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Source: Wildlife Biology, 3(3/4) : 177-186

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.1997.022>

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Survival of black grouse *Tetrao tetrix* in the French Alps

Alain Caizergues & Laurence N. Ellison

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

Survival rates are necessary for calculating allowable harvests and for modelling population performance. Survival rates for 93 black grouse *Tetrao tetrix* equipped with radio tags in two populations of the southern French Alps were estimated. Annual survival rates of hens (0.68, SE = 0.075, 0.84, SE = 0.105), but not of cocks (0.56, SE = 0.09, 0.66, SE = 0.122), tended to be higher than those of juveniles (0.52, SE = 0.071, sexes combined). The lower survival of juveniles was due to higher predation, mostly by raptors, in autumn and winter. Although both autumn and winter were seasons of peak mortality in juveniles, most adult deaths occurred either in spring (hens and cocks), or in early summer (cocks). Causes of mortality were as follows: raptors 51%, mammalian predators 27%, unidentified predators 11%, and hunting 11%. Principal raptors were golden eagle *Aquila chrysaetos* and goshawk *Accipiter gentilis*. Mammalian predators included fox *Vulpes vulpes*, pine marten *Martes martes* and stone marten *M. foina*. Only males could be legally shot, and hunting was a minor mortality factor on our study areas. Nevertheless, the distorted adult sex ratio favouring hens that we observed on our study areas was probably due to hunting of males on and around the study areas. Sensitivity analysis showed that population growth is influenced more by adult survival than by either reproductive success or juvenile survival to one year of age. To prevent shooting from causing highly distorted spring sex ratios, which might compromise reproductive success, harvests should be reduced in years of poor reproduction, and shooting should be oriented towards juvenile males.

Key words: black grouse, French Alps, hunting, Kaplan-Meier, matrix modelling, radio telemetry, survival rates, *Tetrao tetrix tetrix*

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Associate Editor: Ilse Storch

Estimation of demographic parameters is necessary for studying life history strategies (Stearns 1992, Danchin, González-Dávila & Lebreton 1995), mating systems (McDonald & Caswell 1993), and for formulating management recommendations concerning harvests (Ellison, Leonard & Ménoni 1988). Unfortunately, estimates of parameters such as survival are difficult to obtain in natural populations. This is particularly true for secretive bird species living at low

densities, for example forest tetraonids. Consequently, many aspects of forest grouse demography, particularly survival, are poorly known. Information on adult and juvenile survival in grouse is restricted to seven European and North American species (Lindström 1994). However, some of these survival estimates are based on counts rather than on individually marked birds.

Black grouse *Tetrao tetrix* populations have de-

clined in most of Europe as a result of habitat deterioration and increased human disturbance. Hunting has been banned in many areas (for a review see Bergmann & Klaus 1994). In the French Alps, the distribution of black grouse has remained stable over the last 25 years, but since about 1960 densities have declined because of changes in land use practices (development of ski stations, abandonment of mountain agriculture and modification of forestry practices) (Bernard-Laurent 1994).

In the French Alps, black grouse can be hunted in 74% of their range, but shooting is limited to cocks (Bernard-Laurent 1994). The effects of the shooting of males in the French Alps were investigated by comparing sex ratios on hunted and unhunted areas (Ellison et al. 1988). This work led to recommendations for calculating allowable harvests. However, these harvest models used survival rates of black grouse recorded in Sweden (Angelstam 1984) and in the Netherlands (Vos 1983). Winter survival of juveniles was not reported in either of these two studies.

To obtain annual and seasonal survival data applicable to black grouse in the French Alps, we radio-tagged adults and juveniles over 13 years. The resulting data allowed us to estimate the population growth rate λ , and to study its sensitivity to changes in demographic parameters. We also employed a Leslie-type matrix to evaluate the effects of hunting on the adult sex ratio.

Methods

We radio-tagged black grouse in the southern French Alps in two valleys approximately 15 km apart. Birds were captured at Cervières (44°52'N, 6°45'E) from 1982 to 1988, and at Ristolas (44°47'N, 6°57'E) from 1990 to 1995. In both areas, black grouse occur in subalpine forests (1,700–2,400 m a.s.l.) dominated by larch *Larix decidua*, arolla pine *Pinus cembra* and a few mountain pines *Pinus uncinata*. Ground vegetation includes bilberry *Vaccinium myrtillus*, rhododendron *Rhododendron ferrugineum* and grasses *Calamagrostis* spp., *Festuca* spp.

