



HAL
open science

Do migratory movements of black grouse retrace spring dispersal routes of juveniles ?

A. Caizergues, Laurence N. Ellison

► To cite this version:

A. Caizergues, Laurence N. Ellison. Do migratory movements of black grouse retrace spring dispersal routes of juveniles ?. 1997. hal-03986213v2

HAL Id: hal-03986213

<https://hal.science/hal-03986213v2>

Preprint submitted on 18 Apr 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

DO MIGRATORY MOVEMENTS OF BLACK GROUSE RETRACE
SPRING DISPERSAL ROUTES OF JUVENILES?

ALAIN CAIZERGUES^{1,2} AND LAURENCE N. ELLISON¹

¹*Office National de la Chasse, Direction de la Recherche et du Développement, C.N.E.R.A. Faune de Montagne, 8 impasse Champ Fila, 38320 Eybens, France, and* ²*CNRS-CEFE, 1919 Route de Mende, B.P. 5051, F-34033 Montpellier Cedex 1, France*

Author for editorial correspondence:

Alain Caizergues

CNRS-CEFE, 1919 Route de Mende, B.P. 5051, F-34033 Montpellier cedex 1, France

fax: 33-67 41 21 38

phone: 33-67 61 33 00

e-mail: keke@cefe.CNRS-mop.FR

Running head: *Black Grouse Partial Migration*

ABSTRACT.-We examined seasonal movements of radio-marked Black Grouse (*Tetrao tetrix*) in the southern French Alps during 1990-1996. Many hens migrated between summer and winter ranges, whereas males exhibited strong attachment to a single area. Average distance traveled from the winter range to the summer range differed significantly according to sex (males: 1.5 km, females: 2.95 km), and age (yearlings: 4 km, adults: 1.36 km). Birds of all ages displayed strong site fidelity to winter and summer areas. We found no statistical difference between median date of fall dispersal of juveniles (26 October) and median date of migration of birds older than 12 months from summer to winter areas (19 October). Similarly, spring dispersal of yearlings and spring migration of adults from their winter area occurred at the same time (14 April vs. 18 April). Furthermore, dates of movements, including dispersal, were highly repeatable for a given individual. Thus, timing of movements along with data on site fidelity support the view that dispersal and migration are tightly linked in Black Grouse. This is the first study in any Eurasian grouse species demonstrating that migratory movements of adults retrace the spring dispersal route taken when they were 9-11 months old.

Many bird species exhibit both partial and differential migration. Partial migration refers to populations or races in which some individuals migrate and others do not, whereas differential migration concerns differences between sexes, age classes or populations in the timing and/or distance of migration (Lack 1944, Ketterson and Nolan 1983, Terril and Abble 1988). In facultative partial migration, movements may be triggered by changes in carrying capacity of the habitat (e.g. in the Blue Tit *Parus caeruleus*, Smith and Nilsson 1987). In obligate partial migration, movements are under endogenous control (e.g. in the Blackcap, *Sylvia attricapila*, Berthold 1991, 1993).

Several hypotheses have been formulated to explain the evolution of partial migration in birds (Lack 1968, Gauthreaux 1982, Lundberg 1988). Attempts to test them have been performed on long-distance migrants, especially small passerines. Many studies have shown that the migratory behavior has a strong genetic basis (Berthold and Querner 1981, Biebach 1983, Berthold 1984, 1991, see also Berthold and Pulido 1994). But this does not exclude the possibility that non-genetic (environmental) factors influence the decision to migrate or not (e.g. Hildén 1982, Adriaensen and Dhondt 1990).

Formerly, partial migration was considered to be an "evolutionary stable state" only if lifetime reproductive success (LRS) of migrants and non-migrants was equal (Lack 1954, 1968, von Haartman 1968; Berthold 1984, Gauthreaux 1982, Newton 1989). Only recently did Lundberg (1988) suggest that partial migration can evolve even though payoffs of the two strategies may be unequal. Indeed, some field studies have shown that LRS is higher in residents than in migrants (e.g. Adriaensen and Dhondt 1990).

Although there are few studies on seasonal movements in grouse (*Tetraonidae*), several North American species exhibit either partial migration (Zwickel et al. 1968, Hoffman and Braun 1975, Herzog and Keppie 1980, Schroeder 1985, Schroeder and Braun 1993) or differential migration of the sexes (Weeden 1964, Bendell and Elliott 1967, Irving et al. 1967, Cade and Hoffman 1993). Seasonal movements of Eurasian tetraonids have been less thoroughly studied, but partial migration has been documented in the Capercaillie *Tetrao urogallus* (Rolstad 1989, Storch 1993), and in two populations of Black Grouse *Tetrao tetrix* (Willebrand 1988, Ellison et al. 1989). Migration in grouse differs from long distance partial migration of passerines by shorter distances, greater variation in individual distances, direction and timing of movements. However, like in long-distance partial migrants, more female grouse than males migrate, and hens travel longer distances (but see Cade and Hoffman 1993). Although partial

migration may be the rule rather than the exception in tetraonids (Schroeder and Braun 1993), in some populations all individuals migrate (Bendell and Elliott 1967), and in others none migrate (Eng and Schladweiler 1972).

