Spatial arrangement of kin affects recruitment success in young male red grouse

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Models have shown that population cycles might be driven by time lags resulting from positive feedback between kin structure and population change, coupled with negative feedback between density and population change. One such model operates through kin favouritism facilitating the recruitment of young cock red grouse. We investigated whether recruitment by young cocks depended on the presence and spatial arrangement of elder relatives in the territorial population. We used molecular genetic estimates of relatedness, and checked for effects of covariates including natal territory size, hatching date, body size, parasite burdens and local density. Philopatric recruitment by cock red grouse led to the formation of clusters of contiguous territories owned by kin. The probability that an individual young cock would establish a territory increased with the number of kin in his father's cluster. This pattern might have been due to genetic quality determining both recruitment success and the size of the paternal cluster. If so, there should have been a positive correlation between a young cock's probability of recruitment and the number of his relatives in the population, irrespective of their spatial distribution. This did not occur and so the effect of cluster size is unlikely to have been confounded by genetic quality. The only morphological measure correlated with recruitment success was supraorbital comb size. The results are consistent with the prediction that kin tolerance affects recruitment but were at the level of the individual within years, rather than the population among years. Hence an experimental test of the kin favouritism hypothesis for population cycles, by manipulation of relatedness in populations among years, is now required.

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Regular fluctuations in animal numbers have fascinated ecologists since the fur returns of the Hudson Bay Company were described by Elton (1924) and Elton and Nicholson (1942). Model population cycles can be produced by two-part systems with time lags that cause delayed density dependence in the growth of each part (Krebs 1994). Parts can be trophic levels such as predator-prey or host-pathogen (Hutchinson 1948, Berryman 1978, Royama 1981). They may also be segments of a population structured according to age, physiology, space or kinship.

Although few empirical studies have addressed the question directly, kin favouritism could have profound effects on population dynamics (Greenwood et al. 1979, Lambin and Krebs 1993, Watson et al. 1994, Lambin and Yoccoz 1998, Pusenius et al. 1998). Mountford et al. (1990) proposed that cyclic fluctuations in numbers of red grouse (*Lagopus lagopus scoticus* Lath.) are caused by differential behaviour towards kin and non-kin, and models show how this might occur (Mount-

ford et al. 1990, Hendry et al. 1997, Matthiopoulos et al. 1998). Here for the first time we test the key assumption of this hypothesis, that clusters of elder relatives influence the recruitment of young cocks to the territorial population.

Red grouse populations in Britain commonly show cyclic dynamics with periods of four to ten years (MacKenzie 1952, Moran 1952, Williams 1985). Studies in north-east Scotland showed that the main demographic cause of changes in numbers of territorial males from year to year was variation in recruitment. This depended partly on the reproductive rate and partly on the proportion of fully-grown young cocks that established territories (Moss and Watson 1991, Moss et al. 1996). Red grouse take territories and breed in their first year, and birds that fail to get territories usually die before the next breeding season. Territory establishment takes place in the autumn and, despite overwinter mortality, recruitment into the autumn territorial population has been a good predictor of recruitment into the spring population (Watson 1985). In any year there are some young cocks ('recruits') that establish a territory, and some ('non-recruits') that do not (Jenkins et al. 1963, MacColl 1998).

Moss and Watson (1984) suggested that changes in the size of red grouse populations might be caused by changes in behaviour linked to kin selection among males. Mountford et al. (1990) formulated this kinship hypothesis explicitly as an analytical model. The hypothesis assumes that related birds will be more tolerant of one another in territorial competition (Watson et al. 1994). At low density, established territorial cocks are hypothesised to facilitate territorial establishment by their sons close to their natal territories ('philopatric recruitment'). This results in an increase in density and the formation of clusters of territories occupied by related cocks. Tolerant behaviour among members of these clusters favours the recruitment of their joint offspring to the clusters, and results in positive feedback between recruitment and the number of territorial cocks in a cluster. As population density increases, and space becomes limiting, tolerance among relatives declines and recruitment is curtailed. Without high rates of recruitment to maintain them, clusters rapidly decay because of mortality that is naturally high in grouse populations (Moss and Watson 1991). Thus the balance between recruitment and mortality favours recruitment to the population and its constituent clusters during the increase phase, but shifts to favour the decay of kin clusters at peak and declining densities. Therefore, in the decline, kin clusters are smaller than at equivalent densities in the increase phase. This results in a continued restriction of recruitment that drives density into a trough. That this model can produce realistic population cycles has been confirmed in both analytical (Matthiopoulos et al. 1998) and spatially explicit simulation models (Hendry et al. 1997).