Numbers of adults and juveniles were determined by total counts with pointing dogs during the brood-rearing period in August (Ellison, Bernard-Laurent, Corti, Gindre & Magnani 1984). Birds were censused on a reference area of 750 ha at Cervières (1977–1987), and on a reference area of 840 ha at Ristolas (1988–1995).

Both populations were stable during the studies, and mean numbers of adults in summer were: Cervières, 15 cocks and 35 hens; Ristolas, 27 cocks and 55 hens. Hunting occurred between mid-September and 11 November in both valleys, as well as in habitats surrounding both valleys. At Cervières, over half the males present in summer were shot in some years, so that hunting largely explained the skewed sex ratio (Ellison et al. 1988). At Ristolas, the hunting pressure was much lower because the hunting bag was limited to a quota based on current breeding success. Nevertheless, hunting in surrounding areas could have affected the adult sex ratio at Ristolas.

Grouse were captured by three methods. First, drop-nets were used on leks in spring. Secondly, lily-pad traps (Liscinsky & Bailey 1955) were spaced over feeding sites in spring, summer and fall. Last, pointing dogs were used in August to locate juveniles, which were flushed into nets. Birds were classified as juveniles (1 to ~ 12 months), or adults (≥ 12 months) on the basis of primary feather pigmentation (Helminen 1963).

At Cervières, grouse were fitted with either backpack or necklace radio tags. At Ristolas, only necklace tags were employed. Tags included an activity and/or a mortality sensor that activated after five hours of inactivity. Expected lifespan of tags was 1–2 years depending on the model. Tags weighed 10–15 g for juveniles, and 15–24 g for older birds, or less than 2.5% of body mass at the time of capture.

Birds were located from the ground with a portable receiver and a hand-held Yagi-antenna. If the signal was lost, an aerial search was undertaken. Grouse were located at least once a week at Ristolas, and about every two weeks at Cervières. Raptor and mammalian predators were distinguished by evidence at kills, e.g. tags buried or not, tooth marks on tags, feathers sheared off near the base, beak marks on feathers. Potential black grouse predators in both study areas included golden eagle *Aquila chrysaetos*, goshawk *Accipiter gentilis*, eagle owl *Bubo bubo*, red fox *Vulpes vulpes*, pine marten *Martes martes* and stone marten *M. foina*.

We computed annual and seasonal survival probability functions and estimated corresponding endpoint survival rates using the Kaplan-Meier product-limit method modified for staggered entry (Pollock, Winterstein, Bunck & Curtis 1989). Assumptions of the method are: 1) radio-tagged birds constitute a random sample from the population, 2) newly marked individuals have a survival distribution similar to pre-

viously marked birds, 3) survival times for individuals are independent, 4) handling and radio tags do not influence survival and, 5) censoring mechanisms are independent of the fate of animals (loss of signal not equivalent to death). To estimate natural survival rates, we right censored hunting mortality (shot birds considered still alive at end of tracking). Therefore, the survival rates reported here approximate those that would have been recorded in unhunted populations. Birds dying within two weeks after tagging were excluded from the analyses. When the exact date of death was unknown, we assumed that death occurred midway between the day the bird was last known to be alive and the day it was found dead.

We calculated annual survival functions and survival rates on the basis of a calendar year (1 January - 31 December) by taking the product of birds surviving successive weekly intervals. Seasonal survival functions were computed on the basis of periods of equal length (13 weeks): winter (1 January - 31 March), spring (1 April - 30 June), summer (1 July - 30 September) and autumn (1 October - 31 December) so that survival rates corresponding to seasons were directly comparable. However, for young birds, summer survival includes both birds ~12 months old in July and those 4-10 weeks old in August and September. Therefore, results involving survival rates of juveniles in summer should be carefully interpreted.

Variances and standard errors were calculated following Cox & Oakes (1984). Two age classes were considered in the analyses: juveniles ≤ 1 year old and adults >1 year old. Juveniles 'became' adults in the first week of August, at 12-13 months of age. Birds surviving from previous calendar years were censored on 31 December and reintroduced as new independent observations on 1 January.

Because few birds were tracked each year, data from different years were combined to obtain acceptable precision of survival estimates. We assumed no between-year differences in annual and seasonal survival functions, although this was probably not true (Willebrand 1988).

