combination. Rock ptarmigan in Japan are not afraid of humans and are easy to catch (Nakamura 2010). We recorded morphometries of captured individuals including mass and wing length. We determined age class by comparing pigmentation patterns of the two outermost primaries (9 and 10) to adjacent remiges. Yearlings (i.e. 1 year old) had pigmented feathers, whereas adults (i.e. 2+ year old) had white feathers. We ringed captured individuals with plastic rings (A.C. Hughes, size no. 10) with five colours: red, white, black, light-blue and yellow. We used four rings to identify each individual with a unique colour combination and we attached two rings to the right leg and two to the left leg.

When we found a ptarmigan nest, the age i of the nesting female and the number of eggs in the nest were recorded to estimate age-specific clutch size C_i. We defined clutch size as the number of eggs in the first nesting attempt during the incubation period. We had detailed clutch-size data only for age classes up to six-year-old females ($i = 1, 2, ..., 6$). However, we confirmed that females lived up to 10 years. We, therefore, assumed six age classes ($i = 1, 2, ..., 6+$) for purposes of our analysis. We regularly revisited nests to record presence of unhatched eggs or egg shell remains to estimate nest success, hatching success and cause of predation.

Analysis and modelling

We estimated total hatching success, $S_{\text{egg to hatch}}$, defined as the probability of an egg successfully hatching, as the product of nest success and hatchability. We estimated nest success using the Mayfield method (Mayfield 1961, 1975). Most nests were found during the incubation period, but we did not know either the initial date of egg laying or the length of the laying period, so we estimated nest success during the incubation period. We first calculated daily nest survival using the nest survival procedure in the program MARK, version 4.3 (White & Burnham 1999).

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

The mean incubation period was 22 days (Omachi Alpine Museum 1992) and total nest success was calculated as the daily survival rate raised to the 22nd power. Hatchability was calculated as the proportion of eggs that successfully hatched and chicks that left the nest. This proportion was calculated only using successful nests ($\geq$ 1 egg hatched). The 95% confidence interval was calculated by the Wald procedure as modified by Agresti & Coull (1998). Because the number of eggs was large enough, we assumed that total hatching success was estimated as a constant without any estimation error.

Difference in clutch size and hatchability among age classes was analysed using program R, version 2.15.0, and tested by Tukey's and contingency tests, respectively. Difference in daily survival rates among age classes was analysed by post hoc comparisons of survival using program CONTRAST (Hines & Sauer 1989).

We tracked the presence of hatched birds to the next breeding season. To estimate survival rate during this period, we divided the period into three subperiods; $S_{\text{hatch to independence}}$ included after hatching to independence from parental care in late September, $S_{\text{independence to October}}$ included after independence to late October and $S_{\text{October to next year}}$ included after late October to the next breeding season when birds are one year old (yearlings). We estimated chick survival rate after hatching to independence $S_{\text{hatch to independence}}$ by dividing the average brood size in late September just before independence by the brood size within a week after hatching. We only used marked females that hatched eggs successfully and all broods were pooled because the number of females in each age class was not large. The 95% CI was calculated in the same way as for hatchability. We began capturing and marking chicks and juveniles in early September. As some chicks and juveniles could not be sexed at the timing of capture, we estimated $S_{\text{independence to October}}$ and $S_{\text{October to next year}}$ using all banded birds within the year of their birth. We here assumed that no juvenile emigrated from our study area and none immigrated from other local populations for the sake of analytical simplicity. These assumptions were likely justified because Mt. Norikura is an isolated mountain, located too far ($>$ 20 km) from neighbouring local populations for juvenile to disperse. We therefore conducted a direct estimate of juvenile survival from mark-recapture data.

