BioOne COMPLETE

Survival in an expanding hazel grouse Bonasa bonasia population in the southeastern French Alps

Authors: Montadert, Marc, and Leonard, Patrick

Source: Wildlife Biology, 9(4) : 357-364

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.2003.025

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 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Survival in an expanding hazel grouse *Bonasa bonasia* population in the southeastern French Alps

Marc Montadert & Patrick Leonard

Montadert, M. & Leonard, P. 2003: Survival in an expanding hazel grouse *Bonasa bonasia* population in the southeastern French Alps. - Wildl. Biol. 9: 357-364.

By use of radio-tracking, we studied hazel grouse *Bonasa bonasia* in the southeastern French Alps from 1998 to 2002. The Kaplan-Meier annual survival rate of adult males (N = 41) was 0.72 (95% C.I.: 0.59 - 0.85), and 0.60 for adult females (N = 15; 95% C.I.: 0.40 - 0.91). For juveniles (sexes combined; N = 29) the survival over nine months (15 September-15 June) was 0.74 (95% C.I.: 0.58-0.90). The seasonal pattern of survival was different for the two sexes. Adult male survival during November-April (S = 0.76; N = 38) was lower than during May-October (S = 0.95; N = 41). Only three of 16 male deaths (ages combined) occurred in summer. Female survival (ages combined) during November-April (S = 0.90; N = 16) was higher than during May-October (S = 0.70; N = 16). Five of six females died between May and July, i.e. during egg laying, incubation or brood rearing. Raptors, red foxes *Vulpes vulpes* or pine martens *Martes martes* accounted for most mortality of adults. The estimated annual survival rates were high compared to those reported for more northern populations, and the difference may be due to an extensive, dense and well-structured habitat that reduces the ability of raptors to kill hazel grouse. The high survival rates may explain the range expansion currently occurring in the southeastern French Alps.

Key words: Bonasa bonasia, causes of mortality, hazel grouse, radio-tracking, range expansion, survival

Marc Montadert, Laboratoire d'Ecologie et d'Ecophysiologie, EA 3184 MRT, UC INRA, Université Franche-Comté, Place Leclercq 25300 Besançon, France - e-mail: marc.montadert@wanadoo.fr
Patrick Leonard, Office National de la Chasse et de la Faune Sauvage, CNERA FM, Micropolis, La Bérardie, 05000 Gap, France - e-mail: p.leonard@oncfs.gouv.fr

Corresponding author: Marc Montadert

During the last few decades, the hazel grouse *Bonasa bonasia* has disappeared from many lowland habitats of western and central Europe due to changes in habitats and silvicultural practices (Bergmann & Klaus 1994, Lieser 1994, Storch 2000). Contrasting this, the occupied range appears to be stable in most alpine regions and is increasing in parts of southeastern France (Deloche & Magnani 2002). We assume that this expansion is largely related to the abandonment of grazing activities and the subsequent spontaneous reforestation of pastures, which has led to an optimal forest habitat for hazel grouse. Expansion into new habitats suggests that individuals are immigrating from nearby populations with good reproduction or survival. We therefore initiated a research programme near the colonising front in the southeastern French Alps to determine the demographic characteristics of a local hazel grouse population. In this paper, we compare our data on survival and reproduction with those obtained in declining or stable populations in northern France and Fennoscandia.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

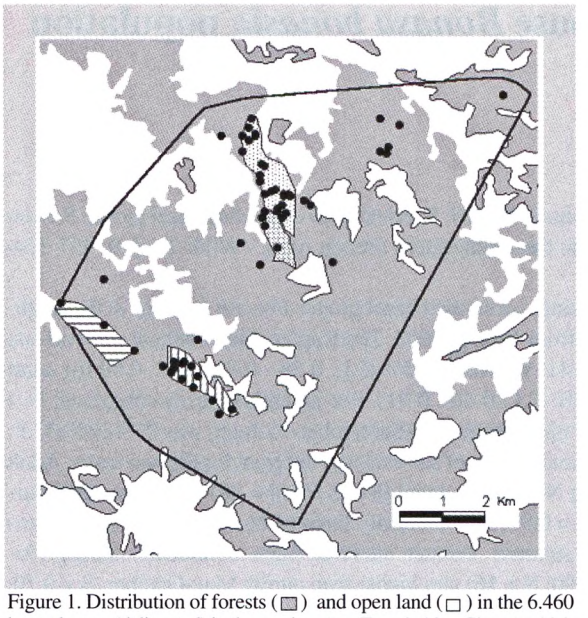


Figure 1. Distribution of forests (▨) and open land (□) in the 6.460 ha study area (delineated) in the southeastern French Alps. Sites at which hazel grouse were captured (●) and locations of the four forests (Fissac ▫, Peyronnière ▩, Sansenu ▥, Pinée ▤), for which the vegetation was described in detail, are shown.