Two hypotheses, not mutually exclusive, have been advanced to explain partial migration in grouse. First, where habitats preferred for breeding and wintering are separated, the tendency for some individuals to migrate might reflect differences in habitat selection (Zwickel et al. 1968, Herzog and Keppie 1978, Cade and Hoffman 1993). Second, migratory movements might be related to differences in the tendency of individuals to disperse in spring from the first winter range to the first breeding range, followed by fidelity to the two ranges (Herzog and Keppie 1980, Schroeder 1985, Schroeder and Braun 1993). However, because of the difficulty in marking large numbers of birds, few studies provide evidence supporting either of these hypotheses (but see Herzog and Keppie 1980, and Schroeder 1985).

None of the two studies on seasonal movements of Black Grouse (Willebrand 1988, Ellison et al. 1989) explained why some individuals migrated and others did not. Furthermore, Marjakangas et al. (1991) did not find any fidelity of yearling Black Grouse hens to their first winter range, but he did not exclude the possibility that some birds were migratory.

Earlier studies of black grouse movements in the French Alps concerned only marked adults (Ellison et al. 1989). Here, we examine seasonal movements of radio marked adults and juveniles. The aim of our study was to determine if migratory movements retrace natal spring dispersal routes.

STUDY AREA AND METHODS

The study was conducted from 1991 to 1996 in the southern French Alps at Ristolas (44°47' N, 6°57' E). There, black grouse occur in discontinuous subalpine forest (1700-2400m) dominated by larch (*Larix decidua*), arolla pine (*Pinus cembra*) and a few mountain pines (*Pinus uncinata*). Ground vegetation consists mainly of bilberries (*Vaccinium myrtillus*), rhododendron (*Rhododendron ferrugineum*) and grasses (*Calamagrostis sp.*, *Festuca sp.*).

Birds were captured on a 500-ha area in spring, summer, and autumn using three methods. First, drop-nets were used on leks during spring display. Second, grouse were caught in lily-pad traps (Liscinsky and Bailey 1955) spaced over feeding grounds (20 trappings sites over an area of 250 ha). Third, pointing

dogs were used to locate broods, and young were then flushed into nets. Age of birds captured was determined by the method of Helminen (1963). Following Herzog and Keppie (1980), we recognized three age classes: juveniles (0 to 9 months), yearlings (9 to 21 months) and adults (> 21 months). Juveniles become yearlings on 1 April.

Twenty-five males (11 adults, 3 yearlings, 11 juveniles) and thirty females (16 adults, 2 yearlings, 12 juveniles) were equipped with necklace tags with an expected lifespan of 1 to 2 years. Grouse were located from the ground at least once a week, using a portable receiver and a hand-held Yagi antenna. Radio-determined locations were plotted on a 1:25,000 map to the nearest 50 meters. For some birds wintering in inaccessible areas, birds were located from distances of 500 to 1,500 meters, and map locations were therefore approximated. When signals were lost, emigration outside the study area was controlled for by aerial searches.

Seasons were defined *a priori* as winter (1 December to 31 March), summer (1 June to 31 August), with spring and autumn in between. Summer includes the laying, incubating and brood period.

We defined spring dispersal as movement of yearlings from their first winter range to first summer range (breeding range). In our terminology, spring dispersers are therefore yearlings. We defined migration as subsequent movements of yearlings and adults between a summer and a wintering range (the birds are termed migrants). Autumn dispersal was movement of juveniles from brood range, or summer range, to winter range. We do not treat the details of autumn dispersal in this paper.

The straight-line distance between winter and summer ranges (migration and spring dispersal) was measured by plotting the bivariate median values of all locations in winter and all locations in summer (X and Y UTM coordinates, zone 32). Summer and winter home ranges were plotted by the convex polygon method (Mohr 1947). The minimum number of locations used to define these ranges was ten. We included in the analyses data from two adult females with incomplete records, but of known winter range and nest site (both migrated respectively 8.5 and 4 km).

Movements between winter and summer areas were classified as follows (Fig. 1):

(1) Long distance movements: the distance between the summer and the winter range (a) exceeded the average distance between the most widely separated points within the winter and the summer ranges $((b+c)/2)$.

(2) Short distance movements: $((b+c)/2) > a$, with no overlap between winter and summer ranges, or $((b+c)/2) < a$, with a slight overlap between the winter and the summer ranges.

(3) No movements (sedentary birds): when both winter and summer ranges overlapped and $((b+c)/2) > a$.

This method avoids an arbitrary distinction of migrants or dispersers vs. sedentary birds, which may occur if one tries to distinguish the two classes by the distribution of distances moved between winter and summer ranges. This latter method would lead to classifying some short-distance migrants or dispersers as sedentary birds. But, a limitation of our method is that some birds with partially overlapping winter and summer ranges may have erroneously been considered to be migrants, and migration is assumed to occur only if ranges do not overlap (Baker 1978). Therefore, we performed the same analysis using the proportion of birds with non-overlapping and overlapping winter and summer ranges.

