

Territorial status and survival in red grouse *Lagopus lagopus scoticus*: hope for the doomed surplus?

**Kirsty J. Park, Martha M. Hurley and Peter J. Hudson**

Park, K. J., Hurley, M. M. and Hudson, P. J. 2002. Territorial status and survival in red grouse *Lagopus lagopus scoticus*: hope for the doomed surplus? – *J. Avian Biology* 33: 00-00.

A previous study of survival in territorial and non-territorial red grouse *Lagopus lagopus scoticus* conducted between 1957 and 1967 found that territorial status in the autumn pre-determined over-winter survival. A very high proportion of territorial birds survived and virtually all non-territorial birds died or emigrated. We tested the hypothesis that over-winter survival was dependent on territorial status within four grouse populations in Scotland between 1986 and 1993. In contrast to the previous study, 66% of non-territorial birds survived over winter, compared to approximately 70% of territorial birds. There was no significant effect of territorial status on the survival estimates. Moreover, some of the birds considered to be non-territorial during autumn went on to successfully raise a brood. We suggest that on our study sites, territory ownership in autumn did not greatly influence over-winter survival, and territorial behaviour did not determine breeding density as previously supposed. We postulate differences with other studies may reflect variations in scale and predation pressure.

*K. J. Park (correspondence) and P.J. Hudson, Centre for Conservation Science, Department of Biological Sciences, University of Stirling, Stirling, FK9 4LA, UK. Email: k.j.park@stir.ac.uk*

*M. M. Hurley, Department of Ecology and Evolutionary Biology, Princeton University, New Jersey 08544, USA.*

The relative importance of intrinsic mechanisms, such as territorial behaviour, versus extrinsic mechanisms, such as predation, in regulating animal population densities has been a central issue in population ecology (Hannon 1986, Newton 1998). Some have considered that territorial defence, resulting in the spacing of individuals, can only operate through mechanisms such as shortage of food or suitable breeding sites (Lack 1966, review in Davies 1978, Bergerud et al. 1985). In contrast, others have argued that these conditions are not necessary and spacing behaviour can limit population density over a range of densities, and that year to year variations in spacing behaviour can generate population cycles (Chitty 1967, Watson and Moss 1970, Matthiopoulos et al. 2000). Support for this hypothesis comes in the form of removal experiments and the observation that territorial status is a prerequisite for breeding (Newton 1998).

Red grouse *Lagopus lagopus scoticus* are monogamous territorial birds, restricted to heather uplands *Calluna vulgaris* of Britain. In late summer, family groups break up and males establish autumn territories, which are maintained throughout winter except during periods of snow cover or poor weather. Females settle within these territories and pairs usually remain together until after the following breeding season (Jenkins et al. 1963, Watson and Jenkins 1964). In support of the territorial-spacing hypothesis, Watson (1985) recorded that winter losses (mortality/emigration) of territorial birds was just 1.7% whereas of individuals without territories it was 96.6%. Through this mechanism almost all territorial birds in autumn survived to breed in the following spring whereas non-territorial birds died or emigrated, supporting the hypothesis that territorial behaviour limited population density by excluding non-territorial birds. Errington (1945) called these birds the 'doomed surplus' since they made no further contribution to population change and were usually taken by predators.

The work by Watson (1985) was undertaken on two grouse populations in north-east Scotland during two overlapping periods of seven years when predator pressure was relatively low and population densities were relatively high (Hudson 1990, 1992). To determine whether

the patterns observed by Watson (1985) were consistent between populations we used radio-telemetry techniques to monitor large numbers of red grouse. Specifically we tested the hypothesis that territorial status in red grouse pre-determined over-winter survival in four grouse populations in Speyside, Scotland, over eight years from 1986 to 1993.

