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SHORT COMMUNICATION

Short communication articles are short scientific entities often dealing with methodological problems or with byproducts of larger research projects. The style is the same as in original articles

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We radio-tagged and tracked 22 hen and three cock capercaillie *Tetrao urogallus* in northeast Scotland during 1989-1995. Natal dispersal distances of 13 first-year hens ranged within 1-30 km (median: 11 km). There were two main periods of dispersal, autumn and spring, with much individual variation. Some hens dispersed in autumn, some in spring, some in autumn and again in spring, and some moved little. Of 10 hens that nested, seven did so in their first year, two not until their second and one in her third year. After their first year, hens were quite sedentary, but some showed increased movement in April as they attended leks. Capercaillie in Scotland live in fragmented woodlands. How far they disperse is an important consideration when managing woods for their benefit.

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Dispersal of juveniles is crucial to the dynamics and survival of animal populations in fragmented habitat. Here we report on the dispersal of juvenile capercaillie *Tetrao urogallus* in Scotland where, as in much of western Europe (Storch 2000), the bird is in peril of local extinction because once-continuous woodland habitat is fragmented by agriculture or development. Their survival depends partly upon the size and distribution of woods, and arranging these for the benefit of capercaillie requires an understanding of how far birds disperse between suitable woodland patches. But information on dispersal of capercaillie is sparse (Segelbacher et al. 2003).

The last record of native Scottish capercaillie was in 1784 when Scottish forests were greatly depleted. Birds were reintroduced from Sweden, Norway, Austria and Finland from 1836 onwards and subsequently became

abundant in replanted woodlands, reaching their maximum spread shortly before the First World War (Pennie 1950, 1951). In the 1970s they are thought to have numbered about 20,000, but by 1992-1994 there were only 2,000-3,000 (Catt et al. 1998) and in 1998-1999 about 1,000 left (Wilkinson et al. 2002). Following removal of forest fences and somewhat improved breeding success in 2001-2003, they recovered to about 2,000 in 2003-2004 (95% confidence interval: 1,300-2,800; the Royal Society for the Protection of Birds, unpubl. survey). In Britain, they occur only in Scotland, with six geographically and genetically (S.B. Piertney, K. Kortland, F. Marshall, G. Segelbacher & R. Moss, unpubl. data) distinct subpopulations in Easter Ross, Moray, Speyside, Deeside and Donside, Perthshire and around Loch Lomond in Argyll.

Material and methods

Well-grown poults were caught in hand nets and radiotagged in late July or early August during 1989-1995 in the Dee valley, west of Aberdeen in northeast Scotland. We report on 20 hens and three cocks caught in the 12 km^2 Caledonian forest remnant in Glen Tanar (southwest of Aboyne), plus two hens from plantations in nearby Finzean (southeast of Aboyne). Picozzi et al. (1999) describe methods and study areas. The birds dispersed through much of the Dee valley and some beyond. The landscape comprised a heterogeneous mixture of semi-natural and commercial forest stands separated by moorland and farmland, broadly coarse-grained at the hectare scale and fine-grained at the km^2 scale.

Birds were routinely located about once a week although a month or more sometimes elapsed until we found hens that had suddenly moved long distances. To find some birds we flew up to 3,000 m altitude in a hot-air balloon. Date of movement was recorded as when a bird was relocated, irrespective of time elapsed, because that was when the movement was discovered. Distances were measured in a straight line 1) between successive observations of each bird and 2) between each observation of a bird and its site of tagging. In the literature, rate of movement is sometimes measured as the distance d between two observations divided by the number of days t between them (d.t^{-1}, units km.day^{-1}). This one-dimensional model implies, unrealistically, that after t days a bird is t times as far from its starting point as it is after one day. A two-dimensional random walk, in which d is proportional to the square root of t, is a better approximation (Brown & Rothery 1993, Turchin 1998). We therefore measured rate of movement as d^2.t^{-1} (km^2.day^{-1}).

On the few occasions when the same hen was recorded twice in the same day, we calculated distance from tagging site for each observation but estimated rate of movement from the first observation only.