Here we use molecular genetic estimates of relatedness to test the hypothesis that clusters of elder established relatives affect the recruitment of young cocks into the territorial population. In particular we examine the assumption that, within years, young cocks from larger kin clusters are more likely to establish a territory philopatrically. If this applied among years, it could provide feedback between past recruitment and demography which would be likely to destabilise population dynamics.

Methods

Study area

A population of individually marked red grouse was studied in a 140-ha area of heather moorland at Glas Choille (57°07′ N, 3°19′ W; Fig. 1), 60 km west of Aberdeen in the foothills of the Cairngorm Mountains,
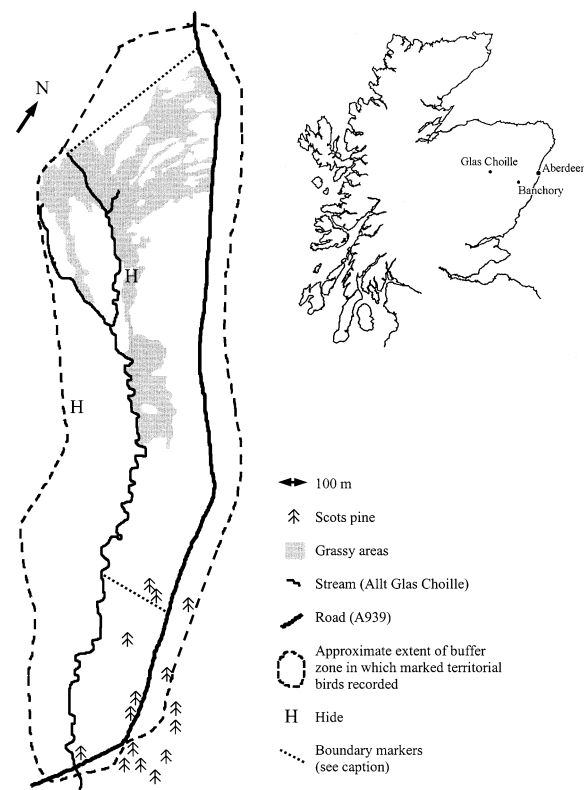

Fig. 1. The study area at Glas Choille, Aberdeenshire, and its position within Scotland. Our study concentrated on marked individuals within a core (65 ha) area delimited by the road, the west edge of the stream and the northern boundary marker. We worked less intensively in a buffer zone, delimited by the dashed line, which extended the total study area to 140 ha. Densities of territorial birds were calculated from a 52 ha central part (delimited by the road, the west edge of the stream and the northern and southern boundary markers) of the core which had been continuously monitored since 1993.

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Scotland from August 1995 until November 1996. Glas Choille is a small glaciated valley, lying between 400 m and 550 m altitude, about a kilometre wide and 2.5 km long, with a stream running through it. The vegetation of Glas Choille, which is managed for red grouse by rotational burning, comprises a mosaic of patches of heather (*Calluna vulgaris*) and other Ericaceae of different ages, juniper (*Juniperus communis*) bushes, and wetter areas comprising a mixture of heather, grasses, rushes and sedges (MacColl 1998).

Data collection

From 1993 onwards, most territorial cocks in the study area (Fig. 1) were marked, and their territories mapped either by X. Lambin (unpubl.) or in the present study, when all territory holding cocks within the core 65 ha of the study area were marked, or unmarked but individually recognisable from their plumage (total seven individuals). Territories were mapped twice a year, on 1:2500 scale vegetation maps, in autumn (September and October) and spring (mid-March till early May), as in Jenkins et al. (1963). Summer (May–August) survival of adult cocks was 95% and 76% in 1995 and 1996, respectively and birds usually keep the same territory until they die (Watson et al. 1994). Hence the spring territory map was a good approximation of the positions of old territorial cocks immediately before young males began to establish territories in late August and early September. When calculating spatial relationships between birds in the autumn, we excluded adult cocks that had died over the summer, and assumed that their spring territories were unoccupied at the beginning of autumn.

Interpretation of the present study depends partly upon knowing the dynamics of the population. We therefore estimated the population density in the study area from 1993 to 1997. Estimates of population density were based on the number of males holding territories in a central 52 ha of the core study area that had been continuously monitored since 1993 (Fig. 1). Density estimates were made at the end of April (breeding density), and at the end of October (post-recruitment density). In October 1997, when effort was reduced, the density estimate was based on a 30-ha subsection of the central 52 ha.