We tested for age, sex and seasonal differences in endpoint survival estimates using the normal approximation ($\sim Z$). We conducted one-tailed tests when we expected differences in survival rates, i.e. lower annual survival rates for adult males than for adult females, and lower annual and winter survival rates for juveniles than for adults. Otherwise, we performed two-tailed tests. We assessed significance of tests at $\alpha = 0.05$. For multiple comparisons, i.e. sur-

vival by season, we lowered the Type I error rate using the method of Dunn-Sidak (Sokal & Rohlf 1981: 241-242). Hence for $k = 6$, the significance level was assessed at $\alpha' = 0.01$. The log-rank (LR) test of Pollock et al. (1989) was used to test for differences in survival functions. The $\sim Z$ test is suitable to compare two survival rates at any particular time, e.g. the end of the year. The log-rank test is designed to compare the shape of two survival functions. This latter test is very useful to assess, for example, whether two groups of individuals with the same annual (seasonal) survival rate differ with respect to their seasonal (monthly) pattern of mortality. Because of small sample sizes, the power of most of the above tests was low.

We used General Linear Models (GLIM software, NAG 1986) with a binomial error distribution (binary response data), and with backward deletion of non-significant effects, to: 1) assess the randomness of right censoring by comparing date of premature signal loss to expected date of loss predicted by battery life, 2) test for age, sex, season and site differences in causes of mortality (particularly avian vs mammalian predation).

We incorporated annual survival estimates from the present study, and data on reproductive success from summer censuses at Ristolas (1988-1995), into two deterministic stage-structured matrix models (Caswell 1989). We simulated a female population with two age-classes (juveniles and adults). This allowed us to compute the population growth rate λ and to determine its sensitivity to variations in demographic parameters. The confidence interval of λ was estimated following Houillier, Lebreton & Pontier (1989). Next, we ran an alternate model including juveniles and adults of both sexes, to see if sexual differences in survival could explain the skewed adult sex ratio observed in the summer counts. Both models were run using ULM software, specifically designed to compute matrix models (Legendre, Clobert & Ferrière 1993, Legendre & Clobert 1995).

Results

We equipped 25 adults (15 cocks, 10 hens) from 1982 to 1989 at Cervières, and 68 birds (11 cocks, 16 hens, 23 juvenile males and 18 juvenile females) from 1990 to 1995 at Ristolas with radio tags. At Ristolas, 17 birds equipped as juveniles were later followed as adults. Two juveniles (one male and one female) that

died within 15 days after marking were excluded from analyses.

Signal loss before the date predicted by theoretical battery life led us to right censor four cocks, three hens and one juvenile female at Ristolas, and six cocks and three hens at Cervières. Censoring was not related to sex (likelihood ratio (LHR) test, $\chi^2 = 1.004$, $df = 1$, $P = 0.31$) or site (LHR test, $\chi^2 = 0.624$, $df = 1$, $P = 0.43$). The interaction term (sex*site) was not significant (LHR test, $\chi^2 = 0.185$, $df = 1$, $P = 0.66$).

Adult survival by sex

Although adult males seemed to experience higher annual mortality than females both at Cervières and Ristolas (Fig. 1a, 1b, Table 1), the differences were not significant (Cervières ~Z one-tailed, $P = 0.14$, log rank (LR) test, $P = 0.54$; Ristolas ~Z one-tailed, $P = 0.16$, log rank (LR) test, $P = 0.53$). Furthermore, at Cervières, no significant differences were found in the seasonal survival rates of hens and cocks (~Z two-tailed all P values ≥ 0.32 , LR tests all P values ≥ 0.35). But at Ristolas, hens survived better than cocks in summer (~Z two-tailed = -2.02, $P = 0.043$; LR test = 2.89, $P = 0.089$). Therefore, hens and cocks cannot be pooled to calculate a single adult survival rate.

Survival by site

Annual survival and survivorship functions of adults of both sexes appeared to be higher at Cervières than at Ristolas (see Table 1), but the differences were not significant (cocks ~Z = 0.68, $P = 0.24$, LR test = 0.003, $P = 0.956$; hens ~Z = 1.25, $P = 0.105$, LR test = 0.36, $P = 0.54$). Despite this absence of statistical difference in annual survival estimates, we think it would be imprudent to combine the data from the two sites to calculate a unique survival rate for hens and a