Site fidelity was assessed using the distance between the bivariate medians of locations of successive winter or summer ranges. We tested for possible differences in site fidelity according to season, sex, age and status (migrants or dispersers vs. sedentary or residents). Additionally, we examined whether or not home ranges in winter and summer overlapped in different years.

Dates of dispersal of juveniles in autumn, of yearlings in spring and dates of migration were taken as the mid-point of the dates between the last successful search on a given range and the next unsuccessful search on that same range. Date of movement of two adults hens were added to the analyses as if they were migrants, even though they occasionally visited their breeding area during winter.

We used a General Linear Model (GLIM package, NAG 1986) with a:

1) Poisson Error distribution (multinomial analyses) to compare proportions of birds belonging to the following classes: long-distance or short-distance migrants or spring dispersers, non-migrants, and non-dispersers.

2) Binomial Error distribution (logit link) to compare proportions of birds with overlapping and non-overlapping winter and summer ranges, and to compare proportion of migrants among adults to proportion of dispersers among yearlings.

3) Normal Distribution to compare distances (distance of migration or spring natal dispersal, and distance between consecutive winter or summer ranges) ($\ln+1$ transformed distances).

All tests were performed with stepwise backward deletions of variables with non significant effects.

RESULTS

Thirteen birds (6 males, 7 females) were tracked from their winter range to their summer range, 11 (5 males, 6 females) from their summer range to their winter range, and 13 (4 males, 9 females) were followed in both directions.

Site fidelity.-Fidelity to winter and summer areas varied independently of age, sex, and status of movement (migratory or spring dispersers vs. sedentary). However, there was a trend toward higher fidelity for the summer than for the winter range ($F_{1,23} = 4.19, P \cong 0.05$).

Distances between successive summer ranges of yearling and adults were small ($\bar{X} = 368 \pm 96$ m, range 50-965 m, $n = 4$ males and 6 females). In fact, the summer ranges of all of these birds overlapped in consecutive years.

Inter-nest distance of hens monitored in consecutive years averaged 240 m \pm SE of 45 m ($n = 10$). These distances varied independently of age (yearlings = 246 m, range 71 - 428 m, $n = 4$) vs. adults = 234 m, range 10 - 405 m, $n = 6$), and status (migrants or spring dispersers = 199 m, range 71-327 m, $n = 4$ vs. sedentary = 265 m, range 10 - 428 m, $n = 6$) (ANOVA with $\ln+1$ transformed distances, $P > 0.05$). Distance between nests in consecutive years did not differ from distance between first nest and second nests (replacement clutches) within the same year (mean = 200 m \pm 60 m, $n = 4$)(Mann Whitney U -test, $U = 15, P = 0.48$).

The average distance between successive winter ranges was 1.3 \pm 0.4 km (range 0.035-2.855, $n = 7$ males and 7 females). The consecutive winter areas of all of these birds overlapped. In addition, two hens (one adult, one yearling) returned to their previously occupied winter area in autumn but were lost or died before winter. Therefore, three yearling females that dispersed in spring (respectively ca. 4, 10 and 14 km) returned to their original wintering site occupied as juveniles. One additional juvenile female that dispersed in autumn but not in spring, spent two consecutive winters (and summers) in the same area.

To sum up, all age classes exhibited a strong fidelity to both their winter and summer range.

Proportions of migrants.-More females than males exhibited both long distance (7/22 females vs. 1/15 males) and short distance (7/22 females vs. 2/15 males) movements between winter and summer areas

($\chi^2_2 = 5.85, P = 0.053$) (Table 1). Long and short distance spring dispersal of yearlings occurred at the same rate as long and short distance migration of adults ($\chi^2_2 = 4.261, P > 0.10$). In other words, the proportions of yearlings that were sedentary, dispersed a short distance or dispersed a long distance did not differ from the proportions of older birds that were sedentary, migrated a short distance or migrated a long distance. The results remained unchanged either by pooling long and short distance movements (age x sex, ns; age, ns; sex $\chi^2_1 = 5.03, P = 0.025$), or by comparing proportions of birds with overlapping and non-overlapping winter and breeding ranges (age x sex ns, age ns, sex $\chi^2_1 = 4.53, P = 0.03$) (Table 2).

Distance of movements.-Distance between winter and summer ranges ranged from 0.09 to 13.7 km (mean = 2.95 ± 0.76 km, $n = 22$) for females and from 0.18 to 3.6 km (mean = 1.5 ± 0.34 km, $n = 14$) for males ($F_{1,34} = 5.49, P = 0.027$) (Fig. 2). Spring dispersal distance of yearlings exceeded distance of migration (spring natal dispersal: $\bar{X} = 4.0 \pm 0.98$ km, range 0.49-13.7 km, $n = 7$ females and 7 males vs. migration: $\bar{X} = 1.36, \pm 0.38$ km, range 0.09-8.165 km, $n = 15$ females and 7 males, $F_{1,33} = 18.5, P < 0.001$).