Of the 22 hens, four moved < 2 km from their tagging site, while others moved up to 44 km between successive observations and 30 km from tagging. Movement data typically comprised long periods of short movements within a relatively small range, punctuated by occasional, sudden longer movements of exploration or dispersal, mostly in spring or autumn. Consequently, frequency distribution plots were bimodal with many shorter movements around one mode and a few longer ones around a second. 'Sudden long movements' fell around the second mode. All birds that survived their first spring showed this pattern, although the longer movements were hundreds of metres for some, kilometres for others. No parametric transformation brought all the data into a single useful distribution. We therefore summarised seasonal patterns of movement, independently of the scale of movement, as follows:

For each analysis, data were ranked (the lowest datum getting the smallest rank) and from the ranks normal scores were calculated according to the Blom method (SAS (2001); rank procedure). This involves taking the inverse cumulative normal (probit) function of $(r_i - 3/8)/(n + 1/4)$ where r_i is the rank of datum i and n the total number of data ranked. We then performed mixed model analyses of variance (SAS mixed procedure) that explained distance or movement in terms of the fixed effects month, age or breeding status. Individual hen and calendar year were entered as random effects, so accounting for correlations among observations from individual hens or years. We checked for artefacts of transformation by comparing analytical results with conclusions reached by examining maps of movement.

Hens were classed as first-year (August-May), second-year (June-May) or older. Some hens did not nest in their first year and so another classification was nesting or not-nesting. Natal dispersal was the distance from a hen's site of tagging to her first nest. For hens that survived their first spring but did not live to nest, we used 'first-winter dispersal' as a surrogate for natal dispersal. This was the distance between tagging site and position in mid May. 'Autumn dispersal' occurred from tagging to late November, 'spring dispersal' was in April-May and 'juvenile dispersal' a general term that included all four.

Results

We consider birds (22 hens, three cocks) that were

Table 1. Natal and autumn dispersal distances (in km) of 13 capercaillie hens. First-winter dispersal distances are shown for birds that did not nest in their first year. Autumn and first-winter dispersal were from tagging to late November and mid-May, respectively. The three (2+) died before nesting. The second 'first-winter' dispersal distance for hen AR3 was from tagging to her second May. Hen AR7, killed against a fence in mid-May, was excluded from the statistical analyses.

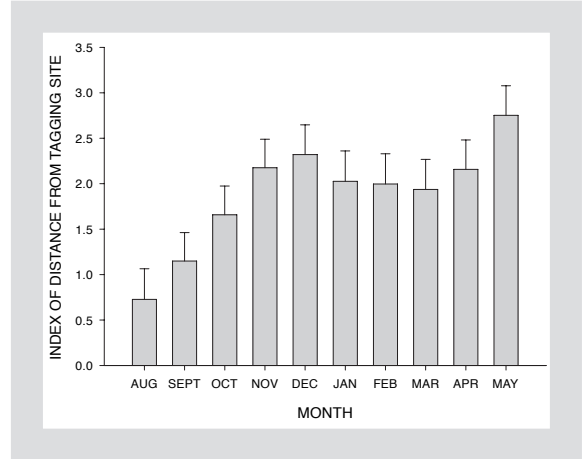| Hen	Year of first nest	Dispersal		
		Autumn	First-winter	Natal
AR7	1	0.4	-	1.1
BM2	1	4.1	-	4.6
M5	1	0.8	-	9.4
RB2	1	2.0	-	11.3
BA2	1	9.4	-	12.1
F3	1	2.5	-	18.0
RB4	1	15.0	-	25.2
AR5	2	21.4	3.2	3.0
RB1	2	0.3	11.1	11.1
D6	(2+)	0.5	4.6	-
D8	(2+)	0.3	28.1	-
BA1	(2+)	20.0	29.8	-
AR3	3	0.8	1.7, 2.7	2.4

Figure 1. Seasonal variations in distance from site of tagging for 12 first-year hens (with S.E. of estimate). The distance indices are estimates from a mixed model of data ranked as described in the text, with month as the sole fixed effect, and bird and year as random effects ($F_{10,375} = 16.8$, $P < 0.0001$); coded by adding two to make all estimates positive. We took weeks to find some long-distance movers in autumn and spring. Hence, for example, the increased distance index for May included some movements that occurred in April.

tracked at least until the end of their first November, so including any autumn dispersal. We followed 15 first-year hens until spring (April-May). Of these, one died on hitting a fence in May. The radio signals of two were lost in April and May 1990, respectively, possibly because they emigrated and we did not search far enough afield.