## **Methods**

### **Radio-tracking grouse**

Male and female red grouse were caught between July and October within four populations at sites in Speyside (South Drumochter, Ralia, Crubenmore and Glen Banchor). Trained pointing dogs were used to locate broods of grouse before brood break-up so these could be caught and radio-tagged. Additional grouse were captured by night lamping (Hudson and Newborn 1995) in late summer and early autumn and fitted with radio-transmitters. Only juvenile grouse weighing more than 300 g were fitted with the 15 g radio-transmitters (BioTrack, Wareham, UK). The radio-transmitters represented  $\leq 5\%$  body mass of juveniles and on average 2.2% and 2.4% of male and female body mass respectively. Previous studies have found no evidence that radio tags have a deleterious effect on the survival of red grouse although the authors noted that the power of the statistical analysis was weak (Thirgood et al. 1995). Radio-tagged birds were usually located at least once a week, using a Telonics TSR-2 receiver (Telonics, Arizona, USA) and a 3-element hand-held Yagi Antenna (Mariner, Lowestoft, UK), over the winter months until they either initiated a breeding attempt in spring, or died.

Territorial status was determined between mid-October and late December, by carefully following the descriptions of territorial behaviour stated by Watson (1985). Territorial activity is most likely to be observed in the morning (Watson 1985), and birds were typically located within the first four hours after sunrise (63%), with 43% of fixes being taken within the first three hours after sunrise. The location of each bird was plotted on a map and a six-figure grid reference recorded. Data were also collected on paired status and other territorial behaviour such

as displays (ground calls, song-flights, territorial aggression, boundary disputes, etc.) and calling when flushed. Males and females regularly paired with a bird of the opposite sex were considered territorial. As any definition of 'regularly paired' will be arbitrary we adopted two definitions of regularly paired and carried out two analyses using these different criteria:

Definition A: male or female paired on  $\geq 25\%$  of observations during the mid-October (week 42) to late-December (week 52) period.

Definition B: male or female paired on  $\geq 50\%$  of observations during the mid-October (week 42) to late-December (week 52) period.

Non-territorial males will not be paired but a male can hold a territory without attracting a mate; for males not considered regularly paired, we therefore examined whether they were regularly recorded on a territory between mid-October and late December. In order to determine this, the birds' positions at each observation was recorded on a map, and additional indicators of territoriality such as calling and territorial aggression were taken into account. Territorial birds would occasionally be absent from their territory. These birds were searched for, and if they subsequently returned to their territory would still be considered territorial. Birds establishing territories elsewhere would also be considered territorial but if they continued to move widely in flocks we (as per Watson 1985) considered them to be non-territorial. Evidence from intensive dawn observations recorded that the autumn territorial competition (rate of territorial behaviour) occurred primarily in September (i.e. before the birds in this study were classed as territorial or non-territorial), and did not vary between sites (Hudson 1992).

As chicks from the same brood may not provide independent data on territoriality and survival, one chick from each brood was selected at random for the purposes of calculating monthly and over-winter survival estimates and for ascertaining the influence of territorial status on over-winter survival. Where broods had dispersed prior to capture, or birds were caught as adults, relatedness was not known and birds were considered independent.

The fate of missing birds was determined by extensive radio-tracking and searching for corpses. As Watson's study was based on resightings of birds marked with back-tabs, it was not always possible for him to determine whether a bird that disappeared was dead or had emigrated, and birds that disappeared were referred to as 'winter losses' (Watson 1985).

### **Estimation of survival rates**

The mark-relocation data were analysed using the software MARK, and applying the Known Fate model (White and Burnham 1999). For each occasion (survey period) the animals' status (alive or dead) was entered. There were a small number of occasions (6% from a total of 672 occasions) where grouse in this study were not located, and therefore their status for this period was unknown. It is possible to enter a code for unknown status in the Known Fate model which is equivalent to right censoring in other survival analyses.

The models created had six encounter occasions each of four weeks duration (relating approximately to October, November, December, January, February and March). The first step in MARK is to create a set of starting models which contain no explanatory variables (such as territorial status). In these models, survival estimates are allowed to vary between months or periods of winter, for example, a model may state that survival in the first three months was the same, but differed from that in the last three months. The model that best describes the data is then used for further analyses incorporating explanatory variables. Link functions were required as survival data, by their nature, are not normally distributed. For models with no explanatory variables, the sine link function is regarded as the most appropriate (White and Burnham 1999).