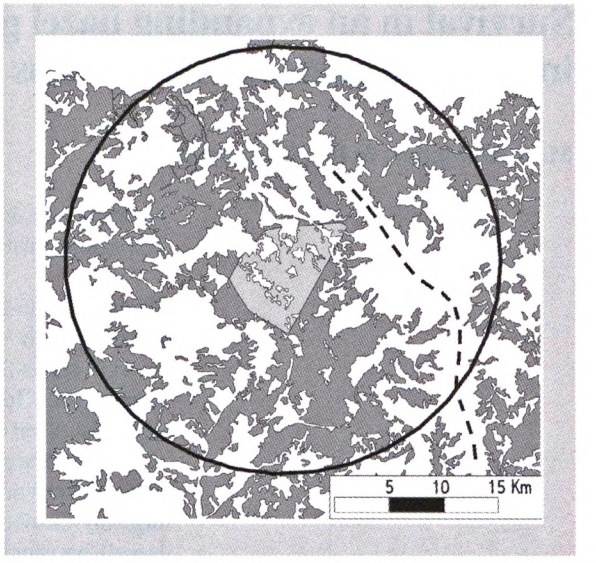


Figure 2. Forest cover at a landscape scale in the southeastern French Alps, with indication of the forest cover of the study area (▩), the forest cover outside the study area (■), the natural barrieres > 2,000 m a.s.l. (---) and the circular area of 40 km diameter.

Material and methods

Study area

The study was carried out in the Alpes-de-Haute-Provence in the southeastern French Alps (~UTM coordinates: 285 000 E, 4908 000 N, 32 T), in an area of 6,460 ha situated at 1,200-1,700 m a.s.l. (Fig. 1). The climate in the area is somewhat Mediterranean, with an average annual precipitation of 950 mm, in which snow from December through March is included, and a mean annual temperature of 7°C. The hazel grouse 'population' in the study area was not isolated, but was connected to surrounding populations through movements. The study area was situated ca 50 km from the southern limit of the expanding hazel grouse range. Interviews with local hunters and poachers suggest that hazel grouse first colonised the study area in the 1950s, and that by the 1970s the species was quite common. Large inter-connected tracks of forests cover 76% of the study area (see Fig. 1). Open land includes pastures, cultivated valleys, alpine meadows, and at higher elevations, rocky ridges. At a larger scale, i.e. within the 40-km diameter circular area (shown in Fig. 2) centred in the study area, the forest cover made up only 46%, and the habitat was more fragmented (see Fig. 2). High elevations exceeding 2,000 m (indicated in Fig. 2) formed natural barriers to hazel grouse movements.

Most forests are the results of natural regeneration. About half of the forested area was covered by old stands (> 100 years), the remainder being young stands originating from either clear-cutting 40-50 years ago or from natural reforestation of abandoned pastures. The vegetation of the four separate forests Fissac, Peyronnière, Sansenu and Pinée in the study area was described either in 10-m radius plots regularly spaced at a density of four per ha (for Fissac = 154 ha, Peyronnière = 46 ha and Sansenu = 83 ha) or in 18 1-ha squares in the Pinée forest (180 ha). In these plots we recorded: number of trees and number of species of all mature trees (i.e. with a diameter at breast height (DBH) of > 17.5 cm), number and species of deciduous shrubs and small trees, canopy cover of deciduous and coniferous trees at three layers, cover of field layer and an index of horizontal cover of the understorey using a 60 x 60 cm checkerboard mounted on a 1.2 m pole (Table 1).

In the study area, > 80% of the stands were dominated by conifers such as spruce *Picea abies*, Scots pine *Pinus sylvestris* or white fir *Abies alba*, and it was especially characteristic for the forests Fissac and Peyronnière. Mature deciduous trees were scarce in these stands. However, a sparse but diversified broad-leaved understorey was usually present and included the following plant species: mountain ash *Sorbus aucuparia*, whitebean *S. aria*, wild cherry *Prunus avium*, hazel *Corylus avellana*, hawthorn *Crataegus monogyna*, willow *Salix* spp., silver birch *Betula pendula*, wayfaring tree *Viburnum lantana*, snowy mespilus *Amelanchier ovalis*, wild cotoneaster *Cotoneaster integerrimus*, fly

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Table 1. Vegetation characteristics of the four forests Sansenu, Fissac, Peyronnière and Pinée in the study area in the southeastern French Alps. Diameters at breast height (DBH) of < 7.5 cm, 7.5-17.5 cm and > 17.5 cm are indicated by *, ** and ***, respectively.