Of 10 hens that nested, seven did so in their first year, two not until their second and one in her third year (Table 1). Three hens that did not nest in their first year died before their second spring.

Causes of death throughout the study included flying into forest fence (six hens) or power line (one hen), red fox *Vulpes vulpes* (four hens), golden eagle *Aquila chrysaetos* (one cock), unidentified bird of prey (one hen) and an unidentified predator (one hen). Radio signals were lost from four hens and one cock. Signal loss was more likely for long-distance dispersers than for short-distance dispersers, so our results may be biased against long-distance dispersers. Five hens and one cock survived the study.

First-year hens

Movements of young hens began in August while they were still with their mothers and continued during brood break-up in late August and then in autumn. Figures 1 and 2 show seasonal variations in activity, independently of scale of movement. The average hen dispersed from her tagging site between August and November (see Fig. 1), showing longer daily movements (see Fig. 2) in Sep-

tember-November, before settling in a small range from December to March. She was most active in April and May, attending one or more leks in late April, and then dispersed to her nesting site or, if not nesting, to her May range.

This average comprised much individual variation. In autumn, seven out of 22 hens showed a distinct phase of autumn dispersal associated with a short, sudden increase in their rate and distance of movement (Table 2) and six hens had a less distinct pattern of autumn move-
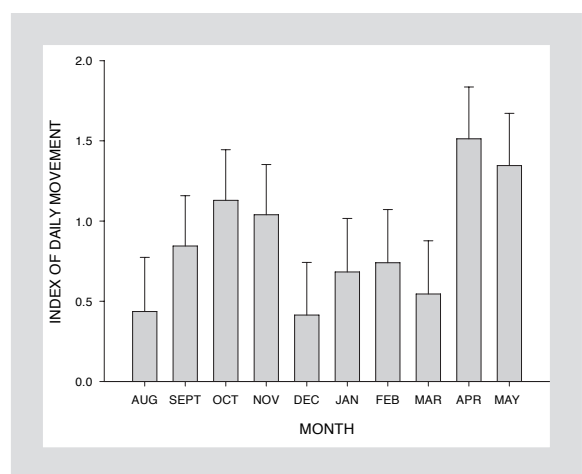

Figure 2. Seasonal variations in daily movement rates for 12 first-year hens (with S.E. of estimate). The rate indices are estimates from a mixed model of data ranked as described in the text, with month as the sole fixed effect, and bird and year as random effects ($F_{10,258} = 6.55$, $P < 0.0001$); coded by adding one to make all estimates positive.

Table 2. Autumn dispersal of 22 young capercaillie hens. For definition of sudden long movement, see text. Sudden long movements were recorded for seven hens in late September (one hen), October (three hens), October-November (two hens) or October-December (one hen). However, the latter three could have completed their autumn dispersal in October because they moved 10, 15 and 20 km, respectively, from their tagging site, and we took weeks to find them.

Number of hens	Sudden long movement	Distance moved
9	No	< 1 km
6	No	1-5 km
3	Yes	2-3 km
4	Yes	10-22 km

ment. They showed no sudden increase in their rate of movement, but slowly drifted away from their tagging site between August and October, remaining within 1-5 km of it. The remaining nine hens stayed within 1 km of their tagging site throughout autumn.

All but one hen moved little during December to March. The exception (AR5; see Table 1) moved 22 km from her tagging site in October and then in December-February flew back and forth between two separate areas (Crathie and Coilacriech) about 4 km apart within continuous woodland. In spring, she returned to Glen Tanar some 3 km from where she had been marked.