We studied the recruitment of all marked young males known to be alive within the study area at the end of August in 1995 and 1996. We focussed on recruitment to the autumn population, in order to reduce complications resulting from overwinter mortality of territorial cocks, and the secondary replacement of these by non-territorial cocks. Young males were considered to have recruited (established a territory) if, by the end of the autumn period of territory mapping, they had been seen displaying unchallenged territorial behaviour on at least three separate days (Watson and Jenkins 1964). 'Recruitment success' of each young male was therefore a binary variable, taking a value of one for young males that were recruited and zero for others.

Measurement of birds and their properties

Individual birds were caught at two times of the year. In late June and early July chicks were caught with the aid of pointing dogs while they were still in broods and 10–50 d old. They were weighed to the nearest gram, aged from primary feather development (Parr 1975), ringed, and marked with coloured plastic (PVC coated nylon) patagial tabs (80 to 110 × 4 mm) (Boag et al. 1975). In August to November ('autumn') young males were caught by spotlighting at night (Hudson 1986) and body measurements (see Table 1) made. These included males previously marked as chicks and some previously unmarked males. Blood samples were taken from a wing vein and stored in sterile isotonic SSC buffer solution (Bruford et al. 1992). Birds were ringed and marked with 150 × 5 mm patagial tabs. Birds previously marked as chicks now had their small tabs replaced with large ones. The birds were either released immediately, or held overnight to obtain a caecal dropping for counts of caecal threadworm (*Trichostrongylus tenuis*) eggs, which can be used to estimate worm burdens (Table 1).

Marked cocks holding territories on the study area in springs 1995 and 1996, and young cocks caught in autumn, were genotyped at nine dinucleotide (Piertney and Dallas 1997) and up to seven tetranucleotide (Piertney et al. 1998) microsatellite loci using standard radio-labelling and electrophoretic techniques (Sambrook et al. 1989). Genotype data were used to assign young males to putative fathers from among tagged territorial males using the exclusion method (Chakraborty et al. 1988), and to calculate pairwise relatedness coefficients (*R*; Queller and Goodnight 1989) among all marked males present on the study area in spring and autumn. Relatedness coefficients calculated from electrophoretic data in this way take account of background levels of allele sharing, and are thus measures of identity by descent (Grafen 1985). They have previously been shown to be robust, and sufficiently precise to infer correctly relationships between individuals of unknown pedigree (Piertney et al. 1999).

Measures of social environment (Table 2) and other covariates (Table 1) were made for each individual young cock. The testing of the hypothesis required some measure of the size of spring clusters of territorial cocks. Our two definitions focussed on a young cock's father, involved the position and relatedness of his male kin, and had to result in cluster sizes which varied enough to be useful as predictor variables.

Table 1. Covariates, other than those concerning the social environment of young cocks, used in analyses of the factors affecting recruitment probability (considered to be continuous variables unless stated otherwise).

Covariate	Description
Year	Year of the study (class variable).
Father's age	Age of a young cock's father (class variable).[1]
Father's territory size	Size of a young cock's father's spring territory (ha).[2]
Hatching date	Back calculated from the mean estimated age of all the chicks (Parr 1975) in each brood caught as chicks.
Chick condition	Residuals from the regression of chick weight on age for each year calculated separately (Moss et al. 1993).
Weight	Residuals from the regression of autumn weight on capture date.[3]
Tarsus	Length of the tarsometatarsus (mm), in autumn. There was no evidence that this was still growing at this time.
Residual comb size	Residuals from the regression of size of supra-orbital comb (maximum height × maximum width) on date of capture.[4]
Condition	A subjective score of the condition of each bird.[5]
Worm burden	Calculated from the number of *Trichostrongylus tenuis* eggs in caecal faeces.[6]
Local density	The number of territory centres within 200 m of a bird's father's territory in the previous spring.[7]

[1] 'young' for one year old fathers (i.e. first breeding attempt) or 'old' for fathers older than one year.

[2] Measured using a planimeter (Allbrit, England) from maps of the territorial behaviour of breeding cocks made during the previous spring (Watson and Miller 1971).

[3] Birds were weighed at night in autumn, when they usually had full crops. We calculated residuals from the best fitting linear or quadratic regression of these weights on date of capture in each year, and used these as an indication of the deviation of individuals from their expected weight from the date on which they were captured (MacColl 1998).

[4] This had units of mm^2 although it is not a true estimate of area of the supra-orbital comb, which is more elliptical, than rectangular, in shape. Combs in red grouse are a secondary sex trait, displayed during intra-sexual conflict. Their size is correlated with hormonal status and aggression (Moss et al. 1979).