### **Model selection**

Akaike's Information Criterion, corrected (AICc) is commonly used to select the model that most closely describes the data (Anderson and Burnham 1999), with the smallest AICc representing the 'best' model. The classic approach is then to statistically test between models

using the likelihood ratio test (LRT) (Lebreton et al. 1992). Recently, however, the role of LRTs in model selection has been questioned, and it has been suggested that use of AICc alone may be more relevant and desirable than a combination of the two methods (Cooch and White 1998, Anderson and Burnham 1999). In addition, it is not possible to test models that are not nested (where model I is the equivalent to a reduced model II if one or more of the constraints from model I is removed). In these cases, it is acceptable to use AICc to identify which model most accurately describes the data (Cooch and White 1998). Anderson and Burnham (1999) suggest that models in which  $\Delta\text{AICc}$  (the difference between the AICc of the model and the smallest AICc) differ by less than two are nearly tied. The degree of support for one model over another is defined as  $[(\text{AICc weight of model 1}) / (\text{AICc weight model 2})]$  following White and Burnham (1999).

One assumption of AICc is that there is no overdispersion in the data ( $\hat{c} = 1.0$ ). A variance inflation factor,  $\hat{c}$  (observed deviance/ expected deviance), can be used to adjust for overdispersion. The  $\hat{c}$  calculated during model selection are shown in Table 1. A  $\hat{c}$  deviating from 1.0 necessarily means that the AICc calculated are defined as Quasi AICc (QAICc).

### **Relations between territorial status and survival**

A series of models were constructed in which factors thought to influence survival, such as year, site, sex and territorial status were included. This was done by adding the factors to the starting model, and constraining the survival parameters to be a function of these factors. Models containing one or more (using all possible combinations of the four factors) constraints were compared, and model selection proceeded as before. In particular, a model containing only territorial status A was included in order to maximize power and increase the likelihood of finding an effect of territorial status if one existed. An intercept was included in each model, and a logit link function used, as this is the recommended link function for models that include

constraints (White and Burnham 1999). The models were repeated using definition B of assigning territoriality.

Median distance moved (km) between subsequent radio-tracking occasions (mid-October to late December) was calculated for each female, and used to ascertain whether the criterion “paired status” used to define territoriality was consistent with the expectation that non-territorial birds should range further than territorial birds (Jenkins et al. 1963, Watson 1985). Although birds will not move in a straight line between observations, this figure allows us to distinguish between those birds that ranged widely and those that remained within a small area. Only females were used for this analysis as regularly paired was the only criterion used for assigning territorial status in females. The paired status criterion was tested using a General Linear Model to test for differences between the median distance moved (dependent variable) of territorial and non-territorial birds (factor). Year, site, sex (factors), and number of observations made (covariate) were included in the starting models. Data were log +1 transformed to achieve normality and homoscedasticity and were analysed using MINITAB release 13 (Ryan et al. 1985).

Finally, an additional analysis in MARK was carried out using the median distance moved in place of territorial status. Model selection proceeded as above.

## **Results**

A total of 112 birds (56 females, 56 males) were followed over winter and assigned territorial status. The numbers of territorial and non-territorial birds monitored under the different territoriality criteria were: 79 and 33 (A), and 72 and 40 (B) respectively. Of these, 67 survived to spring, 36 died (21-24 territorial and 12-15 non-territorial) and in nine (6-7 territorial and 2-3 non-territorial), radio-transmitters failed or the birds disappeared before the end of winter. Between 10 and 21 birds (mean = 14) were monitored each year, and the number of birds at each site ranged from six to 59 (mean = 28; Table 1). We were unable to calculate median distance



moved for one bird so this bird was omitted from analyses using distance. Of the 112 birds monitored, 89 were caught and tagged in the same year they were born, 15 were adults, and for eight age was unknown.

### **Starting model**

In this study, the model in which survival in the first three months was the same, but differed from that in the last three months ( $\phi_{\text{winter-half}}$ ) received 1.25 times more support than the next ‘best’ model (in which survival was the same throughout winter: the  $\phi_{\text{winter}}$  model). These two models can, therefore, be regarded as nearly tied. However, LR tests indicated that the  $\phi_{\text{winter-half}}$  model described the data significantly better than  $\phi_{\text{winter}}$  model ( $\chi^2_1 = 5.98$ ,  $p < 0.05$ ). In the  $\phi_{\text{winter-half}}$  model, survival estimates for the first half of winter (mid-October to mid-December) were 0.96 (95% confidence intervals 0.93 – 0.97), a higher estimate of survival than during the second half of winter (mid-December to mid-March) which was 0.90 (0.86 – 0.93). In the  $\phi_{\text{winter}}$  model survival estimates were 0.93 (0.91 – 0.95) over the whole winter.