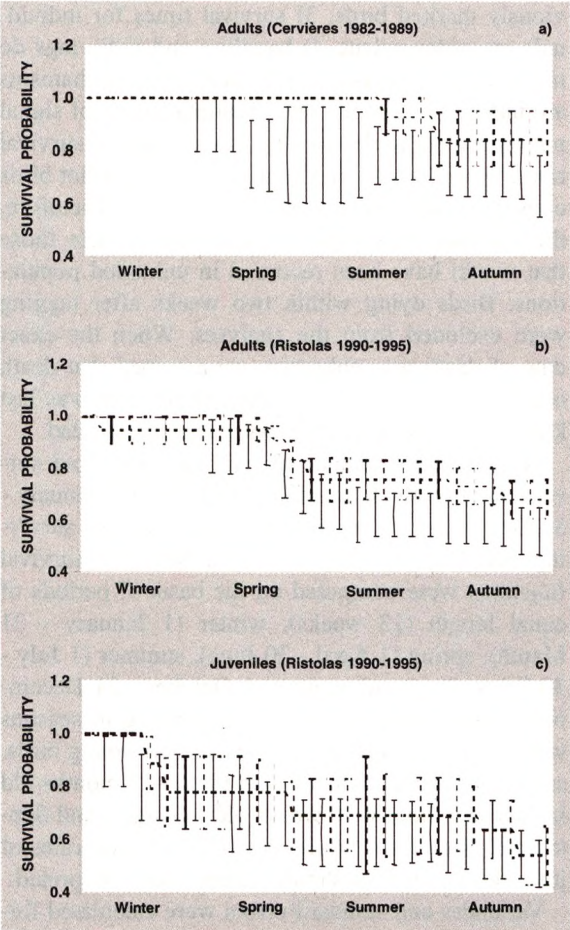


Figure 1. Kaplan-Meier natural survival functions for radio-marked black grouse in southern French Alps: (a) Adult males (—) and females (---) at Cervières from 1982 to 1989; (b) Adult males (—) and females (---) at Ristolas (c) Juvenile males (—) and females (---) at Ristolas (1990-1995). Vertical lines indicate standard errors (SE) calculated following Cox & Oakes (1984). Winter (1 January - 31 March), Spring (1 April - 30 June), Summer (1 July - 30 September), Autumn (1 October - 31 December).

Table 1. Mean annual and seasonal natural survival rates (S) for radio-marked black grouse by age and sex at Cervières (1982-1989), Ristolas (1990-1995), southern French Alps. Winter (1 January - 31 March), Spring (1 April - 30 June), Summer (1 July - 30 September), Autumn (1 October - 31 December). Standard errors (SE) are calculated following Cox & Oakes (1984). N = endpoint sample sizes used to estimate both S and SE (Pollock et al. 1989).

Season	Cervièrës									Ristolàs											
	Adults						Adults						Juveniles								
	Cocks			Hens			Cocks			Hens			Males			Females			Combined		
	S	SE	N	S	SE	N	S	SE	N	S	SE	N	S	SE	N	S	SE	N	S	SE	N
Winter	0.9	0.1	8	1	0	8	1	0	10	0.94	0.053	17	0.81	0.126	8	0.78	0.138	7	0.79	0.093	15
Spring	0.87	0.155	4	1	0	8	0.73	0.101	14	0.81	0.076	22	0.78	0.121	9	0.89	0.105	8	0.83	0.082	17
Summer	1	0	16	0.93	0.069	12	0.86	0.071	21	1	0	28	1	0	12	1	0	7	1	0	19
Autumn	0.85	0.104	10	0.91	0.087	10	0.9	0.069	17	0.91	0.056	26	0.81	0.09	15	0.78	0.11	11	0.79	0.071	26
Annual	0.66	0.122	10	0.84	0.105	10	0.56	0.09	17	0.68	0.075	26	0.51	0.092	15	0.54	0.11	11	0.52	0.071	26

unique rate for cocks. As to seasonal survival, there was a tendency for cocks to experience lower summer survival at Ristolas than at Cervières ($\sim Z$ two-tailed = 2.0207, $P = 0.021$; LR test = 0.667, $P = 0.41$). Similarly, hens from Ristolas tended to experience lower spring survival than hens from Cervières ($\sim Z$ two-tailed = 2.62, $P = 0.009$; LR test = 1.49, $P = 0.22$). All these comparisons between Cervières and Ristolas should be interpreted with care, because data were collected in different years on the two areas (observed differences could be due either to site or temporal effects).

Juvenile survival

Because there was no indication of any difference between juvenile males and females at Ristolas in either annual survival or seasonal pattern of survival (Fig. 1c, see Table 1, $\sim Z$ all P values ≥ 0.26 and LR tests all P values ≥ 0.65), we pooled the data for both sexes in further analyses.