We defined age-specific fertility, F_i, as the number of female offspring that survived to the next breeding season/female aged i, and estimated this as:

$$F_i = C_i \times S_{\text{egg to hatch}} \times 0.5 \times S_{\text{hatch to independence}} \times S_{\text{independence to October}} \times S_{\text{October to next year}} \quad (1),$$

where C_i was drawn from a normal distribution with the estimated age-specific mean of clutch size with 95% CI, and $S_{\text{egg to hatch}}$ was an age-specific constant of total hatching success, 0.5 was the ratio of females assuming an equal primary sex ratio of 1:1, and $S_{\text{hatch to independence}}$, $S_{\text{independence to October}}$ and $S_{\text{October to next year}}$ were drawn from beta distributions with the estimated mean with 95% CI for each subperiod, respectively. We repeated this process 100,000 times to generate distribution of F_i's.

We defined age-specific apparent survival rates of adults (S_i,i = 1, 2, ..., 6+) as the probability that a female aged i survived to the next breeding season to be one year older. We assumed again that there was no dispersal of adult birds, although occasional dispersal that is too rare to affect our estimate of survival rates may occur. Therefore, to estimate S_i, we analysed mark-recapture data using program MARK in which encounter histories (recapture probabilities) were explicitly considered. We assumed the following three global models for mark-recapture data; $\varphi_{\text{ju-1ac,t}}$, $\varphi_{\text{yr-5ac}}$, $\varphi_{\text{ad-1ac}}$ and p_t. The model $\varphi_{\text{ju-1ac,t}}$ had one age class and time dependent survival rate, which included all birds marked as chicks or juveniles within the year they were born. The model $\varphi_{\text{yr-5ac}}$ had five age classes for birds captured as yearlings and $\varphi_{\text{ad-1ac}}$ had one age class including all individuals aged $>$ 6 years. All models assumed time dependence (t) in the probability of encounter p_t.

We conducted post hoc comparisons of age-specific survival rates with the program CONTRAST. All banded birds of known age were used and we pooled multiple years to estimate age-specific variation in demographic parameters.

Deterministic population model

Once we determined a set of age-specific demographic parameters of fertility F_i and annual survival rates S_i (i = 1, 2, ..., 6+), we constructed a projection matrix A that described deterministic dynamics of age-structured population as follows (Caswell 2001):

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

$$\mathbf{A} = \begin{pmatrix} F_1 & F_2 & F_3 & F_4 & F_5 & F_6 \\ S_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_4 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_5 & S_{6+} \end{pmatrix}$$

where F_i was drawn from the distribution generated by equation (1) and S_i was drawn from a beta distribution with corresponding estimated average and 95% CI. The finite rate of population change λ was given by the dominant eigenvalue of A. We repeated this process 100,000 times to derive the distribution of λ. The risk of population extinction was evaluated as the proportion of λs that were < 1.

We considered two scenarios to construct our projection matrices: 1) that females stopped breeding after the age of six, in which annual survival rate of 6+ class, S_{6+}, was set to zero in the (6, 6) element of A (females aged over six did not contribute reproduction at all), and 2) that females aged over six continued breeding with the same reproductive performance and survived as those of age six. The former can be seen as a minimum estimate and the latter as a maximum estimate of reproductive performance extrapolated after six years of age.

We conducted sensitivity and elasticity analysis of λ to F_i and S_i using standard formulas (Caswell 2001) to evaluate how perturbation in these parameters affects λ. In these analyses, we only focused on females assuming equal primary sex ratio of 1:1 at hatching. We also assumed that the population was closed and that no emigration or immigration occurred.

An individual-based stochastic population model

The deterministic model based on the projection matrix completely ignores demographic stochasticity that can be important for small populations because there is a risk of extinction by chance even when $\lambda > 1$ (Shaffer 1981). To compliment the deterministic model, we constructed an individual-based stochastic population model in which birth and survival of individual birds were simulated as follows:

1) Each individual was assigned a set of properties that affected breeding performance and survival rate. In this model we assigned non-negative integer-valued age to each individual (age 0 was chick, age 1 was yearling and ages > 2 were adults).
2) Each female completed a clutch whose size followed a normal distribution with the estimated average and 95% CI depending on its age. Actual clutch size was truncated to the nearest integer value. Because this truncation inflated the variance in clutch size, we used standard errors that were 5% smaller than the estimated value so that the simulated clutch sizes matched the estimated age specific 95% CIs.
3) Each egg hatched, and its sex was set as female with equal primary sex ratio of 1:1 and survived one year to be yearling with the probability $S_{\text{egg to hatch}} \times 0.5 \times S_{\text{hatch to independence}} \times S_{\text{independence to October}} \times S_{\text{October to next year}}$ where each of the three subperiod survival rates after hatching was drawn from a beta distribution with the estimated mean and 95% CI. Yearlings and adults survived one year with age specific annual survival rate S_i that followed a beta distribution with the estimated average and 95% CI ($i = 1, 2, ..., 6+$). As with the deterministic model, annual survival rate for females aged > 6 was set to zero in the minimum scenario, while it was set to S_{6+} in the maximum scenario.
4) At the beginning of breeding season, the age of all birds was incremented by one. These rules of birth and survival were implemented by program language C and constituted the individual-based stochastic population model in which population size was non-negative integer.

Starting from an initial population where the numbers of individuals with certain ages were given, we projected the population dynamics for 30 years. Using the same initial population, we repeated the projection 1,000 times. We calculated the average over the 1,000 trials and derived annual growth rate by linear regression of logged data. The risk of population extinction was evaluated by the percentage of trials in which the population size was ≤ 1 during 30 years. As in the deterministic model, we only focused on females and no immigration was considered.

Results

Demographic parameters

Table 1 summarises age-specific clutch size, nest success, hatchability and total hatching success, S_{egg}

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Table 1. Age-specific clutch size, nest success, hatchability and total hatching success of Japanese rock ptarmigan at Mt. Norikura, Japan, during 2006-2011.

Age i	Clutch size (N)	Daily survival rate	Total nest success	Hatchability (N)	Total hatching success, $S_{egg\ to\ hatch}$
1	5.50 ± 0.223 (16)	0.986 ± 0.008 (15)	0.733 ± 2.130	0.853 (68)	0.625
2	6.27 ± 0.196 (11)	0.982 ± 0.011 (11)	0.671 ± 2.578	0.962 (52)	0.645
3	5.78 ± 0.520 (9)	0.987 ± 0.013 (9)	0.750 ± 3.608	0.978 (45)	0.733
4	6.00 ± 0.269 (8)	0.977 ± 0.024 (8)	0.599 ± 4.320	1.000 (29)	0.599
5	5.63 ± 0.421 (8)	1.000 ± 0.000 (8)	1.000 ± 0.000	0.824 (34)	0.824
6+	5.71 ± 0.359 (7)	1.000 ± 0.000 (6)	1.000 ± 0.001	0.839 (31)	0.839
Total	5.78 ± 0.131 (59)	0.987 ± 0.004 (57)	0.750 ± 1.201	0.907 (259)	0.680

Mean ± SE (N) or frequency (N)

$_{to\ hatch}$. Clutch size was not different among the six age classes (Tukey's test: $F_{5,\ 58} = 0.97$, $P = 0.51$). Hatchability was different among the six age classes (Contingency test: $\chi^2_5 = 14.4$, $P < 0.05$); it was low for the age 1 and 5 and 6+ classes. Total hatching success, $S_{egg\ to\ hatch}$, tended to be higher for older age classes.

Survival rate after hatching to independence, $S_{hatch\ to\ independence}$, was significantly lower than survival rates after independence, $S_{independence\ to\ October}$ and $S_{October\ to\ next\ year}$ (Table 2); chicks suffered a high mortality before independence.

Table 3 summarises age-specific fertility F_i and annual survival rate S_i of females aged i (i = 1, 2, ..., 6+). Fertilities did not depend on the age and there was no significant dependency of survival rates on age (Post hoc test by Program R Contrast: $\chi^2_5 = 9.07$, $P = 0.106$).