Timing of movements.-Birds left their winter ranges between 2 April and 6 May (median = 18 April)(Fig. 3). Departure date from the winter area was independent of age (yearlings vs. adults)(Mann-Whitney U -test, $U = 24.5, P = 0.46$) and status (short vs. long distance movements)(Mann-Whitney U -test, $U = 23.5, P = 0.39$). There was no difference in the variance of departure dates from the winter range for yearlings vs. adults (Test for Equality of Variances $F_{6,8} = 1.4, P = 0.32$) or for birds moving short vs. long distance between winter and summer ranges ($F_{8,6} = 1.64, P = 0.28$).

If we exclude two females that left their breeding range prematurely, that is just or soon after predation of their clutch on 19 June or 6 July, all birds ($n = 18$) undertook the migration to winter range (adults) or autumn dispersal (juveniles) between 4 October and 24 December (Fig. 3). Departure dates did not differ between dispersing juveniles and migrating adults (Mann-Whitney U -test, $U = 24, P = 0.67$). Neither did departure dates differ for birds moving short vs. long distances (Mann-Whitney U -test, $U = 46, P = 0.76$). There was no significant effect of age or status of movement on the variances of departure dates from

birth area for juveniles, or departure from summer range for adults ($F_{13,3} = 2.359, P > 0.1$ and $F_{9,9} = 1.109, P > 0.1$) respectively.

Birds apparently completed dispersal and migration rapidly: eight movements between winter and summer ranges or the opposite, were completed within a maximum of 72 h, even though some individuals migrated or dispersed more up to 14 km. One female completed a 9-km migration between her destroyed nest and her winter range within a maximum of 24 h.

DISCUSSION

Like Ellison et al. (1989), we found that the black grouse in the southern French Alps is a partial migrant according to the terminology of Terril and Abble (1988). Some individuals migrated or dispersed up to about 14 km between winter and summer (breeding) ranges, while others remained in more or less the same area all year round.

Willebrand (1988) reported partial migration in a Swedish population of black grouse. In his study, migration was frequent in females, whereas males tended to stay in the vicinity of their lek all year round. We also found that more females than males migrated or dispersed between winter and summer ranges, and that females moved farther. Other studies have reported migration biased toward females in grouse (Bendell 1955, Kobriger 1965, Hoffman and Braun 1975, Herzog and Keppie 1980, Schroeder 1985, Hines 1986, Rolstad 1989, Schroeder and Braun 1993). Migration favoring females is consistent with the pattern of segregation of sexes observed in winter in several grouse species (Weeden 1964, Irving et al. 1967, Beck 1977, Ellison et al. 1981). Moreover, female grouse move farther than males during natal dispersal (Bowman and Robel 1977, Keppie 1979, Jamieson and Zwickel 1983, Dunn and Braun 1985, Schroeder 1986, Martin and Hannon 1987, Small and Rusch 1989, Keppie and Towers 1992, Beaudette and Keppie, 1992, Giesen and Braun 1993). These movements biased toward females correspond to the general pattern found in birds, whereas in mammals males are more likely to disperse (Greenwood 1980, Greenwood and Harvey 1982).

Our results suggest that the higher frequency of migration in hens vs. cocks, and the longer distances migrated by hens, are a consequence of higher spring dispersal rates and longer dispersal distances of yearling hens (Herzog and Keppie 1980, Schroeder 1985, Schroeder and Braun 1993). Four

lines of evidence support this idea. First, we found that the proportion of yearlings dispersing long and short distances in spring was not different of the proportion of older birds migrating long and short distances. Second, birds exhibited strong site fidelity to the first winter range occupied as a juvenile and the first summer range occupied as a yearling, and older birds returned each year to their former winter or summer range. Recall that the two ranges of some birds were separated by more than 14 km. Third, spring dispersal of yearlings occurred at the same date that adults migrated from their winter range to their summer range. Fourth, young that later became migrants (i.e. with separate winter and summer ranges as adults) continued to leave their winter range at about the same date in spring at which they had dispersed as yearlings. However, we found that distances moved were somewhat longer for spring natal dispersal than for migration. We believe that this difference was due to an artifact resulting from small sample sizes, because the juveniles that we followed a year or more, and that dispersed as yearlings, later retraced their spring dispersal route between summer and winter ranges (point two above).

Several authors have suggested that habitat selection may explain the differences in seasonal movements of the sexes (Zwickel et al. 1968, Hoffman and Braun 1975, Ellison et al. 1989, Cade and Hoffmann 1993). However, in our study, some radio tagged birds of both sexes were year round residents on the trapping area, that moreover was used by radio-tagged birds of both sexes either in summer or in winter. Moreover, among migrants, most individuals of both sexes passed over potential wintering or summering habitats during their migratory movements (see also Willebrand 1988, Marjakangas et al. 1991). Therefore, differences in habitat preferences between males and females were probably of minor importance in determining the pattern of movements that we observed. Other authors have also suggested that habitat selection is not the main factor explaining sexual differences in the tendency to migrate in grouse (Schroeder 1985, Willebrand 1988, Schroeder and Hoffmann 1993).

Among birds in general, three important questions remain unanswered. First, why do yearling females disperse more frequently and farther than yearling males? Second, why do dispersing birds bypass suitable habitats before establishing a winter and summer range? Third, why does a bird return to its first winter range occupied as a juvenile, and its first summer range occupied as a yearling?