Survival by age at Ristolas

Annual survival of juveniles (sexes combined) did not differ from that of cocks (see Table 1, $\sim Z$ one-tailed = 0.35, $P = 0.36$; LR test = 0.118, $P = 0.36$). However, the pattern of seasonal survival was somewhat different. As predicted, juveniles apparently exhibited lower winter survival than cocks ($\sim Z$ one-tailed = 2.25, $P = 0.0122$) and higher summer survival ($\sim Z$ two-tailed = 2.0207, $P = 0.043$). But, probably because of small sample sizes, log-rank tests failed to detect any differences in survival functions during these seasons (winter: LR test = 2.506, $P = 0.11$; summer: LR test = 2.445, $P = 0.11$). Yearlings (sexes combined, birds 11–12 months old) tended to experience higher survival in July than adult cocks (adults are 23 months old or older), but the difference was not significant ($\sim Z$ two-tailed = 1.59, $P = 0.11$; LR test = 2.45, $P = 0.12$). No mortality occurred in yearling or older cocks, or in juveniles (sexes combined), from August until the end of September.

Annual survival of juveniles (sexes combined) did not differ from that of hens (see Table 1) ($\sim Z$ one-tailed = 1.53, $P = 0.063$; LR test, $P = 0.27$). Survival of juveniles tended to be lower than that of hens in winter and autumn, but again the differences were not significant (winter $\sim Z$ one-tailed = 1.47, $P = 0.07$; LR test = 1.905, $P = 0.16$; autumn $\sim Z$ two-tailed = 1.177, $P = 0.23$; LR test = 1.102, $P = 0.29$). No mortality occurred in either yearling or older hens from July until the end of September.

Seasonal pattern of survival (between season comparisons)

At Cervières, we failed to detect any effect of season on survival of cocks or hens (see Table 1, $\sim Z$ all P values ≥ 0.15 for males and 0.29 for females; and LR tests all P values ≥ 0.24 for males and 0.34 for females), but the sample size was small. At Ristolas, cocks tended to experience high mortality rates during spring and summer, but only the difference between winter and summer survival rate (end point estimates) approached significance ($\sim Z = 2.64$, $P = 0.008$; LR test = 3.098, $P = 0.078$, $\alpha = 0.01$, see Methods). Endpoint survival estimates of hens were higher in summer than in spring ($\sim Z = 2.62$, $P = 0.009$). Similarly, survival functions of hens tended to be different between spring and summer (LR test = 5.946, $P = 0.014$).

Juveniles tended to survive better in summer than in autumn, but no significant difference was found in the survival functions between the two seasons ($\sim Z = 2.91$, $P = 0.003$; LR test = 3.28, $P = 0.07$). No mortality occurred in summer among birds 11–12 months old, nor among the young followed from early August (birds about four weeks old) until the end of September (about 12 weeks old).

Causes of mortality

Among 37 cases of mortality at Ristolas, the causes were as follows: raptors 21, mammalian predators 8, unknown predators 5 and hunting 3 (Table 2).

Avian vs mammalian predation varied according to season (likelihood ratio LHR test, $\chi^2 = 11.77$, $df = 3$, $P = 0.008$), with an increase in mammalian predation in spring. Raptor mortality tended to be higher in both juveniles and cocks than in hens, but the differences were not quite significant (sex effect: LHR test, $\chi^2 = 3.68$, $df = 1$, $P = 0.055$; age effect: LHR test, $\chi^2 = 3.79$, $df = 1$, $P = 0.0515$).

Table 2. Cause-specific mortality of black grouse by age and sex at Cervières (1982–1989) and Ristolas (1990–1995), southern French Alps.

			Predation			Hunting
			Raptor	Mammal	Unknown	
Cervières	Adults	Cocks	1	3	0	2
		Hens	1	1	0	-
	Total		2	4	0	2
Ristolas	Juveniles	Cocks	5	1	2	1
		Hens	3	3	1	-
	Adults	Cocks	7	1	0	2
		Hens	6	3	2	-
	Total		21	8	5	3

Eight cases of mortality were recorded at Cervières: raptors 2, mammalian predators 4, and hunting 2 (see Table 2). Avian predation was significantly lower at Cervières than at Ristolas ($\chi^2 = 8.81$, $df = 1$, $P = 0.003$), with a marked effect of season (the same pattern as above, $\chi^2 = 11.04$, $df = 3$, $P = 0.011$). It should be noted, however, that because data were not collected in the same years on the two areas, we cannot claim that avian predation was always lower at Cervières.