Deterministic model - Finite rate of population change and the risk of extinction

We estimated the mean finite rate of population change to be $\lambda = 1.105 \pm 0.063$, 95% CI = 0.985-1.231 in the minimum scenario and $\lambda = 1.114 \pm 0.062$, 0.996-1.239 in the maximum scenario. The proportion of λs that were < 1 was 4.4 and 2.9% (4,440 and 2,933 in 100,000 trials, respectively) in the minimum and the maximum scenario, respectively.

Table 2. Survival rates of Japanese rock ptarmigan after hatching to the next breeding season at Mt. Norikura, Japan, during 2006-2011.

			95%CI	
Period	Estimate	SE	Lower	Higher
From hatch to independence, $S_{hatch\ to\ independence}$	0.305	0.031	0.247	0.369
From independence to late October, $S_{independence\ to\ October}$	0.832	0.059	0.682	0.919
From late October to the next breeding season, $S_{October\ to\ next\ year}$	0.955	0.011	0.928	0.97

Sensitivity and elasticity analysis

Improvement of fertility in the age 1 class resulted in the highest contribution to λ, and that of survival of the age 1 class the next highest (Table 4). The sensitivities to fertilities and survival rates decreased nearly exponentially as age increased. The elasticities also showed the same tendency; they continuously

Table 3. Age-specific fertility, F_i (A), and apparent annual survival rates, S_i (B), of female Japanese rock ptarmigan during 2006-2011.

A) Fertility

			95% CI	
Age i	Estimate	SE	Lower	Upper
1	0.417	0.086	0.261	0.597
2	0.490	0.080	0.344	0.658
3	0.513	0.153	0.230	0.832
4	0.435	0.078	0.294	0.598
5	0.562	0.139	0.308	0.853
6+	0.580	0.122	0.360	0.836

B) Apparent annual survival rate

			95% CI	
Age i	Estimate	SE	Lower	Upper
1	0.739	0.047	0.637	0.82
2	0.624	0.064	0.493	0.740
3	0.513	0.087	0.348	0.676
4	0.732	0.151	0.376	0.925
5	0.447	0.220	0.123	0.823
6+	0.486	0.089	0.320	0.656

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Table 4. Sensitivity and elasticity of λ to age specific fertility, F_i, and annual survival rate, S_i (i = 1, 2, ..., 6+).

	F_1	F_2	F_3	F_4	F_5	F_{6+}	S_1	S_2	S_3	S_4	S_5	S_{6+}
Sensitivity	0.435	0.289	0.161	0.074	0.049	0.034	0.411	0.261	0.156	0.065	0.045	0.032
Elasticity	0.163	0.127	0.074	0.029	0.025	0.018	0.273	0.146	0.072	0.043	0.018	0.014

decreased as age increased with the elasticity to the survival rate of the age 1 class being highest.

Stochastic population dynamics - risk of extinction for a small-sized population

Our simulated population eventually grew in size when the population was initially set small (15 females 6-years old) with an annual growth rate of 1.106 and 1.110 in the minimum and the maximum scenario, respectively (Fig. 1). In the minimum scenario, population size tended to decline in the early years because initial females of age 6 reproduced only once in the first year and then stopped breeding. The risk of extinction (population size ≤ 1 during 30 years) was 8.9% and 2.7% (89 and 27 in 1,000 trials) in the minimum and the maximum scenario, respectively.

Discussion

We evaluated age-specific fertilities and survival rates of rock ptarmigan population breeding on Mt. Norikura, Japan. Overall, clutch size tended to be lower in our population compared with others; mean clutch size was 8.3 on Attu Island in the Aleutian Islands (Kaler et al. 2010), 6.5 and 5.9 in the French Alps and the eastern Pyrenees, respectively (Novoa et al. 2011). But annual survival rates were similar to Attu Island