	Sansenu	Fissac	Peyronnière	Pinée
Number of plots	331	613	183	72
Main forest stand types of plots	Mixed and coniferous	Coniferous	Coniferous	Deciduous and mixed
Mean number of species of tall trees*	2.6	1.8	1.6	1.9
Mean number of species of deciduous shrubs	3.7	4.5	1.9	2.3
Index of horizontal cover of understorey	0.51	0.41	0.46	0.4
Mean tree density* (number/ha)	354	268	227	306
Mean cover of high coniferous trees*	21%	26%	24%	9%
Mean cover of medium coniferous trees**	6%	13%	21%	2%
Mean cover of small coniferous trees***	2%	18%	12%	1%
Mean cover of high deciduous trees*	24%	1%	0%	33%
Mean cover of medium deciduous trees**	9%	2%	0%	21%
Mean cover of small deciduous trees***	5%	4%	0%	12%
Mean cover of coniferous branches 2 - 7 m high	20%	35%	30%	5%
Mean cover of deciduous branches 2 - 7 m high	33%	4%	0%	33%
Mean number of *Crataegus* sp./plot	1.3	1.3	0.1	0.2
Mean number of *Coryllus* sp./plot	4.1	1.4	0.1	0.1
Mean number of *Sorbus* spp./plot	1.1	7.6	0.7	2.3
Mean number of *Salix* sp./plot	1.6	1.5	0.2	0.5
Mean number of *Betula* sp./plot	2.6	2.7	0.4	0.1
Mean cover of herbaceous plant	29%	37%	52%	24%
Mean cover of *Arctostaphyllos* sp.	0%	4%	2%	0%
Mean cover of raspberry *Rubus* sp.	3%	6%	4%	5%
Mean number of clearing-forest edges between two plots	0.41	0.95	0.27	0.31

honeysuckle *Lonicera xylosteum*, dog rose *Rosa canina* and burnet rose *R. pimpinellifolia*. The remaining 20% of the stands were either beech *Fagus silvatica* mixed with a few conifers (in the Pinée forest) or mixed stands rich in both coniferous and deciduous trees (in the Sansenu forest; see location in Fig. 1).

The Fissac and Peyronnière forests were grazed in summer and autumn by cattle. Forest management was usually extensive. Private forests often remained unexploited for decades, and when logging did occur tree species of no economic value were left behind. The communal forests were managed by the National Forestry Service which made use of selective cutting that resulted in a fine-grained mosaic of tree patches of different ages.

The community of predators is diversified and the raptors likely to capture young or adult hazel grouse are sparrow hawk *Accipiter nisus*, goshawk *Accipiter gentilis*, buzzard *Buteo buteo*, golden eagle *Aquila chrysaetos*, kestrel *Falco tinnunculus*, eagle owl *Bubo bubo* and tawny owl *Strix aluco*. The main carnivores are red fox *Vulpes vulpes*, pine marten *Martes martes* and beech marten *M. foina*. Stoat *Mustela erminea* and polecat *Mustela putorius* are rare. Shooting of hazel grouse is prohibited in the Alpes-de-Haute-Provence.

Capture, radio-tracking and census

Between 1998 and 2001, we captured hazel grouse in spring (March-April) and in autumn (September-October) by luring them into nylon fishing nets with whistles that imitate the song of either the male or the female (Swenson 1991). Capture was biased towards males because they responded better to the whistle.

To obtain a representative sample of birds for estimating survival rates, we captured birds throughout the study area and in most forest types (see Fig.1). The dispersion of juveniles of up to 25 km from the study area (M. Montadert, unpubl. data) further increased the variety of habitats sampled to study survival.

Birds were weighed and equipped with a radio-necklace tag weighing 7 or 11 g that included a mortality sensor. The life expectancy of the tags was 12 months, but some functioned two years. Adults were distinguished from juveniles (< one year old) by aspect of the clear band of the first primary (Stenman & Helminen 1974, Bonczar & Swenson 1992). Because all juveniles were captured in autumn after broods break up, we have no data on juvenile survival from hatching to late August.