Matrix modelling

The female-only and the both-sex models were computed using estimates of annual survival from Ristolas (i.e. annual survival probability of 0.68 (SE = 0.075) for hens, 0.56 (SE = 0.09) for cocks and 0.52 (SE = 0.071) for juveniles). Both models were run using the mean reproductive success estimated at Ristolas by means of pointing dogs from 1988 to 1995, that is 1.4 juveniles/hen in August (juveniles 2–8 weeks old). We assumed that reproductive success did not vary with age class of females, and that the sex ratio of juveniles was 1:1. Thus, females of both age classes were assumed to raise on average 0.7 (SE = 0.16) juveniles of each sex per year. These parameters led to a value of 1.044 for λ (95% confidence interval = 0.804 – 1.284). Sensitivity analysis (Table 3) indicated that λ was more sensitive to variations in survival than to changes in reproductive success. Using elasticity (E) values one can calculate the effect of a proportional change in any parameter (survival or reproductive success) on λ (in %). For example, if adult survival increased by 5%, λ would increase by $5 \times 0.65 = 3.25\%$, whereas a 5% increase in reproductive success would raise λ by only $5 \times 0.22 = 1.1\%$ (if juvenile survival increased by 5%, λ

would increase by 1.7%, see Table 3). The both-sex model predicted that 43% of the adults should be cocks in August, whereas the mean value obtained with dogs over eight years was 32% (minimum = 27%, 95% confidence interval = 18.6 – 36.1; maximum = 41%, 95% confidence interval = 31.2 – 52.1).

Discussion

Potential biases in survival estimates

Right censoring mechanisms appeared to be random. However, if any signal losses represented dead birds, then the calculated natural survival rates may be too high (Pollock et al. 1989, White & Garrott 1990). At Ristolas, four out of eight premature losses of signal were known to be due to transmitter failure, i.e. broken antenna or battery failure verified by recovery of tag. The fate of the other four was unknown. At Cervières, one hen was censored because she lost her radio collar, and eight other signals were lost for unknown reasons. We cannot rule out the possibility that signals lost for unknown reasons were lost due to predation. For this reason, our survival estimates are perhaps positively biased, particularly for Cervières.

The positive bias could be partly offset by a negative effect of radio tags on survival, although previous radio-tracking studies on black grouse concluded that radio collars had no measurable effects on survival (Willebrand 1988). Furthermore, it is generally accepted that radios weighing no more than 2–3% of body weight have no effect on survival, unless they are fitted as backpacks or ponchos (e.g. Thirgood, Redpath, Hudson, Hurley & Aebischer 1995; for a review see White & Garrott (1990) and Calvo & Furness (1992)). Radios may affect survival if they are highly visible or noisy in flight (Marks & Marks 1987), but our tags were neither conspicuous nor noisy. In our study, only two birds fitted as juveniles died within 15 days of capture and they were excluded from analyses. Consequently, we have no reason to suspect that the use of radios greatly biased our survival estimates.

Annual survival

Our estimates of annual survival rates of adults at Ristolas (0.56, SE = 0.09 for cocks and 0.68, SE = 0.075 for hens) and at Cervières (0.66, SE = 0.122 for cocks and 0.84, SE = 0.105 for hens) are higher or comparable to those reported in earlier studies: 0.53 in Finland (Lindén 1981), 0.54 in Sweden (Angel-

Table 3. Sensitivity S_i and elasticity E_i (relative sensitivity) of the population growth rate λ to changes in survival and reproductive success. Population growth rate $\lambda = 1.044$. Generation time $T \approx 3$ years. Sensitivity S_i is the effect on λ of an absolute change in a demographic parameter, for example, increasing adult survival from 0.68 to 0.73 would lead to an increase in λ from 1.044 to $1.044 + (1 \times 0.05) = 1.094$. Elasticity E_i is the effect on λ of a proportional change in a demographic parameter, for example, increasing adult survival by 5% ($0.68 + (5\% \times 0.68) = 0.71$) would lead to an increase in λ of $5\% \times 0.65 = 3.25\%$, and λ would now be $1.044 + 3.25\% \times 1.044 = 1.078$ (see Caswell 1989).

	Survival		Reproductive success	
	Juveniles	Adults	Juveniles	Adults
Sensitivity, S_i	0.7	1	0.18	0.33
Elasticity, E_i	0.34	0.65	0.12	0.22

stam 1984), 0.28-0.52 in Sweden (Willebrand 1988), and 0.66 (hens) in the Netherlands (Vos 1983). In our study, sexual differences in annual survival were not statistically significant in adults. Annual survival rates of juvenile males and females were nearly equal (males 0.51, SE = 0.09, females 0.54, SE = 0.11).