[5] This took a value between 1 (skeletal) and 5 (fat), based on the plumpness of the bird's pectoralis muscles. Most birds fell in the range 2 (thin) to 4 (good).

[6] *T. tenuis* eggs in caecal faeces from captured birds were counted using a modified McMaster technique (MAFF 1986, Delahay 1995). An estimate of the number of adult worms in the gut of each bird was made using the regression equation of Moss et al. (1990: 635). We calculated worm burden as natural logarithm of (number of adult worms + 1).

[7] When the 200-m radius overlapped with the edge of the study area, the number of territory centres in the nearest 12.57 ha (equivalent to a circle of radius 200 m) of the study area was counted.

We defined the 'number of related neighbours' (Table 2) as the number of territorial cocks adjacent to the father and related to him by a coefficient ≥ 0.375. This cut-off has been shown (Piertney et al. 1999) to be suitable for separating first order (parent-offspring and full-sibling) from other lower order relationships with minimal type-I or type-II error. Relatedness was continuously distributed in the population (Piertney et al., 1999) and so small changes in the choice of this and other cut-offs (below) were unlikely to affect the outcome.

'Chain size' was an alternative definition of cluster size. This was calculated by constructing, for each father in spring, chains of contiguous territorial cocks that had a relatedness coefficient ≥ 0.5. This definition incorporated only the most closely related of birds, and resulted in chains of suitably variable length, that did not link across the whole study area.

Number of related neighbours and chain size are spatially explicit measures of cluster size, an aspect of the relatedness structure of the previous generation as experienced by young cocks. The kin favouritism hypothesis therefore predicts that they should be positively related to probability of recruitment, and in testing for their significance, one-tailed tests were used. In addition, we calculated a measure of social environment that was not spatially explicit. This was 'total male relatives': the number of adult male relatives of each young bird, of relatedness coefficient ≥ 0.25, present in the study area in autumn. This definition includes all a cock's neighbouring and non-neighbouring relatives and is loosely equivalent to the size of his extended family. We assume that this measure reflected the recent success of a bird's lineage in establishing itself in the study area.

To check for possible artefacts at the boundary of the study area (edge effects) we scored each young cock's father according to his position in the study area. Position was considered a class variable and took integer values from 1 to 4 (respectively, 25%–49%, 50%–74%, 75%–99% and 100% of territorial boundary shared with cocks of known relatedness).

Statistical analysis

The recruitment success of a young cock, a binary measure, was modelled using logistic regression so that different covariates and their interactions could be analysed simultaneously. Some young cocks were brothers, and some of the covariates (e.g. attributes of fathers) were measured at the brood level. To control for non-independence among brothers, and for effects of relatedness not explicitly included in the models, each brood's father was included in models as a random factor. It was therefore necessary to use generalised linear mixed models (GLMMs). These were implemented using the GLIMMIX macro in SAS (Lit-

Table 2. Measures of the social environment of young cocks used in analyses of the factors affecting recruitment probability (these are continuous variables unless stated otherwise).

Covariate	Description
Father's presence	Whether or not a young cock's father held a territory during the young bird's first autumn (class variable).
Number of related neighbours	The number of immediate territorial neighbours of the cock's father in the previous spring that were related to the father by a coefficient ≥ 0.375.
Chain size	For each father in spring, the length of the chain of contiguous territorial cocks that had a relatedness coefficient ≥ 0.5
Total relatives	The number of adult male relatives of the young cock, of relatedness coefficient ≥ 0.25, present in the study area in the autumn.
Brothers	Number of known male siblings that each young cock had, present on the study area in autumn, determined from microsatellite data. It is possible that having brothers could alter an individual's probability of recruiting through cooperation or competition.
Competitors	The sum of the known number of sons of a cock's father's immediate spring neighbours.
Position	Position of a cock's father within the study area in the previous spring. (class variable).

tell et al. 1996). Models were constructed by a stepwise selection procedure, adding terms one at a time, and dropping the least significant in the subsequent model until only terms significant at the 5% level, using SAS type III tests (SAS 1990), remained. Use of Akaike's Information Criterion (AIC) (Hilborn and Mangel 1997) led to the same final model, showing that this was the most parsimonious description of the data.