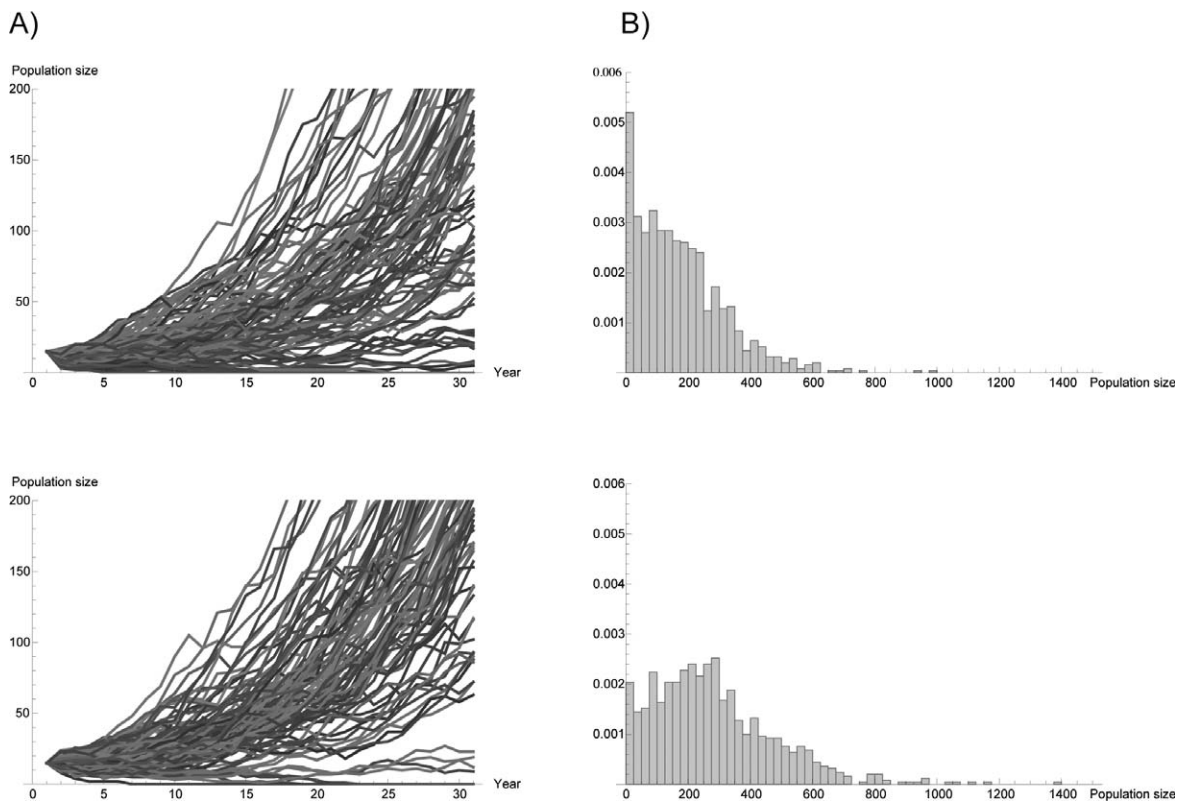


Figure 1. Stochastic population simulation of a Japanese rock ptarmigan starting with a population of 15 females of age 6. Temporal changes in population size after 100 trials (A) and distribution of population size at the 30th year calculated from 1,000 trials (B). The top and bottom two figures are for the minimum and the maximum scenario, respectively.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

(0.38 - 0.75; Kaler et al. 2010) and the French Alps (0.7 - 0.61; Novoa et al. 2011).

Population viability analysis using the deterministic population model and the estimated demographic parameters predicted that the local population of rock ptarmigan at Mt. Norikura would be stable in the near term. Our corresponding stochastic population model also showed that, although extinction could happen by demographic stochasticity, the risk was small; this risk we predicted to be no greater than 8.9%, even for a small-sized isolated population of about 30 birds (15 females with equal sex ratio). This result was similar to population growth estimate of willow ptarmigan *Lagopus lagopus* in Canada ($\lambda = 1.13 \pm 0.20$), but differed from white-tailed ptarmingan *L. lecurus* in the USA ($\lambda = 0.65 \pm 0.07$; Sandercock et al. 2005a) and rock ptarmigan in the northern French Alps and the eastern Pyrenees ($\lambda = 0.935$ and 0.804; Novoa et al. 2011).