Lower annual survival rate of juveniles than of adults is frequently observed in grouse (Bergerud 1988, Lindström 1994). In Sweden, survival of juvenile male black grouse tended to be lower than that of adult cocks from autumn to early February (Angelstam 1984) and from mid-March to late June (Willebrand 1988). Our findings partly support such a difference in black grouse, because survival rate of hens (but not of cocks) was almost significantly higher than survival rate of juveniles (sexes pooled).

Seasonal mortality

Spring is generally a period of high mortality in tetraonids (Angelstam 1984, Willebrand 1988, Storch 1993) and other galliformes (Palmer, Hurst, Stys, Smith & Burk 1993, Roberts, Coffey, & Porter 1995, Wright, Paisley & Kubisiak 1996). High mortality in spring might be expected in grouse for the following reasons: 1) mobility in juveniles of both sexes is high in early spring (Willebrand 1988, Marjakangas, Aspegren & Kyllönen 1991), which might increase vulnerability to predators, 2) display activity of cocks (reviewed in Andersson 1994 and Höglung & Alatalo 1995), associated energy costs (Vehrencamp, Bradbury & Gibson 1989) and/or their bright plumage (Promislow, Montgomerie & Martin 1992, Götmark & Hohlfält 1995) might result in increased predation, and 3) the temporal and energetic costs to hens of egg formation, incubation and feeding activities during nest recesses probably also increase predation risk (Angelstam 1984). The season of lowest mortality in black grouse hens is probably the brood rearing period in late July and August (Angelstam 1984, Willebrand 1988). The low mortality of hens in July and August may be due to a combination of factors: abundant food at this time for both hens and predators, low hen mobility, and lower energy expenditure by hens for brood rearing than for laying or incubation. Natural mortality of most grouse species in autumn and winter has been shown to vary annually (Willebrand 1988, Wegge, Larsen, Gjerde, Kastdalen, Rolstad & Storaas 1990) and to be higher in inexperienced immatures than in adults (Rusch & Keith 1971, Myrberget 1972, Bowman & Robel 1977, Angelstam 1984).

Our data fit most of the seasonal patterns of mortality described above: low survival in spring (except for Cervières), increased survival in summer, and survival in autumn and winter either low (juveniles) or high (adults). At Ristolas, summer was the period of lowest mortality for hens and juvenile females and also for males several weeks old and those approaching 12 months of age. Mortality of cocks older than 23 months was high in summer. Lower summer survival in old cocks could be the consequence of the energetic cost of reproduction. Black grouse cocks have been found to experience heavy weight loss during display (Angelstam 1984), and energetic cost of displaying has been shown to be high in sage grouse *Centrocercus urophasianus* (Vehrencamp et al. 1989). In our study, all radio-tracked cocks showed high lek attendance (1 May until the end of June) and most deaths occurred in early July soon after the end of the display season. Therefore, our data support the hypothesis of reproductive costs resulting in higher post-display mortality.

Mortality of cocks and hens in autumn and winter appeared to be lower than in the breeding season. Both snow roosting and flocking behaviour may contribute to reduced mortality in adults in these seasons (Marjakangas 1990, 1992).

In contrast to adults, juveniles suffered heavy losses in both autumn and winter, probably because of inexperience with predators. Dispersal alone did not seem to explain the high juvenile losses, because mortality was high in both sexes, and females disperse farther than males (Caizergues & Ellison, unpubl. data). Juveniles exhibit lower thermoregulatory capacity than adults (Rintamäki, Saarela, Marjakangas & Hissa 1983) and thus they may be more vulnerable than adults to low temperatures.

Cause-specific mortality

Birds of prey are the main predators of forest grouse (Bergerud 1988). In Sweden, the goshawk was responsible for most black grouse kills in all seasons (Angelstam 1984, Willebrand 1988). At both Cervières and Ristolas, predation apparently accounted for all natural mortality. Most kills were made by golden eagles and goshawks. Vulnerability of females to foxes and martens, however, increased in spring. Of seven females killed in spring, two died during laying (both killed by raptors) and four during incubation (three mammals, one raptor). Only two were killed on or near the nest. Our results seem similar to those of Angelstam (1984), who found that most

incubating females were killed away from the nest. Willebrand (1988) also reported high predation on females in spring. In his study, raptors were the main predators before mating and during laying, but mammalian predators took most of the females killed during incubation.