Denominator degrees of freedom were calculated, in SAS, using Satterthwaite's formula (Littell et al. 1996). Parameter values for class variables were estimated by fitting the final model with no intercept. For main effects which had significant interaction terms, parameter values for different levels of the main effects were estimated directly as those of the interaction terms when the main effects were dropped from the model. Regression models with normal error structure, in which no random term was necessary, were implemented using PROC GLM in SAS (SAS 1990). Tests of significance are two-tailed except where stated.

Sample sizes for some subsidiary covariates (Table 1) were smaller than those for the full set of birds for which we had genetic and behavioural data. Some males, for example, were caught for the first time when fully grown and so for them we had no measure of chick condition. This must have reduced our power to detect effects of some of the subsidiary covariates. It might also have led to biases in the results involving them, though we have no evidence to support this possibility.

Results

The density of territorial males on the central 52 ha increased from 39 territories km^{-2} in October 1993 to 100 territories km^{-2} in October 1996 (Fig. 2). Young cocks that were recruited were seen to display unchal-

lenged territorial behaviour on average on 9.2 d (range 3–23). Recruits differed significantly from non-recruits in three measures (Table 3): (1) the number of related neighbours, (2) the total number of relatives and (3) the residual comb size.

Number of related neighbours

A young cock's probability of recruitment increased with his father's number of related neighbours, as predicted by the kinship hypothesis (Figs 3 and 4). The magnitude of these effects was large: a change of two standard deviations (minus one to plus one) in the mean number of related neighbours led to a 72% increase in recruitment probability in 1995 and 109% in 1996 (Table 4).

Total number of relatives

Total relatives was an aspatial measure that presumably reflected the recruitment success and survival of the members of the focal cock's lineage in the study area in previous years. The statistical relationship between
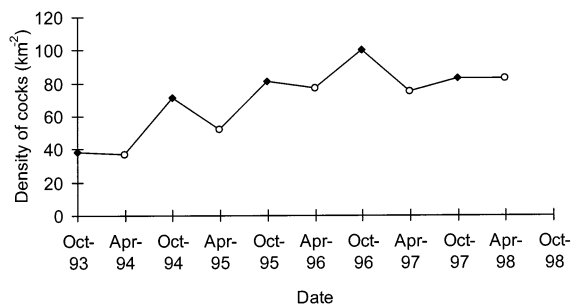

Fig. 2. Density of territorial cocks at Glas Choille. Points are October (post recruitment) and April (breeding) densities.

Table 3. Generalised linear mixed model (GLMM) for probability of recruitment. F values and probabilities for non-significant terms are those obtained when the terms were added alone to the model containing all significant terms. The P values associated with number of related neighbours, chain size and position are for one-tailed tests of their significance. The model included Father and Year × Father as random effects. Estimates (logit scale) of their variance were 0.21 and 0.00, respectively.

Source of variation	df	F	P
Year	1,74	6.41	0.014
Comb size	1,74	6.15	0.015
Total relatives	1,74	4.12	0.05
Number of related neighbours	1,42	3.20	0.04
Year × Total relatives	1,73	7.96	0.006
Non-significant terms			
Year × Comb size	1,74	0.03	0.87
Year × No. of related neighbours	1,53	0.01	0.90
Total relatives × No. of related neighbours	1,72	1.86	0.18
Father's presence	1,37	0.56	0.46
Chain size	1,42	0.00	0.50
Brothers	1,47	0.12	0.73
Competitors	1,54	1.61	0.21
Position	3,39	0.96	0.21
Father's age	1,41	0.77	0.38
Father's territory size	1,61	2.88	0.10
Hatching date	1,27	0.81	0.38
Chick condition	1,23	0.07	0.79
Weight	1,70	0.54	0.46
Tarsus	1,72	2.24	0.14
Condition	1,73	0.97	0.33
Worm burden	1,52	1.33	0.25
Local density	1,42	0.61	0.44

a) 1995

b) 1996

Fig. 4. Number of fathers with different numbers of related neighbours for recruits (open bars) and non-recruits (filled bars) for a) 1995 and b) 1996. Each father is counted only once in each year, but where a father had sons of different recruitment success he is split among recruits and non-recruits in the appropriate fractions. This figure does not control for the effects of other covariates on recruitment.