We relocated radio-tagged birds by approaching them to ≤ 100 m, once per week in winter, and 2-3 times per week during the other seasons. Locations were determined with an accuracy of ±25 m and coordinates stored in a GIS. Causes of deaths were classified by appearance of remains as being due to raptors, mammals, disease or accidents. Birds killed by raptors were recognised by a pile of intact feathers (rachis or shaft not sectioned) that included the tag. Mammals (fox or mustelids) did not pluck the bird completely on the capture site. The tag was generally found with the necklace cut open, lying near some feathers sectioned near the base of the rachis.

We evaluated reproductive success between 1999

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

and 2001 on a 140-ha area at the end of July (in the Fissac forest), using a drive-count method derived from Rajala (1966) and modified by Leclercq (1984). The results were expressed as the percentage of juveniles among all birds seen (age ratio). Sexes could not be distinguished. We compared these results with those obtained by the same method in two other study areas in the Jura mountains (northeastern France; Desbrosses 1997, B. Leclercq, unpubl. data, M. Montadert, pers. obs.). Just before break up of broods (in mid-August-beginning of September) we also recorded, partly for modelling purposes, the number of juveniles reared per radio-tagged hen that had been alive in mid-June.

Data analysis

We estimated survival rates using the Kaplan-Meier procedure modified by Pollock, Winterstein, Bunck & Curtis (1989), assuming that: 1) the probabilities of capture are independent, 2) newly marked individuals have the same subsequent survival probability as the birds previously marked, 3) survival times of different individuals are independent, 4) marking does not influence survival of the birds, and 5) loss of signal is independent of the fate of the animal.

Of the birds followed more than one year, eight males and one female were reintroduced into the calculations as new individuals. Juveniles entered the group of adults on 15 June, i.e. at about one year of age. Of four birds that died because their radio collar became entangled in branches, two had survived for more than one month, and we included them in the data set as being still alive at end of tracking. We considered one case of 'premature signal loss' (i.e. after < 6 months duration) to be due to tag failure and not to mortality. For this individual, we ruled out emigration by performing an aircraft search and considered the bird to be alive at the time of signal loss.

We calculated an annual survival rate for adults. For juveniles we calculated survival over nine months, including the period from 15 September (shortly after brood break up) to 15 June. We assumed no between-year differences in annual and seasonal survival and combined data from different years to obtain acceptable precision of survival estimates. Variance and standard error were calculated by use of the method of Cox & Oakes (1984). A normal Z test was used to compare survival rates by sex and age (Pollock et al. 1989). We retained a significance level of $\alpha = 0.05$.

We compared survival rates during two 6-month periods which differed in vegetation cover, and which therefore might have affected the vulnerability to predators. The periods were: May-October (leaves on deciduous trees and shrubs) and November-April (leaves absent and snow often present).

The relative importance of the causes of deaths was evaluated by computing cause specific mortality rates with MICROMORT software (Heisey & Fuller 1985). With this method, the probability that an individual succumbs to a specific cause of mortality during a definite lapse of time can be estimated. Annual variation in reproductive indices was analysed by a r x k Fisher test.

To estimate the population growth rate, λ, we employed a deterministic matrix population model (Caswell 1989) with two age classes of females (juveniles and adults). Adult survival was calculated for 15 June-15 June, juvenile survival for 15 September-15 June. The mean reproductive rate of hens was calculate as the number of juveniles reared by hens into late August divided by the number of hens carrying radios and being alive in mid-June. Calculations were done using ULM software (Legendre & Clobert 1995).

Results

Survival

We captured and radio-tagged 65 hazel grouse during March 1998-October 2001, of which 49 were males (26 adults, 23 juveniles) and 16 females (10 adults, six juveniles). The annual survival rate of adult males was 0.72 (95% C.I.: 0.59-0.85) and 0.60 (95% C.I.: 0.40-0.91) for adult hens (Table 2). Although the two rates were not significantly different (one-tailed Z = 0.683, P = 0.25), we did not calculate a common adult survival rate because the seasonal pattern of mortality differed (see below). The survival rate during 15 September-15 June of immature males was 0.71 (95% C.I.: 0.53-

Table 2. Mean survival rates (S) of radio-tagged hazel grouse in the southeastern French Alps during 1998-2001. N is the number of radio-tagged hazel grouse, N' the endpoint sample sizes used to estimate both S and standard error (SE).