Sensitivity and elasticity analysis showed quantitatively similar results to previous analysis of ptarmigan, that survival of juveniles and yearlings had stronger influence on λ than survival of adults (Sandercock et al. 2005b). Thus, conservation activities designed to increase nesting success and survival of chicks and yearlings will be desirable. Therefore, our results support the current conservation activity at Mt. Norikura where special care is being taken for chicks after hatching by providing them with a shelter from predators in order to increase their survival rate (H. Nakamura, unpubl. data).

Similar modelling approaches using matrix projection models and stochastic population models have been applied to the rock ptarmigan and related bird species (Caizergues & Ellison 1997, Johnson & Braun 1999, Grimm & Storch 2000, Sandercock et al. 2005a,b, Novoa et al. 2011, Wilson & Martin 2011). But, the classification of age classes was crude in these previous studies, with a maximum of three age classes assumed. Our study featured finer resolution by using six age classes. Although we did not find significant dependency of fertility and survival rate on female age, our study will enhance conservation planning by allowing more focused managing to improve survival of specific age classes.

The results of our analyses should be taken with caution because all analyses were based on the demographic data that were collected from the local population at Mt. Norikura. Thus, each local population in the Japanese Alps will likely have different environmental characteristics and would likely face different threats of environmental degradation and predation pressure. Therefore, demographic parameters may differ significantly among local areas. Further studies are needed to estimate demographic parameters in other local populations.

In the broader context of population dynamics of Japanese rock ptarmigan, there is a small ($\sim$ 30 individuals) local population that is found on Mt. Hiuchi (2,462 m) in the Niigata prefecture, about 40 km away from the core population breeding in the Northern Alps. This small population has persisted during the past 30+ years (H. Nakamura, unpubl. data), and it has been suggested that occasional and rare immigration to the small population could make it possible for it to persist for a long time (Nakamura et al. 2003). Although the risk of local extinction within 30 years is low in our simulation (see Fig. 1), it would be very unlikely that the Hiuchi population has the same demographic parameters as our study population on Mt. Norikura because the potential breeding area and the number of potential territories are much smaller at Mt. Hiuchi than at Mt. Norikura (Nakamura 2003). Thus, the Hiuchi population may behave as a sink population, and occasional dispersal from the core population in the Northern Alps may play an important role in persistence of this and other small populations. Martin et al. (2000) show that external recruitment is vital for the persistence of local populations of ptarmigan, but few data are available to estimate dispersal rates among local populations in Japan. We suggest that future research focus on dispersal and genetic variability to understand the mechanisms by which these locally isolated populations persist, and whether they function as either interacting meta-populations or independent populations.

Acknowledgements - we thank members of the laboratory of ecological research at Shinshu University, who helped us observe and collect data on rock ptarmigan demography since the 1970s. We also thank participants of the 12th International Grouse Symposium in Matsumoto, July 2012 for valuable feedback and comments on how to improve the analyses in this paper. Our special thanks go to B.K. Sandercock and an anonymous reviewer, and to R.J. Gutiérrez for valuable advice and comments to improve our paper.

References

Agresti, A. & Coull, B.A. 1998: Approximate is better than "exact" for interval estimation of binomial proportions. - American Statistician 52: 119-126.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Caizergues, A. & Ellison, L.N. 1997: Survival of black grouse *Tetrao tetrix* in the French Alps. - Wildlife Biology 3(3-4): 177-186.

Caswell, H. 2001: Matrix population models. 2nd edition. - Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts, USA, 722 pp.

Grim, V. & Storch, I. 2000: Minimum viable population size of capercaille *Tetrao urogallus*: results from a stochastic model. - Wildlife Biology 6(4): 219-225.

Haneda, K., Nakamura, H., Koiwai, A., Iizawa, T. & Tajima, K. 1985: Distribution and density of the rock ptarmigan *Lagopus mutus* in the Southern Japan Alps. - Tori 34: 33-48. (In Japanese with an English summary).