The differences in the sexes and the bypassing of suitable habitats may result from dispersal having evolved in response to an interaction among four factors: habitat variability in space or time, competition

for resources, competition or mates, and inbreeding (Greenwood 1980, Dobson and Jones 1982, Pusey 1987, Johnson and Gaines 1990, Lidicker and Stenseth 1992, Clobert et al. 1994). In other words, dispersal is probably at least under genetic control. However, studies in grouse have not yet shown conclusively that dispersal behavior is inherited (Keppie 1980, Schroeder and Boad 1988).

As to the third question about fidelity to widely separated ranges, part of the explanation may be that searching for a closer range would take more time and energy than returning directly to a known site (Switzer 1993, Pärt 1995). Moreover, return to a familiar habitat probably confers an advantage over potential competitors (e.g. Krebs 1982, Lambrechts and Dhondt 1988) and may make both exploitation of resources (food, nest sites, territories on lek) and predator avoidance more efficient (Hinde 1956, Metzgard 1967).

ACKNOWLEDGMENTS

We thank A. Bogtchalian, R. Corti, P. Guilhem, F. Kopko, P. Leonard, P. Longchamp, H. Poudroux, D. Thiolière, T. Grzeganeck , C. Leenhardt and J. P. Serres for field assistance. We are grateful to O. Dehorter, M. Gibernau, M. Lambrechts and J. Blondel for comments on earlier versions of 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 CEFÉ (Centre d'Ecologie Fonctionnelle et Evolutive)-CNRS, Montpellier, France.

LITERATURE CITED

- ADRIAENSEN, F. AND A. A. DHONDT. 1990. Population dynamics and partial migration of the European Robin (*Erithacus rubecula*) in different habitats. *Journal of Animal Ecology* 59:1077-1090.
- BAKER, R. R. 1978. *The evolutionary ecology of animal migration*. Holmes and Meier, New York.
- BEAUDETTE, P. D. AND D. M. KEPPIE. 1992. Survival of dispersing Spruce Grouse. *Canadian Journal of Zoology* 70:693-697.
- BECK, T. D. I. 1977. Sage Grouse flock characteristics and habitat selection in winter. *Journal of Wildlife Management* 41:18-26.
- BENDELL, J. F. 1955. Age, breeding behavior and migration of Sooty Grouse, *Dendragapus odscurus fuliginosus* (Ridgway). Pages 367-381 in *Transactions of the Twentieth North American Wildlife Conference*, March 14, 15 and 16, 1955, Wildlife Management Institute, Wire Building, Washington 5, D.C.
- BENDELL, F. J. AND P. W. ELLIOTT 1967. Behavior and the regulation of numbers in Blue Grouse. *Canadian Wildlife Service Report Series-Number 4*, Ottawa. 76pp.
- BERTHOLD, P. AND U. QUERNER 1981. Genetic basis of migratory behavior in European Warblers. *Science* 212:77-79.
- BERTHOLD, P. 1984. The control of partial migration in birds: a review. *Ring* 10:253-265.
- BERTHOLD, P. 1991. Genetic control of migratory behaviour in birds. *Trends in Ecology and Evolution* 6:254-257.
- BERTHOLD, P. 1993. *Bird migration*. Oxford University Press, Oxford.
- BERTHOLD, P. AND F. PULIDO 1994. Heritability of migratory activity in a natural bird population. *Proceeding and Royal Society London B* 257:311-315.
- BIEBACH, H. 1983. Genetic determination of partial migration in the European Robin (*Erithacus rubecula*). *Auk* 100:601-606.
- BOWMANN, T. J. AND R. J. ROBEL 1977. Brood break-up, dispersal, mobility, and mortality of juvenile Prairie-Chickens. *Journal of Wildlife Management* 41:27-34.
- CADE, B. S. AND R. W. HOFFMAN 1993. Differential migration of Blue Grouse in Colorado. *Auk* 110:70-77.

- CLOBERT, J., M. MASSOT, J. LECOMTE, G. SORCI, M. DE FRAIPONT, & R. BARBAULT 1994. Determinants of dispersal behavior: the common lizard as a case study. Pages 183-206 in *Lizard ecology: historical and experimental perspectives* (L. J. Vitt, & E. R. Pianka, Eds.). Princeton University Press, Princeton, New Jersey.
- DOBSON, F. S., & W. T. JONES. 1985. Multiple causes of dispersal. *American Naturalist* 126: 855-858.
- DUNN, P. O. AND C. E. BRAUN 1985. Natal dispersal and lek fidelity of Sage Grouse. *Auk* 102:621-627.
- ELLISON, L. N., Y. MAGNANI AND R. CORTI 1981. Comparaison entre une population chassée et trois populations non chassées de Tétrás Lyre dans les Alpes françaises. *Bulletin Mensuel ONC, n° Scientifique et Technique Tétráonidés*, Décembre 1981:227-242.
- ELLISON, L. N., E. MENONI AND P. LEONARD 1989. Déplacement d'adultes de Tétrás Lyre (*Tetrao tetrix*) en automne et en hiver. *Gibier Faune Sauvage* 6:245-260.
- ENG, R. L. AND P. SCHALDWEILER 1972. Sage Grouse winter movements and habitat use in central Montana. *Journal of Wildlife Management* 36: 141-146.
- GAUTHREUX, S. A. J. 1982. The ecology and evolution of avian migration systems. Pages 93-168 in *Avian Biology*, vol 6 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). Academic Press, New York.
- GIESEN, K. M. AND C. E. BRAUN 1993. Natal dispersal and recruitment of juvenile White-Tailed Ptarmigan in Colorado. *Journal of Wildlife Management* 57:72-77.
- GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140-1162.
- GREENWOOD, P. J., & P. H. HARVEY 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* 13:1-21.
- HELMINEN, M. 1963. Composition of the Finnish populations of Capercaillie, *Tetrao urogallus*, and Black Grouse, *Lyrurus tetrix*, in the autumns of 1952-1961, as revealed by a study of wings. *Papers Game Research* 23:3-125.
- HERZOG, P. W. AND D. A. BOAG 1978. Dispersion and mobility in a local population of Spruce Grouse. *Journal of Wildlife Management* 42:853-865.