	Adult male				Immature male				Adult female				Immature female			
Period	S	SE	N	N'	S	SE	N	N'	S	SE	N	N'	S	SE	N	N'
November-April	0.76	0.1	38	32	-	-	-		-	-	-	-	-	-	-	-
May-October	0.95	0.033	41	44	-	-	-		-	-	-	-	-	-	-	-
15/09 - 15/06	0.76	0.078	41	23	0.71	0.093	23	17	-	-	-	-	0.83	0.152	6	5
Annual	0.72	0.066	41	33	-	-	-		0.60	0.024	15	7	-	-	-	-

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

0.89) and was similar to that of adult males for the same period (0.76; 95% C.I.: 0.34-0.91; one-tailed Z = 0.427, P = 0.33). The number of adult and juvenile females marked was too small to make a meaningful comparison of their survival during 15 September-15 June. To obtain a conservative estimate of juvenile female survival during 15 September-15 June for the demographic model, we combined the data for the two sexes, which gave a survival rate of 0.74 (95% C.I.: 0.58-0.90).

The survival of adult males during November-April (0.76) was lower than during May-October (0.95; one-tailed Z = 2.52, P = 0.006). Of the 16 male deaths, only three occurred during May-October. The survival of females (adults and juveniles pooled) during November-April (0.90) was probably higher than during May-October (0.70; one-tailed Z = 1.54, P = 0.06). Of the six female deaths, only one occurred during November-April. Of the five females that died during May-October, one died during laying, two were killed on the nest during incubation and two died while they were accompanying broods. In this period, no mortality occurred among hens who had lost their nests. The survival of females during May-October (0.70) was lower than that of adult males for the same period (0.95; one-tailed Z = 2.08, P = 0.02).

Causes of death

We recorded 22 deaths of natural causes (i.e. disease and predation; Table 3). The only case of disease, a colibacillosis, occurred in an adult male in June. We believe that we correctly distinguished between raptor and mammal kills. Although identification of the species was rarely possible, we suspect that most raptor kills were made by goshawks. Among the mammals, red fox and pine marten were the most likely predators. We attributed two deaths to pine martens. In one case, we found a hazel grouse hidden in a squirrel nest 25 m up a fir tree. In the other case, we found the radio tag hidden under a large pile of branches. A red fox probably killed one radio-tagged male whose feathers we found next to a den. Lastly, a dog probably killed a hen incubating at the edge of a road commonly travelled by hikers. Small sample sizes precluded testing for differences in the importance of the various mortality factors given in Table 3.

Table 3. Cause specific annual mortality rates of adult male and female, and for immature (of both sexes) hazel grouse in the southeastern French Alps computed after the method given by Heisey & Fuller (1985). The numbers of deaths recorded are given in parantheses.

	Adult male	Adult female	Immature
Raptor	0.15 (5)	0.22 (2)	0.23 (5)
Mammal	0.12 (5)	0.20 (3)	0.04 (1)
Disease	0.02 (1)	0.00 (0)	0.00 (0)
Survival	0.72	0.58	0.73

Population growth

We retained the following values to implement the simple demographic model: annual survival of adult females = 0.60 (for 15 June-15 June), survival of juvenile females = 0.74 (i.e. the common survival of juveniles; for 15 September-15 June), and reproductive success of adult females (i.e. juvenile females in August/adult females alive on 15 June) = 0.75 (average reproductive rate of 1.5 young per hen in August with an assumed equal sex ratio among the young). According to this model, the rate of increase, λ, was 1.15.

Reproductive rate

Our indices of reproduction varied significantly from 1999 to 2001. For age ratios they were 9, 60 and 23% for juveniles, respectively, and 1.14, 3.00 and 0.25 young per radio-marked hen (Fisher r x k test: for age ratios, P = 0.02, for juveniles per radio-marked hen, P = 0.06). Both methods indicate that reproduction was highest in 2000, when nest success was highest (all five radio-marked hens raised young). Our mean age ratio of 34% was similar to the means recorded in two populations from the Jura Mountains in northeastern France, but our mean density of 6.0 adults/100 ha was higher than in the Risol forest during 1995-2001, where the mean reproductive success was 34% and the mean density 3.1 adults/100 ha; and in the Risoux forest during 1983-2001, where the mean reproductive success was 37% and the mean density 2.1 adults/100 ha.