### **Effect of territorial status**

As a logit link function was used for these analyses, survival became a logit linear function of the variables under consideration. An intercept term was included in all models. MARK was unable to calculate separate survival estimates for territorial and non-territorial birds using the  $\phi_{\text{winter-half}}$  model. This was due to relatively small sample sizes once survival estimates were partitioned between the first and second half of winter. This meant it was not possible to compare directly the  $\phi_{\text{winter-half}}$  model (no constraints) with the same model including constraints. It was, however, possible to calculate survival estimates for territorial and non-territorial birds using the simple winter model ( $\phi_{\text{winter}}$ ) in which survival is constant throughout winter (which had previously been identified as the next ‘best’ model). As a result, three types of models were

compared:  $\phi_{\text{winter-half}}$  model (no constraints),  $\phi_{\text{winter}}$  model (no constraints), and the  $\phi_{\text{winter}}$  model including constraints (Table 2). This was then repeated a further two times, using territorial status B, and distance moved, in place of territorial status A.

The model output for the three models that best described the data, under the different criteria for territorial status, is shown in Table 2. None of the models that included territorial status or distance moved had strong support, indicating that territorial status is not an accurate predictor of survival estimates. Survival estimates for territorial and non-territorial birds after back-transformation are shown in Table 3. LR tests between  $\phi_{\text{winter-half}}$  (no constraints) and  $\phi_{\text{winter}}$  (territorial status/distance included as constraints) were not possible as these models are not nested. LR tests did show, however, that the  $\phi_{\text{winter}}$  model with territorial status/distance as a constraint was not a significantly better fit than the  $\phi_{\text{winter}}$  model (territorial status A:  $\chi^2_1 = 0.48$ ,  $P = 0.49$ ; territorial status B:  $\chi^2_1 = 0.87$ ,  $P = 0.37$ ; distance:  $\chi^2_1 = 0.48$ ,  $P = 0.49$ ).

We tested the paired status criteria used to define territoriality, making the assumption that non-territorial birds range more widely than territorial birds. Using A or B as territoriality criteria, non-territorial females moved significantly further between observations than territorial females (A:  $F_{1,51} = 4.01$ ,  $P = 0.051$ ; B:  $F_{1,51} = 10.87$ ,  $P = 0.002$ ). Values are given here for territorial status B: median distances between observations were 0.21 km (Q1 - Q3: 0.14 – 0.43) for territorial females and 0.37 km (Q1 - Q3: 0.23 – 0.62) for non-territorial females. In both models, site was a significant factor (A:  $F_{3,51} = 3.31$ ,  $P = 0.027$ ; B:  $F_{3,51} = 4.87$ ,  $P = 0.005$ ). Neither model was significantly influenced by differences in the number of observations made for each bird.

There were insufficient data to test for differences in breeding success between birds determined as territorial and non-territorial in the late autumn/winter. However, of the 27 radiotagged birds which could be positively identified as incubating during the following spring, between 10 (definition A) and 11 (definition B) (44 – 41%) were considered non-territorial the

previous autumn. At least some of these nested successfully and hatched chicks, although the fate of the majority is unknown.

## **Discussion**

Few studies have successfully established the survival prospects of territorial and non-territorial individuals, although there has been some indirect evidence that ownership of a territory confers survival advantages (e.g. song sparrows *Melospiza melodia*, Smith and Arcese 1989). The classic study on territorial status and survival is the work on red grouse by Watson (1985). He followed the fate of red grouse from two populations in north-east Scotland and found that virtually all non-territorial birds died over winter or emigrated, whereas almost all territorial birds survived. This provided good evidence that autumn territorial ownership is a prerequisite for breeding and indicated that the number of territorial birds determined the subsequent breeding density. This is part of a larger set of work that has led workers to propose that it is largely intrinsic mechanisms of spacing behaviour, rather than extrinsic mechanisms (such as predation or parasites) that limit population density. Variations in spacing behaviour may lead to population cycles in species such as red grouse (e.g. Watson and Moss 1970, Moss et al. 1994, Moss et al. 1996, Matthiopoulos et al. 2000). Within this system, any mortality that occurs during the winter months removes only the non-territorial surplus birds (the ‘doomed surplus’ (Errington (1945)) called it), leaving the density of breeding birds in spring unaffected. Should a territorial bird die (a rare event), it will be rapidly replaced by any surviving non-territorial individual.