- HERZOG, P. W. AND D. M. KEPPIE 1980. Migration in a local population of Spruce Grouse. *Condor* 82:366-372.
- HILDÉN, O. 1982. Winter ecology and partial migration of the Goldcrest *Regulus regulus* in Finland. *Ornis Fennica* 59:99-122.
- HINDE, R. A. 1956. The biological significance of the territories of birds. *Ibis* 98: 340-369.
- HINES, J. E. 1986. Social organization, movements, and home ranges of Blue Grouse in fall and winter. *Wilson Bulletin* 98:419-432.
- HOFFMAN, R. W. AND C. E. BRAUN 1975. Migration of a wintering population of White-Tailed Ptarmigan in Colorado. *Journal of Wildlife Management* 39:485-490.
- IRVING, L., C. G. WEST, L. J. PEYTON AND S. PANEAK 1967. Migration of Willow Ptarmigan in arctic Alaska. *Arctic* 20:77-85.
- JAMIESON, I. A. AND F. C. ZWICKEL 1983. Dispersal and site fidelity in Blue Grouse. *Canadian Journal of Zoology* 61:570-573.
- JOHNSON, M. L., & M. S. GAINES 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Annual Review of Ecology and Systematics* 21:449-480.
- KEPPIE, D. M. 1979. Dispersal, overwinter mortality, and recruitment of Spruce Grouse. *Journal of Wildlife Management* 43:717-727.
- KEPPIE, D. M. 1980. Similarity of dispersal among sibling male Spruce Grouse. *Canadian Journal of Zoology* 58:2102-2104.
- KEPPIE, D. M. AND J. TOWERS 1992. A test on social behavior as a cause of dispersal of Spruce Grouse. *Behavioral Ecology and Sociobiology* 30:343-346.
- KETTERSON, E. D. AND V. J. NOLAN 1983. The evolution of differential bird migration. *Current Ornithology* 1:357-402.
- KOBRIGER, G. D. 1965. Status, movements, habitats, and food of prairie grouse on a sandhills refuge. *Journal of Wildlife Management* 29:788-800.
- KREBS, J. R. 1982. Territorial defence in the Great Tit: do residents always win? *Behavioral Ecology and Sociobiology* 11:185-194.
- LACK, D. 1944. The problem of partial migration. *British Birds* 37:122-130.

- LACK, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.
- LACK, D. 1968. Bird migration and natural selection. *Oikos* 19:1-9.
- LAMBRECHTS M. M. AND A. A. DHONDT 1988. Male quality and territory quality in the Great Tit *Parus major*. *Animal Behaviour* 36:596-601.
- LIDICKER, W. Z., & N. C. STENSETH 1992. To disperse or not disperse: who does it and why? Pages 21-36 in *Animal dispersal: small mammals as a model* (S. C. Stenseth and W. Z. J. Lidicker, Eds). Chapman & Hall, London.
- LISCINSKY, S. A. AND W. J. J. BAILEY 1955. A modified shorebird trap for capturing Woodcock an grouse. *Journal of Wildlife Management* 19:405-408.
- LUNDBERG, P. 1988. The evolution of partial migration in birds. *Trends in Ecology and Evolution* 3:172-175.
- MARJAKANGAS, A., H. ASPEGREN AND M. KYLLÖNEN 1991. Spring dispersal and subsequent movements of yearling female Black Grouse *Tetrao tetrix* in eastern central Finland. Pages 297-301 in XXth Congress of the International Union of Game Biologists, Gödöllő, Hungary.
- MARTIN, K. AND S. J. HANNON 1987. Natal philopatry and recruitment of Willow Ptarmigan in north central and northwestern Canada. *Oecologia* 71:518-524.
- METZGAR, L. H. 1967. An experimental comparison of Screech Owl predation on resident and transient white-footed mice (*Peromiscus leucopus*). *Journal of Mammalogy* 48: 387-391.
- MOHR, C. O. 1947. Table of equivalent populations of North American small mammals. *American Midland Naturalist* 37: 233-249.
- NAG, 1986. The generalised linear interactive modelling system. The royal statistical society, London.
- NEWTON, I. ed. 1989. Lifetime reproduction in birds. Academic Press, London.
- PÄRT, T. 1995. The importance of local familiarity and search costs for age and sex-biased philopatry in the Collared Flycatcher. *Animal Behaviour* 49:1029-1038.
- PUSEY, A. E. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends in Ecology and Evolution* 2:295-299.
- ROLSTAD, J. 1989. Habitat and range use of Capercaillie *Tetrao urogallus* L. in southcentral Scandinavian boreal forests. Ph.D. dissertation, Agricultural University, Ås, Norway.