Discussion

Annual survival

Our estimation of the annual survival rates for adult males (0.72) and for adult females (0.60) are higher than those reported hitherto on hazel grouse. In Finland, Gaidar (1973) obtained 0.23 from recaptures of ringed birds. These Finnish data likely underestimated the survival because all birds that emigrated from the study area were considered dead. In Sweden, the annual survival estimated by use of the method of Trent & Rongstad (1974) was 0.48 for males and 0.19 for females (Swenson 1991). The values obtained in Sweden were strongly influenced by the proportion of radio-tagged birds that lived in poor forest habitats characterised by a single-layered structure (Swenson 1991). In contrast, the coniferous or mixed forests occupied in the south-

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

eastern Alps were generally well structured with a mixture of young, medium and mature coniferous trees (see Table 1) that offered good protection against predators. We conclude that good cover may largely explain the relatively high survival recorded in France.

Seasonal variation in survival of the sexes

The seasonal distribution of mortality appeared to differ according to sex. Female hazel grouse suffered high predation during the period of reproduction (May-July). The predation risk is high in tetraonid hens at this time (Angelstam 1984, Willebrand 1988, Caizergues & Ellison 1997, Hewitt, Keppie & Stauffer 2001) owing to the energy cost of laying and incubation, and the reluctance of hens to leave their nests or young at the approach of a predator. Predation on males was highest during November-April. In this period the cover is reduced by loss of leaves on deciduous trees and shrubs, which may render singing cocks vulnerable to predators, particularly when the ground vegetation is covered by snow. Display and singing activities of cocks are most frequent in both March-April and September-October. In the latter period, cover is good and the mortality of males was low. Finally, when the cover is poor the conspicuous plumage of males may render them more vulnerable than females to predators (Götmark & Hohlfält 1995).

Juvenile versus adult survival in males

Juvenile tetraonids often survive over winter less well than adults (Lindström 1994), but there are exceptions, for example in spruce grouse *Dendragapus canadensis* (Keppie 1979, Beaudette & Keppie 1992). In our study, the survival of males during 15 September-15 June was similar in juveniles and adults. Thus the dispersal of juvenile males between September and March, with some settling 4-25 km from the study area (M. Montadert, unpubl. data), and their intensive erratic movements in autumn, did not result in higher mortality than in the more sedentary adults. Also in black grouse *Tetrao tetrix* dispersal did not appear to be costly in terms of survival (Caizergues & Ellison 2002).

Cause specific mortality

Like in other galliformes (Bergerud 1988, Marcström, Kenward & Engren 1988, Connelly, Apa, Smith & Reese 2000, Hewitt et al. 2001), predation was the main cause of mortality. The impact of raptors is often higher than that of mammals, especially in open landscapes. Examples are black grouse (Angelstam 1984, Willebrand 1988), willow grouse *Lagopus lagopus lagopus* (Smith & Willebrand 1999), red grouse *L. lagopus scoticus* (Hudson 1992, Thirgood, Redpath, Rothery & Aebischer 2000) and rock partridge *Alextoris graeaca* (Bernard-Laurent 1989, Bernard-Laurent 1990). Raptors were also more important predators than mammals on hazel grouse in Sweden (Swenson 1991) and on black grouse occupying a forest habitat in the Alps (Caizergues & Ellison 1997). In the hazel grouse population we studied, predation by raptors was not markedly higher than that by mammals, despite the fact that raptors are common in the area. We conclude that the discrete behaviour of the hazel grouse associated with a dense and well-structured forest habitat constrained the ability of raptors to detect and predate hazel grouse. Thus we agree with the suggestion put forward by Swenson (1991, 1993) that hazel grouse are more vulnerable to raptors in open forest habitats where the birds are more visible than in denser habitats.

Demographic performance and range extension

The simple demographic model suggests that a closed hazel grouse population with the survival and reproductive rates we estimated could potentially increase at an annual rate of 15%. We believe that in fact some net emigration was occurring from this and other nearby populations in the southeastern French Alps. Reproduction in our study area was no better than that of hazel grouse in the Jura, where low-density populations are stable or declining (Magnani, Cruveille, Huboux, Collard, Roche & Longchamp 1991, Bernard-Laurent & Magnani 1994, Deloche & Magnani 2002). We therefore suggest that the positive growth rate estimated in our study area, and the range expansion in the southeastern Alps, are largely due to high survival of birds > two months.

The forests in our study area are dominated by conifers and are relatively young. The current logging practices, involving selective cutting, result in the fact that these forests are multi-layered, and well structured horizontally in a fine-grained mosaic. Such habitat is found throughout the southern French Alps, including many thousands of hectares not yet colonised by hazel grouse. Conservation of current source populations, and of the unoccupied forests, is required to assure that the hazel grouse continue to expand its range.