The analyses presented here suggest that monthly survival estimates were similar across the whole winter, although there was some evidence that survival in the second half of winter (mid-December to mid-March) was slightly lower than in the first half of winter (mid-October to mid-December). In contrast to findings by Watson (1985), we found that: (1) over-winter survival estimates for non-territorial birds was 0.66 and (2) territorial status was not an accurate

predictor of over-winter survival. Non-territorial birds ranged further between observations, but the median distance moved (in place of territorial status) was not an accurate predictor of over-winter survival estimates. In addition, we were able to ascertain that some of the birds classed as non-territorial in winter were able to gain a territory by the following spring and went on to breed and raise a brood. As such, territorial status in autumn at these sites, during this period of study, was not a prerequisite for over-winter survival and breeding success. It is possible that some non-territorial birds became territorial as the winter progressed since territorial status was classed between mid-October and late December. If a non-territorial bird became territorial before December it is likely that our methods would have identified this and classed this bird as territorial (our hypothesis, based on Watson's results, would then predict that the survival probability for this bird would increase). If the bird switched status after December we would not have recorded a change in territorial behaviour. However, by the end of December in Watson's (1985) study (p495 table 2), an average of 61% of non-territorial males and 65% of non-territorial females had already died. This is clearly different to the present study where the mortality of non-territorial birds across the whole winter (mid October to mid March) was only 34%.

Why do these findings contrast? One explanation is that while more territorial birds die in the Speyside populations, the spacing mechanisms remain the same: territorial birds that die are simply replaced by non-territorial birds (e.g. Jenkins et al. 1963). Survival estimates for these two groups of birds, however, were very similar. A second explanation is that territorial individuals are now more vulnerable to predation, perhaps as a consequence of different weather conditions and/or increased predation pressure. Grouse defend territories from autumn through to spring but during periods of unsettled winter weather, territorial behaviour ceases or birds may only defend territories for brief periods in the morning and spend the rest of the day in groups (Watson and Jenkins 1964). While not on their territories, these birds may be as vulnerable as the non-territorial individuals to predators and this may account for the lack of any

distinction in the survival estimates between territorial and non-territorial individuals. The cause of death on these sites was determined by a concurrent study and was predominantly predation by either foxes or raptors (Hudson et al. 1997). Predation was also clearly greater than in the studies at Glen Esk (Jenkins et al. 1964). Moreover, the frequency of predator sightings in the Speyside sites was greater than the frequency of sightings in the Glen Esk and Kerloch sites supporting the contention that predation pressure differed between sites and periods (Hudson 1992). In addition, the differences in the methodology adopted in the two studies (resightings of marked birds (Watson 1985) versus locating birds through radiotelemetry (this study)) mean that our study is on a larger scale than that of Watson (1985), and indicates that spacing behaviour may be operating locally but perhaps not at the scale of the population.

Most of the birds in this study were caught and tagged in the same year they were born. The age of birds in Watson's study was not reported, so we are unable to ascertain whether age differences could account for the contrasting findings between the two studies. This is, however, unlikely, as a previous study investigating survival of adult and young birds found no significant differences between their weekly survival rates over winter (Hudson 1992).

These observations imply that with low predation pressure, territorial status determined survival, whereas with higher predation pressure there is no such advantage of territoriality. As such, the results from this study suggest that at least part of the winter mortality could potentially be considered additive and thus will have some influence on the subsequent breeding density of birds. In such areas population density may not be limited solely by the spacing behaviour of the grouse as previously reported. Therefore the role of predation in the population dynamics of red grouse may be more important than was previously supposed, perhaps as a consequence of increased predation pressure.