Hunting mortality was low on both study areas. However, the possibility that some signal losses could have been due to hunting or poaching loss cannot be eliminated, especially at Cervières (Ellison et al. 1988). Collisions with powerlines in Norway (Bevanger 1995) and with ski-lift wires in France (Miquet 1990) may cause much mortality in black grouse. We recorded no such mortality, but ski-lifts and powerlines were scarce on our study areas (one ski-tow at Ristolas, no equipment at Cervières).

Sensitivity analysis

Sensitivity analysis showed that black grouse belong to the category of long-lived species for which the generation time (T) is >2 years (Lebreton & Clobert 1991). This means that populations are more sensitive to variations in both juvenile and adult survival than to changes in fecundity. However, the relative effect of survival and reproduction on a population depends also on the magnitude of their variations. Annual survival of grouse may be highly variable. For example, in Swedish black grouse, annual survival varied from 28 to 52% in males, and from 48 to 52% in females (ages combined) (Willebrand 1988). In capercaillie, annual survival varied from 53 to 78% in cocks, and from 45 to 68% in hens (Wegge et al. 1990). Variability in reproductive rates is even higher. At Ristolas, reproductive success varied by a factor of >5 during eight years (0.5–2.7 young per hen in August), and at Cervières by a factor of >14 during 11 years (0.2–2.9 young per hen in August). Furthermore, at Ristolas, we found a positive correlation between change in numbers of cocks in one year and reproductive success in the previous year (cocks $r = +0.79$, $df = 5$, $P = 0.034$; hens $r = +0.66$, $df = 5$, $P = 0.108$). Therefore, reproductive components can influence population dynamics of black grouse.

Finally, the both-sex model predicted a higher percentage of cocks in August (43%) than the average percentage of cocks censused in August (32%). Dogs may have more difficulty in locating cocks than hens (Ellison, unpubl. data), but this cannot entirely explain the unequal sex ratio. We believe the distorted adult sex ratio was largely due to hunting, as was the case at Cervières (Ellison et al. 1988). Higher sur-

vival of hens may also have contributed to the distorted sex ratio, but we could not show that the annual survival of hens was significantly higher than that of cocks.

Management implications

To calculate allowable harvests, Ellison et al. (1988) used survival rates of males estimated from the literature (annual survival of 65% for cocks, and 65% for juveniles from mid-August to 1 May). Our results suggest that annual survival of cocks was between 56% (95% confidence interval = $\pm 18\%$) at Ristolas and 66% ($\pm 23\%$) at Cervières. Survival of young males from mid-August to May was about 57% ($\pm 27\%$) at Ristolas. Therefore, because we do not know if hunting mortality is compensated for by increased survival, it might be prudent to reduce both rates for calculating allowable harvests, at least in fragmented or isolated populations, that by definition are vulnerable to extinction (Ellison 1991a,b, McCullough 1996), and in populations exposed to mortality by ski-lift cables. In other areas, use of the 65% rates should not endanger the populations. In fact, the protection of females is already a highly conservative management policy. Furthermore, application of survival rates of 65% in the past has meant that no harvest was theoretically available in about one year out of four in the southern French Alps, because of reproductive failures. We do not claim that calculation of harvests based on the 65% rates will not affect spring numbers of cocks. But as long as the sex ratio in spring is not reduced below approximately 80 cocks/100 hens (44% cocks), there should be no negative effects on reproduction. Sex ratios as low as 50 cocks/100 hens (33% cocks) appeared to have no short-term effects on reproduction (Ellison et al. 1988).

Our results suggest that over-winter survival of juveniles is lower than that of adults, and the sensitivity analysis shows that adult survival contributes more to population growth than juvenile survival. Thus, hunting regulations should be oriented towards young birds. The pursuit in autumn of singing males, often adults, should be discouraged.

Acknowledgements - we thank A. Bogtchalian, R. Corti, P. Guilhem, F. Kopko, P. Leonard, P. Longchamp, H. Poudroux, D. Thiolière, T. Grzeganeck and J. P. Serres for field assistance. We are very grateful to J.-D. Lebreton and R. Pradel for statistical advice. We thanks two anonymous referees for helpful comments on the manuscript. This work received financial support from: the Office National de la Chasse, the Fédération des Chasseurs des Hautes-Alpes,

the Société de Chasse de Ristolas, the commune de Ristolas, the Conseil Général des Hautes-Alpes, the Conseil Régional Provence-Alpes-Côte-d'Azur and the Groupement d'Intérêt Cynégétique du Queyras. Alain Caizergues received logistic support from the CEFE (Centre d'Ecologie Fonctionnelle et Evolutive)-CNRS, Montpellier, France.

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