probability of recruitment and total relatives was complicated by its interaction with year. This shows that it was only significant in 1996, when recruitment success declined as total relatives increased (Table 4, Figs 5 and 6). In 1995, the relationship was positive, although the magnitude of the effect was smaller, and it was not significant. Total relatives was not related to number of related neighbours ($F_{1,28} = 0.54$, $P = 0.47$, GLMM of the relationship between number of related neighbours
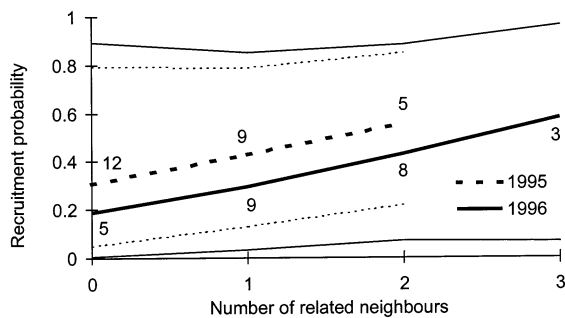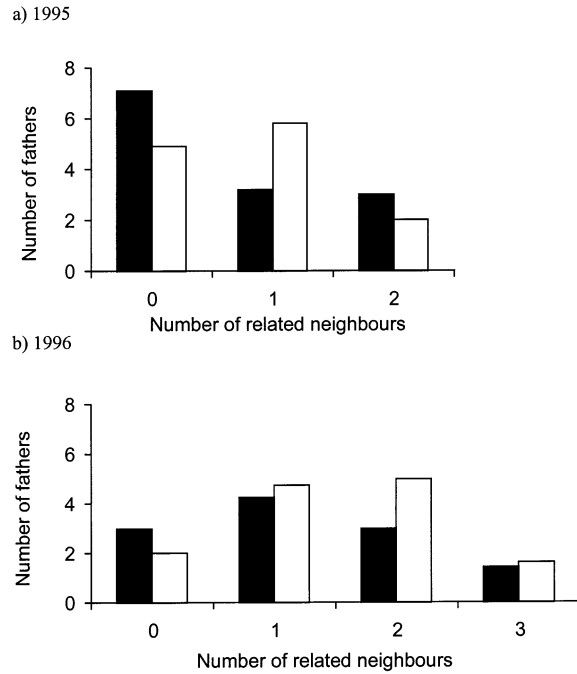

Fig. 3. Probability of recruitment and number of related neighbours. Fitted values (bold) and 95% confidence intervals (faint) are back transformed from the logit scale parameters estimated by a generalised linear mixed model (GLMM). Dashed line = 1995, solid line = 1996. Numbers beside fitted points indicate the number of young cocks for each point.

and total relatives, with year as a covariate and father and year × father as random effects, using a Poisson error distribution and logarithmic link function).

As recruitment was largely philopatric (Watson et al. 1994, MacColl 1998), total relatives might simply reflect local density. However, local density was not useful in explaining variation in recruitment success (Table 3), and total relatives was unrelated to local density ($F_{1,29} = 0.02$, $P = 0.90$, GLMM of the relationship between local density and number of related neighbours, with year as a covariate and father and year × father as random effects, using a normal error distribution and identity link function).

Residual comb size and worm burdens

Residual comb size was the only morphological trait that differed significantly between recruits and non-recruits. Birds with larger combs were more likely to get territories (Fig. 7). A change of two standard deviations (minus one to plus one) in mean residual comb size led to a 152% increase in recruitment probability in 1995 and 74% in 1996.

Recruitment success was unrelated to burdens of the nematode parasite *T. tenuis* (Table 3). Burdens were

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Table 4. Parameter estimates (logit scale) from best fitting GLMM of probability of recruitment. The values of t and P are those associated with the null hypothesis that a parameter equals zero. Test statistics for the two year values (intercepts in the model) are not included because they have no biological meaning, but their parameter estimates are given so that the model is completely specified. Degrees of freedom for the fitting of this model are in Table 3.

Parameter	Estimate	Std error	t	P
Year = 95	−0.800	0.857	–	–
Year = 96	2.527	1.159	–	–
Comb size	0.020	0.008	2.61	0.01
Total relatives, year = 95	0.034	0.049	0.69	0.49
Total relatives, year = 96	−0.192	0.062	−3.08	0.003
No. of related neighbours	0.553	0.317	1.75	0.04

very low in young males in autumn (1995: geometric mean = 27 worms/bird, 95% C.I. 8–91, $n = 42$, 1996: geometric mean = 32 worms/bird, 95% C.I. 6–180, $n = 45$). These values are two orders of magnitude below the level of infection at which pathogenic effects are expected to occur (Hudson et al. 1992).

Discussion

Measures of social environment

The data confirm a key assumption about grouse demography made in the kinship hypothesis: that a young cock's probability of recruitment was related to the number of his elder relatives that had territories next to his father (Mountford et al. 1990, Moss and Watson 1991, Matthiopoulos et al. 1998). This is consistent with the hypothesis that relatives influence the recruitment of their joint offspring. It might be regarded as part of the more general phenomenon of relatives 'helping' their offspring (Macdonald 1983, Stacey and Koenig 1990), though the mechanism is not known (MacColl 1998).