- SCHROEDER, M. A. 1985. Behavioral differences of female Spruce Grouse undertaking short and long migrations. *Condor* 87:281-286.
- SCHROEDER, M. A. 1986. The fall phase of dispersal in juvenile Spruce Grouse. *Canadian Journal of Zoology* 64:16-20.
- SCHROEDER, M. A. AND D. A. BOAG 1988. Dispersal in Spruce Grouse: is inheritance involved? *Animal Behaviour* 36:305-306.
- SCHROEDER, M. A. AND C. E. BRAUN 1993. Partial migration in a population of Greater Prairie-Chickens in northeastern Colorado. *Auk* 110:21-28.
- SMALL, R. J. AND D. H. RUSCH 1989. The natal dispersal of Ruffed Grouse. *Auk* 106:72-79.
- SMITH, H. G. AND J.-Å. NILSSON 1987. Intraspecific variation in migratory pattern of a partial migrant, the Blue Tit (*Parus caeruleus*): an evaluation of different hypotheses. *Auk* 104:109-115.
- STORCH, I. 1993. Habitat use and spacing of Capercaillie in relation to forest fragmentation patterns. Ph. D. dissertation, Munich.
- SWITZER, P. V. 1993. Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology* 7:533-555.
- TERRIL, S. B. AND K. P. ABLE 1988. Bird migration terminology. *Auk* 105:205-206.
- VON HAARTMAN, L. 1968. The evolution of resident versus migratory habit in birds. Some considerations. *Ornis Fennica* 45:1-7.
- WEEDEN, R. B. 1964. Spatial segregation of sexes in Rock and Willow Ptarmigan in winter. *Auk* 81:534-541.
- WILLEBRAND, T. 1988. Demography and ecology of Black Grouse population. Ph. D. dissertation, Uppsala, Sweden.
- ZWICKEL, F. C., I. O. BUSS AND J. H. BRIGHAM 1968. Autumn movements of Blue Grouse and their relevance to populations and management. *Journal of Wildlife Management* 32:456-468.

TABLE 1. Number of adults black grouse that were sedentary, migrated long or short distances, or number of yearlings that dispersed long or short distances between their first winter range and their first summer range.

| | | Migrants or Dispersers | | Non-Migrants or Residents | Total |
|----------------|------------------|---------------------------------------|---------------------------|--|--------------|
| | | Long Distance | Short Distance | | |
| Males | Adults | 0 | 0 | 8 | 8 |
| | Yearlings | 1 | 2 | 4 | 7 |
| | Total | 1 | 2 | 12 | 15 |
| Females | Adults | 3 | 6 | 6 | 15 |
| | Yearlings | 4 | 1 | 2 | 7 |
| | Total | 7 | 7 | 8 | 22 |

TABLE 2. Number fo black grouse captured as adult, yearling or juvenile, with overlapping and non-overlapping winter and breeding areas.

| | | No overlap | Overlap |
|----------------|------------------|-------------------|----------------|
| Males | Adults | 1 | 7 |
| | Yearlings | 1 | 6 |
| | Total | 2 | 13 |
| Females | Adults | 6 | 9 |
| | Yearlings | 4 | 3 |
| | Total | 10 | 12 |

TABLE 3. Estimation of dates of movements for 4 migrant females captured as juvenile or adult.

| Age | Bird n° | Summer-Winter | Winter-Summer |
|-----------------|----------------|---|---------------------------------|
| Adult | 1 | 6 Oct., 20 Oct., 4 Oct. | 15 Apr, 5 Apr. |
| Adult | 2 | 30 Oct, 30 Oct. | - |
| Juvenile | 3 | 30 ^(*) Oct., 9 Oct., 17 Oct. | 24 ^(**) Apr, 30 Apr. |
| Juvenile | 4 | 18 ^(*) Nov., 27 Nov. | 9 ^(**) Apr., 14 Apr. |

(*) Fall natal dispersal.

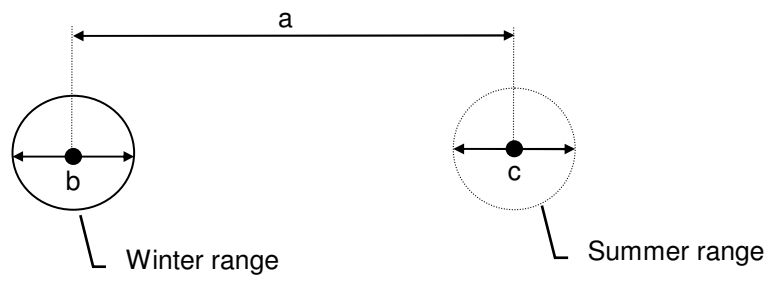
(**) Spring natal dispersal.