Hines, J.E. & Sauer, J.R. 1989: Program CONTRAST: a general program for the analysis of several survival or recovery rate estimate. - Fish and Wildlife Service Report 24, Washington, D.C., USA. - Available at: http://www.mbr-pwrc.usgs.gov/software/doc/contrast.html.

Johnson, K.H. & Braun C.E. 1999: Viability and conservation of an exploited sage grouse population. - Conservation Biology 13: 77-84.

Kaler, R.S.A., Ebbert, S.E., Braun, C.E. & Sandercock, B.K. 2010: Demography of a reintroduced population of Everrmann's Rock Ptarmigan in the Aleutian islands. - Wilson Journal of Ornithology 122: 1-14.

Kobayashi, A. & Nakamura, H. 2011: Seasonal change of food items of the Japanese Rock Ptarmigan. - Japanese Journal of Ornithology 60: 200-215. (In Japanese with an English summary).

Martin, K., Stacey, P.B. & Braun, C.E. 2000: Recurrent, dispersal, and demographic rescue in spatially-structured white-tailed ptarmigan populations. - Condor 102: 503-516.

Mayfield, H.F. 1961: Nesting success calculated from exposure. - Wilson Bulletin 73: 255-261.

Mayfield, H.F. 1975: Suggestions for calculating nest success. - Wilson Bulletin 87: 456-466.

Nakamura, H. 2007: Monograph Japanese Rock Ptarmigan *Lagopus mutus japonicus*. - Japanese Journal of Ornithology 56: 93-114. (In Japanese with an English summary).

Nakamura, H. 2010: Why Japanese rock ptarmigan never fear humans. - Grouse News 40: 32-35. (In Japanese).

Nakamura, H., Kitahara, K. & Tokoro, Y. 2003: Distribution of territories and the number of rock ptarmigan *Lagopus mutus japonicus* on the Mt. Hiuchi. - Bulletin of the Institute of Nature Education in Shiga Heights, Shinshu University 40: 1-8. (In Japanese with an English summary).

Novoa, C., Desmet, J.F., Brenot, J.F., Muffat-Joly, B., Arvin-Bérod, M., Resseguier, J. & Tran, B. 2011: Demographic traits of two alpine populations of rock ptarmigan. - In: Sandercock, B.K., Martin, K. & Segelbacher, G. (Eds.); Ecology, Conservation, and Management of Grouse Studies in Avian Biology No. 39. University of California Press, Berkeley, California, USA, pp. 267-280.

Omachi Alpine Museum 1992: Rock Ptarmigan - Life history and challenge to breeding. - Shinanomainichi Press, Nagano, Japan, 211 pp. (In Japanese).

Sandercock, B.K., Martin, K. & Hannon, S.J. 2005a: Demographic consequences of age-structure in extreme environments: population models for arctic and alpine ptarmigan. - Oecologia 146: 13-24.

Sandercock, B.K., Martin, K. & Hannon, S.J. 2005b: Life history strategies in extreme environments: comparative demography of arctic and alpine ptarmigan. - Ecology 86: 2176-2186.

Sawa, Y., Takeuchi, Y. & Nakamura, H. 2011: Nest site selection and nesting biology of Rock Ptarmigan *Lagopus muta japonicus* in Japan. - Bird Study 58: 200-207.

Shaffer, M.L. 1981: Minimum population sizes for species conservation. - BioScience 31: 131-134.

White, G.C. & Burnham, K.P. 1999: Program MARK: survival estimation from population of marked animals. - Bird study 46 (Suppl.): 120-139.

Wilson, S. & Martin, K. 2011: Life-history and demographic variation in an alpine specialist at the latitudinal extremes of the range. - Population Ecology 53: 459-471.

Zwickel, F.C. & Bendell, J.F. 1967: A Snare for Capturing Blue Grouse. - Journal of Wildlife Management 31: 202-204.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use