Our observation of the relationship between recruitment and cluster size was based on variation among individuals within years and it remains to be seen whether the relationship applies at the population level among years. If so, it would involve a time delay between relatedness structure and recruitment that could destabilise population dynamics.

The evidence goes against the possibility that some genetic quality affected both the recruitment success of a young cock and his father's number of related neighbours. First, the use of father as a random effect controlled for consequences of relatedness that were not explicit in the models. Second, an influence of genetic quality would presumably entail a positive relationship between recruitment success and the previous success of a young cock's lineage. Total relatives is a measure of such success. It was found to be negatively related to recruitment success in 1996, and not related to it in 1995 when density was lower.

The observed relationship between recruitment success and total relatives invites explanation. Under a constant selection regime, one might expect success in

one generation to spawn success in the next. However, this might not be true with density- or frequency-dependent selection. Lineages have mixed fortunes over time, and may be lost from natural populations at high rates (Gompper et al. 1997). Our data could be explained if the effects of kin favouritism on recruitment success were density dependent. The evidence suggests that previously successful lineages showed a synchronised downturn in their fortunes in 1996. A possible explanation involves a mechanism of the type proposed by Chitty (1957, 1964). Perhaps traits selected for in the increase phase of the population cycle were selected against at high density. Moss et al. (1984) reported selection for heritable subordinate behaviour during the increase phase of a population fluctuation, which reversed at peak density. Perhaps individuals from previously successful lineages were recruited poorly in 1996 because they were subordinate types experiencing high density, as would occur if kin favouritism had less effect on recruitment at high density. Breeding (April) densities at Glas Choille were high (Watson et al. 1994, Moss et al. 1996), and changed little between 1996 and 1998 (Fig. 2). The population declined in 1999, and we expect this to be the start of a cyclic decline.

Studies of bird populations from several species have linked population structure either directly to demogra-
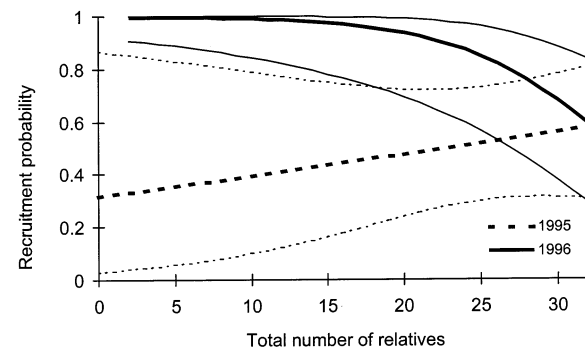

Fig. 5. Probability of recruitment and total number of relatives. Fitted values (bold) and 95% confidence intervals (faint) are back transformed from the logit scale parameters estimated by a GLMM. Dashed line = 1995, solid line = 1996. Sample sizes were 62 young cocks in 1995 and 72 young cocks in 1996.
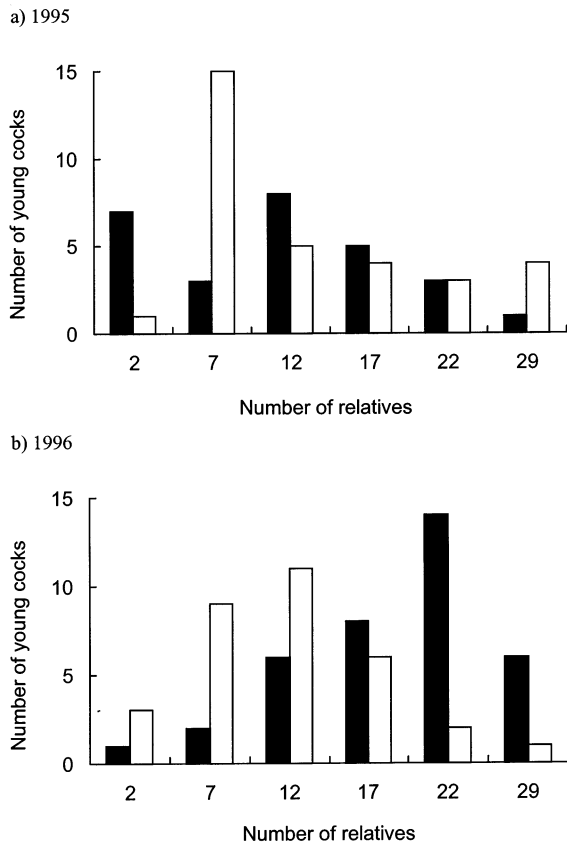
a) 1995

b) 1996

Fig. 6. Number of young cocks with different numbers of total relatives, for recruits (open bars) and non-recruits (filled bars) for a) 1995 and b) 1996. This figure does not control for the effects of other covariates on recruitment.