Of the 15 hens that survived until spring, all but one (BM2) showed increased movement in April-May as they visited leks and in some cases moved to a new spring range. Some hens remained within a few km of their winter range, others embarked upon wide-ranging tours (e.g. BA2). Some, including birds that nested in their first year, moved to a new range just before the main mating season in late April (e.g. RB2 moved 9 km during 2-16 April), some moved during late April (e.g. F3 moved 19 km during 19-25 April) and some in May (e.g. M5 moved 9 km during 7-13 May). The natal or first-winter dispersal distances of 13 hens (see Table 1) ranged within 1-30 km (median: 11, mean: 12.3, SD 9.8).

We checked whether young hens that nested or did not nest in their first year (see Table 1) showed different movement patterns. Mixed model analyses for the 12 hens that survived until the end of May explained rate of movement or distance from tagging site in terms of month (August-May), nesting status (nesting or not) or month*status interaction. There were of course significant differences among months (SAS type 3 tests of fixed effects: rate $F_{9,349} = 6.47$, P < 0.0001; distance $F_{9,366} = 19.1$, P < 0.0001) but no significant effect of nesting status (rate $F_{1,349} = 0.39$, P = 0.53; distance $F_{1,366} = 0.52$, P = 0.47) or month*status interaction (rate $F_{9,349} = 0.94$, P = 0.49; distance $F_{9,366} = 1.18$, P = 0.31).

Older hens

We tracked 12 hens into their second year and three into their third. Second-year and older hens made none of the sudden long-distance movements shown by some dispersing first-year hens. Some older hens nonetheless showed increased movement in April as they attended leks.

Old hens were categorised according to age (second-year or older) and year of first nest (first-year or later; see Table 1). A mixed model showed that different categories had different patterns of movement in April-June (month: $F_{11,565} = 2.71$, P = 0.002; age: $F_{1,565} = 0.33$, P = 0.56; year of first nest: $F_{1,565} = 0.09$, P = 0.77; month*age: $F_{11,565} = 2.49$, P = 0.005; month*year of first nest: $F_{11,565} = 3.86$, P < 0.0001). This was because, after juvenile dispersal in April-May, 1) in June and subsequent May-Junes, birds that nested moved less than birds that did not nest (month*year-of-first-nest interaction was not significant when May and June were dropped from the analysis) and 2) in April-May, birds in their second year moved more than older birds (month*age interaction not significant when April and May were dropped).

Cocks

We report on three cocks that lived in the 12 km² old pinewood of Glen Tanar. The two main leks were about 3 km apart, one in the northwest (lek 1) and one in the southeast (lek 2). Each lek had about 10 displaying cocks.

Cock D4 was tagged in August 1989 and killed by a golden eagle in March 1993. He was tagged on the Drum, about 1 km to the northeast of lek 2. He spent most of his time within 1 km of where he was tagged and was never recorded > 3 km from there. Each spring he became more active and visited lek 2. He did not gain a permanent territory at lek 2, however, and was usually seen displaying on the Drum, either solitarily or with up to two other cocks.

Cock D5 was marked in August 1991, also on the Drum, and was still alive in January 1997. He was never recorded > 1.2 km from where he was tagged. Each spring he became more active and displayed on the Drum. Unlike D4, he was not recorded at a main lek.

Cock M3 was marked in late July 1989 near lek 2. His radio failed in July 1991. In spring 1990 he roamed through the old forest, up to 4 km from where he was tagged, and visited lek 1. From August 1990 he was usually found to the north of lek 1, up to 5 km from his tagging site. In spring 1991 he again roamed, visiting leks 1 and 2.

Discussion

Analysis of data

For statistical analyses of movement, we ranked the data and converted the ranks to normal scores. Mixed models allowed us to combine data from all birds, so providing compact summaries of seasonal variations in activity (see Figs. 1 and 2) independently of how far each bird moved. Numerical results were consistent with inductive conclusions reached by examining maps of individuals' movements, themselves too cumbersome to present here (examples are available from the authors on request).