*Acknowledgements* - Special thanks to the Scottish Trustees for their financial support and Nick Sotherton for his support that allowed us to undertake this research. John and Eira

Drysdale kindly allowed us to work on their estate and the Game Conservancy Trust provided support. John Renton helped with field work. Thanks to Matthew Evans for help with the survival analysis. Steve Redpath and Kate Buchanan made useful comments on previous versions of this manuscript.

## References

- Anderson, D. R. and Burnham, K. P. 1999. Understanding information criteria for selection among capture-recapture or ring recovery models. – *Bird Study* 46 (suppl.): 14-21.
- Bergerud, A. T., Mossop, D. H. and Myrberget, S. 1985. A critique of the mechanics of annual changes in ptarmigan numbers. – *Can. J. Zool.* 63: 2240-2248.
- Chitty, D. 1967. The natural selection of self-regulatory behaviour in animal populations. – *Proc. Ecol. Soc. Aust.* 2: 51-78.
- Cooch, E. and White, G. 1998. Program MARK: a gentle introduction. Available at <http://canuck.dnr.cornell.edu/misc/cmr/mark/docs/book/>.
- Davies, N. B. 1978. Ecological questions about territorial behaviour. – In: Krebs, J. R. and Davies, N. B. (eds.). *Behavioural ecology, an evolutionary approach*. Blackwell Scientific Publications, Oxford, pp. 317-350.
- Errington, P.L. 1945. Some contributions of a fifteen-year local study of the northern Bobwhite to a knowledge of population phenomena. – *Ecol. Monogr.* 15: 1-34.
- Hannon, S. J. 1986. Intrinsic mechanisms and population regulation in grouse – a critique. – *Proc. Int. Ornithol. Congr.* 19: 2478-2489.
- Hudson, P. J. 1990. Territorial status and survival in a low density grouse population: preliminary observations and experiments. – In: Lance, A. N. and Lawton, J. H. (eds). *Red grouse population processes*. British Ecological Society and Royal Society for the Protection of Birds, pp. 20-28.
- Hudson, P. J. 1992. *Grouse in space and time: the population biology of a managed gamebird*. – The Game Conservancy Trust, Fordingbridge.

- Hudson, P. J. and Newborn, D. 1995. A manual of red grouse and moorland management. – The Game Conservancy Trust, Fordingbridge.
- Hudson, P. J., Newborn, D. and Robertson, P. A. 1997. Geographical and seasonal patterns of mortality in red grouse *Lagopus lagopus scoticus* populations. – Wildl. Biol. 3: 79-87.
- Jenkins, D., Watson, A. and Miller, G. R. 1964. Predation and red grouse populations. – J. Appl. Ecol. 1: 183-195.
- Jenkins, D., Watson, A. and Miller, G. R. 1963. Population studies on red grouse, *Lagopus lagopus scoticus* (Lath.) in north-east Scotland. – J. Anim. Ecol. 32: 317-376.
- Lack, D. 1966. Population studies of birds. – Clarendon Press, Oxford.
- Lebreton, J-D., Burnham, K. P. and Anderson, D. R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. – Ecol. Monogr. 62: 67-118.
- Matthiopoulos, J., Moss, R. and Lambin, X. 2000. The kin-facilitation hypothesis for red grouse population cycles: territory sharing between relatives. – Ecol. Model. 127: 53-63.
- Moss, R., Parr, R. and Lambin, X. 1994. Effects of testosterone on breeding density, breeding success and survival of red grouse. – Proc. R. Soc. Lond. B 258: 175-180.
- Moss, R., Watson, A. and Parr, R. 1996. Experimental prevention of a population cycle in red grouse. – Ecology 77: 512-530.
- Newton, I. 1998. Population limitation in birds. – Academic Press, London.
- Ryan, B. F., Joiner, B. I. and Ryan, T. A. 1985. MINITAB Handbook, 2nd edn. PWS-Kent, Boston.
- Smith, J. N. M. and Arcese, P. 1989. How fit are floaters? Consequences of alternative territorial behaviors in a nonmigratory sparrow. – Am. Nat. 133: 830-845.
- Thirgood, S. J., Redpath, S. M., Hudson, P. J., Hurley, M. M. and Aebischer, N. J. 1995. Effects of necklace radio transmitters on survival and breeding success of red grouse *Lagopus lagopus scoticus*. – Wildl. Biol. 1: 121-126.