Acknowledgements - we are indebted to Laurence Ellison, Ariane Bernard-Laurent and Patrick Giraudoux who kindly reviewed the manuscript, and to Roger Izoard for his continuous and effective support. We thank Jon Swenson for showing us how to capture hazel grouse by luring them into nets. We also thank K. Kopko, A. Bogtchalian, D. Thiolière, A. Bombaud, J.C. Cauvin, R. Gayraud, D. Michallet, F. Miguel, R. Papet, J. Richelme, M. Teissier, R. Villecrose, E. Du Verdier and D. Igier of the 'Office National de la Chasse et de la Faune

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Sauvage'; R. Yonnet and D. Reboul of the 'Office National des Forêts'; F. Normand, R. Clement and P. Romain of the 'Fédération Départementale des Chasseurs des Alpes de Haute Provence'; and J. Lenoir and B. & J. Guillet for indispensable field assistance. We received financial support from the 'Federation Departementale des Chasseurs des Alpes de Haute Provence' and from the European Union Leader II - Gal programme, locally managed by the 'Syndicat Intercommunal à Vocation multiple de Seyne-les-Alpes'.

References

Angelstam, P. 1984: Sexual and seasonal differences in mortality of the black grouse Tetrao tetrix in boreal Sweden. - Ornis Scandinavica 15: 123-134.

Beaudette, P.D. & Keppie, D.M. 1992: Survival of dispersing spruce grouse. - Canadian Journal of Zoology 70: 693-697.

Bergerud, A.T. 1988: Population ecology of North American grouse. - University of Minnesota Press, Minneapolis, pp. 578-695.

Bergmann, H.H. & Klaus, S. 1994: Distribution, status and limiting factors of hazel grouse (Bonasa bonasia) in Central Europe, particularly in Germany. - Gibier Faune Sauvage, Game and Wildlife Vol. 11 (Hors série Tome 2): 5-32.

Bernard-Laurent, A. 1989: Importance de la prédation sur une population de perdrix rochassières (Alectoris graeca saxatilis X Alectoris rufa rufa) des Alpes méridoniales. (In French with an English summary: Mortality factors and survival rates of hybrid partridges (Alectoris graeca saxatilis X Alectoris rufa rufa) in the French Alps. - Gibier Faune Sauvage, Game and Wildlife 6: 361-382.

Bernard-Laurent, A. 1990: Biologie de reproduction d'une population de perdrix rochassière Alectoris graeca saxatilis X Alectoris rufa rufa dans les Alpes méridionales. - Revue d'Ecologie (Terre et Vie) 45: 321-342. (In French with an English summary).

Bernard-Laurent, A. & Magnani, Y. 1994: Statut, évolution et facteurs limitant les populations de gelinotte des bois (Bonasa bonasia) en France: synthèse bibliographique. (In French with an English summary: Status, trends and limiting factors of hazel grouse (Bonasa bonasia) populations in France: a literature survey). - Gibier Faune Sauvage, Game and Wildlife Vol. 11 (Hors Série Tome 1): 5-38.

Bonczar, Z. & Swenson, J.E. 1992: Geographical variation in spotting patterns on Hazel Grouse Bonasa bonasia primary feathers: consequences for age determination. - Ornis Fennica 69: 193-197.

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

Caizergues, A. & Ellison, L.N. 2002: Natal dispersal and its consequences in black grouse Tetrao tetrix. - Ibis 144: 478-487.

Caswell, H. 1989: Matrix population models. Construction, analysis and interpretation. - Sinauer Associates, Sunderland, Massachussets, 328 pp.

Connelly, J.W., Apa, A.D., Smith, R.B. & Reese, K.P. 2000: Effects of predation and hunting on adult sage grouse Centrocercus urophasianus in Idaho. - Wildlife Biology 6: 227-232.

Cox, D.R. & Oakes, D. 1984: Analysis of survival data. - Chapman & Hall, New York, 201 pp.

Deloche, N. & Magnani, Y. 2002: Evolution de la répartition communale du petit gibier de montagne en France au cours de la décennie 1990-1999. - Faune de montagne 257 (Supplement): 1-16. (In French).

Desbrosses, R. 1997: Habitats et fluctuations des populations de gelinotte des bois (Bonasa bonasia) dans l'Est de la France. - Unpubl. PhD thesis, Dijon University, France, 169 pp. (In French).