Thus, in their first spring (April-May) hens that nested moved as much as those that did not nest. This reflected hens dispersing in April and early May, some just before they nested. Subsequently, in June of their first year and in May-June of later years, nesting hens moved less than non-nesting hens. Also, as they became older, hens moved less in April-May, although this conclusion was based on a small sample.

Autumn and spring dispersal

Two distinct periods of juvenile dispersal, autumn and spring, have been described for other woodland grouse (e.g. ruffed grouse *Bonasa umbellus* (Small & Rusch 1989, Rusch et al. 2000), spruce grouse *Falcipennis canadensis* (Boag & Schroeder 1992, Keppie 2004), blue grouse *Dendragapus obscurus* (Hines 1986, Zwickel 1992), and black grouse *Tetrao tetrix* (Warren & Baines 2002, Caizergues & Ellison 2002)) and our data are consistent with this. Similarly, cock grouse are usually found to be more philopatric than hens.

Moss (1987) showed that the ratio of young to old capercaillie hens shot in Glen Tanar in 1974-1984 fell suddenly between October and November and concluded that this indicated autumn dispersal. We confirm and amplify this conclusion by showing that dispersal occurs also in spring. Our results resemble those of Warren & Baines (2002), who found that black grouse on open moorland in north England showed two phases of dispersal, autumn (late September - early November) and spring (late March - mid April), with a mean natal dispersal distance for eight first-year greyhens of 9 km (range: 4-19 km).

There have been many studies of radio-tagged adult capercaillie caught at leks, but knowledge about natal dispersal of young birds is sparse. Storch (2001) concluded that whereas most males settle close to their chick range, young females tend to disperse distances of typically 5-10 km. Storch & Segelbacher (2000) summarised known 'juvenile dispersal distances'. They con-

cluded that average seasonal movements of 1-2 km may be expected for adults and median dispersal distances of < 10 km for juveniles. Many of these data, however, were from chicks wing-marked and shot in the same autumn, possibly before they had completed natal dispersal.

Our young hens dispersed a median 11 km from their tagging site to nest, somewhat further than suggested by Storch & Segelbacher (2000). This might be related to the fragmented nature of Scottish forests, but there was much individual variation. Some birds hardly moved from their tagging site while others moved far in autumn or spring.

Individual differences in dispersal patterns might be inherent. Emigration of young birds from Glen Tanar, however, was density dependent (Moss & Weir 1987). Hence, some dispersal could be due to overcrowding. In the Pyrenees, Ménoni (1991) documented aggression among hens in spring as they defended territories encompassing scarce brood habitat. Such aggression might stimulate young hens to disperse. In boreal forest, Borchtchevski & Gubar (2003) speculated that spring dispersal of hens might result from competition for limited supplies of bog-cotton *Eriophorum* spp., a high-quality food.

Although some of our tagged hens did not nest until their second or third year, all the long-distance dispersal movements that we recorded were in their first year. Borchtchevski (1993), however, suggested that, under some circumstances in boreal forest, young birds might leave prime habitat and return as adults. He based this on indirect evidence from age ratios in shot birds.

Dispersal in fragmented woodland

Our sparse data on cocks is consistent with Storch's (2001) generalisation that most cocks tend to settle near their chick range. This raises a problem in fragmented habitats. Although hens may be able to recolonise isolated patches of woodland where capercaillie have died out, cocks may be less likely to do so. Thus, during expansion of the reintroduced Scottish population, hens often preceded cocks (Witherby et al. 1941), leading to many reports of hybrids between black grouse and capercaillie. Similarly, Wegge et al. (1992) suggested that the sex ratio might favour hens in fragmented forests.

Our findings have implications for practical conservation of fragmented woodland grouse populations. Where all woodland fragments are permanently occupied, dispersal of hens among fragments might be enough to maintain genetic diversity and avoid inbreeding depression. In this case, fragments separated by say 5-10 km (Segelbacher et al. 2003) might retain enough genetic diversity to avoid inbreeding depression. In many land-

scapes, birds are likely to die out in some fragments, which must then be recolonised. In this situation, landscape design should take account of the shorter distances moved by dispersing cocks. 'Stepping stone' woods between major woodland fragments, for example, could facilitate cock dispersal.

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