- Watson, A. 1985. Social class, socially induced loss, recruitment and breeding of red grouse. – *Oecologia* 67: 493-498.
- Watson, A. and Jenkins, D. 1964. Notes on the behaviour of the red grouse. – *Brit. Birds* 57: 137-170.
- Watson, A. and Moss, R. 1970. Dominance, spacing behaviour and aggression in relation to population limitation in vertebrates. – In: Watson, A. (ed.). *Animal populations in relation to their food resources*. Blackwell Scientific Publications, Oxford, pp. 157-220.
- White, G. C. and Burnham, K. P. 1999. Program Mark. Survival estimation from populations of marked animals. – *Bird Study* 46 (suppl.): 120-136.

*(Received 15 January 2001, final revisioin 17 August 2001, accepted 23 August 2001).*



Table 1. Numbers of birds radiotracked per year at each site (site 1 = South Drumochter, 2 = Ralia, 3 = Crubemore, 4 = Glen Banchor).

Year	Site				Totals
	1	2	3	4	
1986	6	3	6	6	21
1987	5	6	0	0	11
1988	8	0	6	0	14
1989	10	2	0	0	12
1990	10	0	0	0	10
1991	8	6	0	0	14
1992	5	10	0	0	15
1993	7	8	0	0	15
Grand total					112

Table 2. Model output used for model selection. Constraints (year, site, sex and territorial status: all possible combinations) were added to the model  $\phi_{\text{winter}}$  and compared to two models with no constraints:  $\phi_{\text{winter}}$  and  $\phi_{\text{winter-half}}$ . This was repeated using territorial status B and median distance moved. Because  $\hat{c}$  was more than 1.0 (for territorial status A models average  $\hat{c} = 2.41$ , territorial status B models  $\hat{c} = 2.42$ , distance moved models  $\hat{c} = 2.44$ ), Quasi-Akaike's Information Criterion (corrected) has been used,  $\Delta$  QAICc is the difference between the QAICc of the model and the smallest QAICc, QAICc weight is the relative contribution of the QAICc of the model to the total QAICc of the set of models. The level of support for the first model (within each set of model runs) in comparison to (1) the second model, and (2) the third model is shown (i.e. the level of support for the  $\phi_{\text{winter-half}}$  model was only 1.24x more than that for the  $\phi_{\text{winter}}$  model, but 3.00x more than the  $\phi_{\text{winter}}$  model with territorial status A included as a constraint). This has been calculated by: [(QAICc weight of model 1) / (QAICc weight model 2)] following White and Burnham (1999).

Model	QAICc	$\Delta$ QAICc	QAICc weight	Support
Territorial status A				
$\phi_{\text{winter-half}}$	110.43	0.00	0.36	1.24x, 3.00x
$\phi_{\text{winter}}$	110.89	0.46	0.29	
$\phi_{\text{winter}} +$ territorial status	112.71	2.28	0.12	
Territorial status B				
$\phi_{\text{winter-half}}$	110.26	0.00	0.36	1.29x, 3.00x
$\phi_{\text{winter}}$	110.71	0.46	0.28	
$\phi_{\text{winter}} +$ territorial status	112.39	2.13	0.12	
Distance moved				
$\phi_{\text{winter-half}}$	109.35	0.00	0.30	1.20x, 2.00x
$\phi_{\text{winter}}$	109.76	0.41	0.25	
$\phi_{\text{winter}} +$ distance	110.74	1.39	0.15	

Table 3. Monthly survival estimates and 95% confidence intervals for territorial and non-territorial birds using the two different territoriality criteria (A and B). These estimates were obtained by adding the constraint territorial status to the  $\phi_{\text{winter}}$  model. Values for over-winter survival are shown in parentheses.

Territorial status	Survival estimate	Lower 95% confidence	Upper 95% confidence
Definition A			
Territorial	0.94 (0.69)	0.89 (0.49)	0.97 (0.82)
Non-territorial	0.93 (0.66)	0.91 (0.56)	0.95 (0.74)
Definition B			
Territorial	0.94 (0.70)	0.89 (0.50)	0.97 (0.83)
Non-territorial	0.93 (0.66)	0.91 (0.56)	0.95 (0.74)