Gaidar, A.A. 1973: Ringing of Tetrastes bonasia L. and its results. - Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Biologichskii 78: 120-124. (In Russian with an English summary).

Götmark, F. & Hohlfält, A. 1995: Bright plumage and predation risk in passerine birds: are males easier to detect than females? - Oikos 74: 475-484.

Heisey, D.M. & Fuller, T.K. 1985: Evaluation of survival and cause-specific mortality rates using telemetry data. - Journal of Wildlife Management 49: 668-674.

Hewitt, D.G., Keppie, D.M. & Stauffer, D.F. 2001: Predation effects on forest grouse recruitment. - Wildlife Society Bulletin 29: 16-23.

Hudson, P.J. 1992: Grouse in space and time: the population biology of a managed gamebird. - Game Conservancy Trust, Fordingbridge, 224 pp.

Keppie, D.M. 1979: Dispersal, overwinter mortality, and recruitment of spruce grouse. - Journal of Wildlife Management 43: 717-727.

Leclercq, B. 1984: Dynamique des populations de grand tétras (Tetrao urogallus) dans le Haut-Jura. (In French with an English summary: Population dynamics of the capercaillie (Tetrao urogallus) in the high Jura). - Gibier Faune Sauvage 3: 21-35.

Legendre, S. & Clobert, J. 1995: ULM, a software for conservation and evolutionary biologists. - Journal of Applied Statistics 22: 817-834.

Lieser, M. 1994: Untersuchung der Lebensraumansprüche des Haselhuhns (Bonasa bonasia L. 1758) im Schwarzwald im Hinblick auf Maßnahmen zur Arterhatung. (In German with an English summary: Habitat requirements of hazel grouse (Bonasa bonasia L. 1758) in the Black Forest with regard to the species conservation). - Ökologie der Vögel (Ecology of Birds) 16: 1-117.

Lindström, J. 1994: Tetraonid population studies - state of the art. - Annales Zoologici Fennici 31: 347-364.

Magnani, Y., Cruveille, M.H., Huboux, R., Collard, P., Roche, P. & Longchamp, P. 1991: Entre Rhône et Rhin: grand tétras et gélinotte. Statut territorial et évolution. - Bulletin Mensuel O.N.C. 162: 9-16. (In French).

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Marcström, V., Kenward, R.E. & Engren, E. 1988: The impact of predation on boreal tetraonids during vole cycles: an experimental study. - Journal of Animal Ecology 57: 859-872.

Pollock, K.H., Winterstein, S.R., Bunck, C.M. & Curtis, P.D. 1989: Survival analysis in telemetry studies: the staggered entry design. - Journal of Wildlife Management 53: 7-15.

Pulliam, H.R. 1988: Sources, sinks, and population regulation. - American Naturalist 132: 652-661.

Rajala, P. 1966: Metsäkanalintukannat elokuussa 1966 reittiarviointien mukaan. (In Finnish with an English summary: The number of tetraonids birds and their occurrence in various habitats types in the Oulu district according to route-census). - Suomen Riista 19: 130-134.

Smith, A. & Willebrand, T. 1999: Mortality causes and survival rates of hunted and unhunted willow grouse. - Journal of Wildlife Management 63: 722-730.

Stenman, O. & Helminen, M. 1974: Pyyn ikäluokan määritys siiven perusteela. (In Finnish with an English summary: Aging method for hazel grouse (Tetrastes bonasia) based on wings). - Suomen Riista 25: 90-96.

Storch, I. 2000: Conservation status and threats to grouse worldwide: an overview. - Wildlife Biology 6: 195-204.

Swenson, J.E. 1991: Social organization of hazel grouse and ecological factors influencing it. - Unpubl. PhD thesis, University of Alberta, Edmonton, Canada, 185 pp.

Swenson, J.E. 1993: Hazel grouse (Bonasa bonasia) pairs during the nonbreeding season: mutual benefits of a cooperative alliance. - Behavioral Ecology 4: 14-21.

Thirgood, S.J., Redpath, S.M., Rothery, P. & Aebischer, N.J. 2000: Raptor predation and population limitation in red grouse. - Journal of Animal Ecology 69: 504-516.

Trent, T.T. & Rongstad, O.J. 1974: Home range and survival of cottontail rabbits in southwestern Wisconsin. - Journal of Wildlife Management 38: 459-472.

Willebrand, T. 1988: Demography and ecology of a black grouse Tetrao tetrix population. - PhD thesis, Uppsala University, Sweden, 149 pp.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use