phy (Beletsky and Orians 1989), or to behaviour that could affect demography (Green 1983, Eason and Hannon 1994, Lessells et al. 1994, Sklepkovych 1997). However, either structure was measured by familiarity of individuals, rather than genetic relatedness or kinship (Green 1983, Beletsky and Orians 1989, Eason and
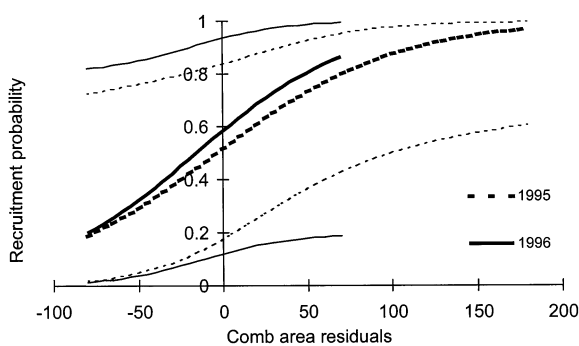

Fig. 7. Probability of recruitment and comb size. Fitted values (bold) and 95% confidence intervals (faint) are back transformed from the logit scale parameters estimated by a GLMM. Dashed line = 1995, solid line = 1996. Sample sizes were 58 young cocks in 1995 and 72 young cocks in 1996.

Hannon 1994), or demographic consequences of structuring were unclear (Lessells et al. 1994, Sklepkovych 1997).

The direct effect of a kinship-based measure of population structure on a demographic process has, to our knowledge, only been studied once before in a bird population (Greenwood et al. 1979). They found that kin-adjacent male great tits (*Parus major*) commenced breeding earlier than males which had non-adjacent relatives in the population. The potential demographic effects of this were not examined, although laying date is known to be an important determinant of local recruitment in great tit populations (Kluijver 1951, Perrins 1965, Perrins and McCleery 1989). Thus there seems to be potential for feedback between kin structure and population change in great tit populations.

Morphology

The probability of recruitment was positively related to the residual comb size of young cocks in both 1995 and 1996. In red grouse, comb size is an effective assay of circulating androgens, particularly testosterone, that in turn affect territorial behaviour (Moss et al. 1979, 1994). Experimental implantation of testosterone leads to territorial expansion through increased territorial behaviour (Watson and Parr 1981, Moss et al. 1994). Comb size is also known to be important in behavioural interactions in rock ptarmigan (*Lagopus mutus*) (Brodsky 1988, Holder and Montgomerie 1993). Therefore it is not surprising to find that recruitment success and comb size were related, although it is likely that a behavioural or hormonal correlate of comb size was more important than residual comb size itself.

Other studies of differences in phenotype between birds with territories ('owners') and those without ('floaters') (e.g. Hannon and Roland 1984, Arcese and Smith 1985, Matthysen 1989, Shutler and Weatherhead 1991, Lozano 1994) have generally been done by removing established owners, and comparing them to individuals that replaced them. These studies have seldom detected differences in morphology between owners and floaters. However, as the removals in these experiments had to be done after territories had been established, the method has two problems: 1) it is usually unknown where the replacement birds came from, and therefore they might be territorial birds from outside the study area. 2) Differences between the two sets of birds could be a consequence, rather than a cause, of territory ownership. In this study we avoided these problems by assessing traits of young birds before they got a territory.

Similar problems apply to previous studies of the relationship between territorial recruitment and body size. Even so, our finding of no simple directional relationship is in accord with most other studies (Han-

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non and Roland 1984, Arcese and Smith 1985, Eckert and Weatherhead 1987, Matthysen 1989, Shutler and Weatherhead 1991, Lozano 1994).

Conclusions

There is increasing experimental evidence that kin structuring in microtines can influence population growth rates and hence act as a destabilising process (Lambin and Krebs 1993, Lambin and Yoccoz 1998, Pusenius et al. 1998). Our evidence for red grouse is consistent with this generalisation but does not prove that kin structure affects the demography or dynamics of populations. This must await further data from the course of a population fluctuation, and experimental tests at the population level.

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