Fig. 1. Distances used to classify grouse into different categories of migrant or disperser (see methods): a = distance between winter and summer range, b = distance between most widely separated points of the winter range and c = distance between most widely separated points of the summer range (black dots represent the bivariate median values of locations).

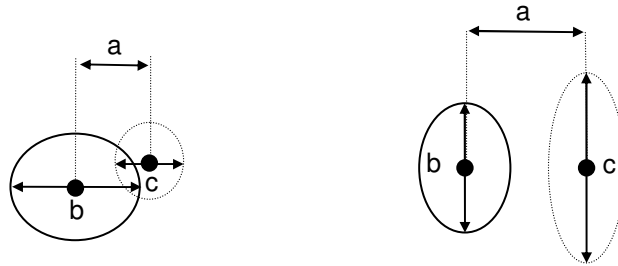
Fig. 2. Distances between summer and winter ranges for 14 males (7 adults, 7 yearlings) and for 22 females (15 adults, 7 yearlings) black grouse at Ristolas, southern French Alps.

Fig. 3. Dates of movements of black grouse undertaking dispersal fall dispersal (juveniles), spring dispersal (yearlings) or migration (adults).

Long distance movements



Short distance movements



Sedentary or residents

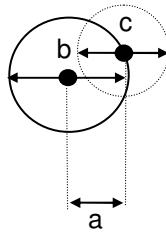


Fig. 1.

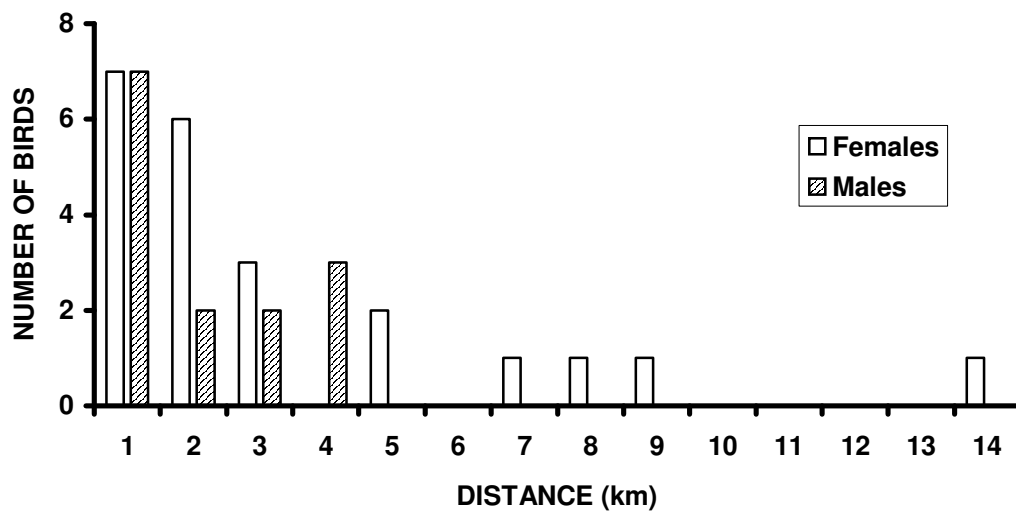


Fig. 2.

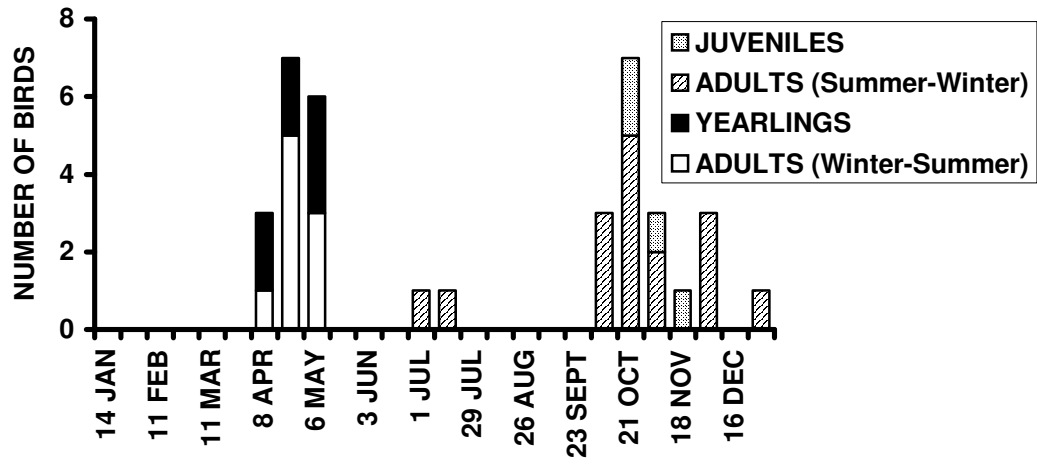


Fig. 3.