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Arroyo, Beatriz; Leckie, Fiona; Amar, Arjun; Hamilton, Jude; McCluskie, Aly; Redpath, Steve. 2005. *Habitat use and range management on priority areas for hen harriers: 2004 report.* NERC/Centre for Ecology & Hydrology, 45pp. (CEH Project Number: C02018)

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HABITAT USE AND RANGE MANAGEMENT ON PRIORITY AREAS FOR HEN HARRIERS: 2004 REPORT

REPORT TO SCOTTISH NATURAL HERITAGE

Contract number: F02AC307

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March 2005

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BACKGROUND

The hen harrier *Circus cyaneus* is listed on Annex 1 of the EU Birds Directive (EEC/79/409). As a signatory to the Directive the UK government is required to set up a series of Special Protection Areas (SPAs) in those areas that are most important for the species, and to maintain the species in a favourable demographic status. Scotland holds the majority of the UK breeding hen harrier population and a series of Scottish Hen Harrier SPAs has been identified (Annex 0).

Knowledge of the spatial and habitat use of breeding harriers is fundamental to the effective management and protection of the species. Recent work to identify the locations and boundaries for hen harrier SPA has highlighted the need to accurately define the areas most used by harriers, ideally without imposing unnecessary restrictions on other land uses. Yet relatively little is known about harrier ranging behaviour or habitat preferences, hindering development of effective habitat and site management for breeding harriers. In particular, more information is needed on how much space harriers require, and the relative values of different habitats. These questions must be addressed through studies of individual range size and habitat preferences (Madders 2003a).

Through the use of modelling and analyses of harrier habitat selection, conclusions can be drawn about the optimal management of habitat to benefit hen harriers. This project focuses especially on supporting SNH conservation management schemes for hen harrier SPAs (Natural Care, www.snh.org.uk/pdfs/natcare/nc-03.pdf), by providing recommendations for habitat management, appropriate targets for hen harrier numbers and productivity, and assessments of the success of the Natural Care programme on hen harrier SPAs.

The primary objective of this project, therefore, is to improve our understanding of the habitat requirements of hen harriers, in order to inform the implementation of Natural Care and other support mechanisms for moorland management.

Specifically, the project included the following objectives:

1. To investigate the ranging behaviour and habitat use of breeding hen harriers on SPAs where Natural Care Schemes have or will be implemented.

In particular, the objectives for 2004 were to get conclusive answers, through radio-tracking data collected this year, together with those collected in previous years, to the following specific questions: the average size of the home ranges for both sexes, the maximum distances at which harriers hunt from the nest, and whether hunting ranges of neighbouring birds overlap. These issues are important in terms of evaluating the optimal distances at which to implement habitat management, and whether management implemented in a given area is likely to benefit more than one pair simultaneously.

2. To develop a model that predicts range use in breeding hen harriers.

Such a model would allow prediction of the relative frequency of hunting across home ranges according to landscape variables and distance to the nearest harrier nest. Management can then be aimed at increasing the availability of preferred landscape components to harriers, and the model would also give indication of where to implement management in relation to nest distribution. Methods to achieve this objective include observations of hunting harriers,

analysed in conjunction with habitat variables in the observation areas. In 2004, we aimed to complete analyses of the relationship between habitat composition and hunting frequency for two areas with long-term data sets (Orkney and Langholm), and a third area (Glen App and Galloway moors) where data was collected in 2004.

3. To produce a set of criteria on which to assess and monitor the success of Natural Care management prescriptions on moorland SPAs for hen harriers.

This will require the development of population models that are specific to individual SPAs and to wider (e.g. regional) areas since it is unlikely that the hen harrier population of any SPA will be isolated from the wider countryside. No work was carried out in 2004 in relation to this objective.

4. To produce a set of management recommendations for every Scottish SPA for breeding hen harriers to inform effective and cost-efficient management prescriptions.

Effective habitat management for hen harriers on moorland SPAs under the Natural Care Scheme requires knowledge of those habitats that are best for hen harriers. Information about the influence of habitat on harrier nest distribution and breeding success allows managers to identify which habitats to favour within protected areas. It is also important to determine whether management rules can be applied to any given area, or must be designed on a site-by-site basis. Analysing whether the relationships between habitat variables and harrier breeding is site-specific or general across areas would allow the latter question to be answered. In 2004, we aimed to finalize the analyses on the relationship between habitat and harrier distribution in four SPAs/pSPA with long-term data sets on harrier breeding.

We present below the detailed up-to-date results in relation to objectives one, two and four. Additionally, we present an assessment of progress towards project objectives.

A- RANGING BEHAVIOUR

A1- EVALUATION OF THE RADIO-TRACKING ACCURACY

Estimates of home range sizes inevitably involve an amount of error. It is critical that this error be quantified, so that the precision of home range estimates can be determined. Such an evaluation was made in the previous study years (Arroyo et al. 2003, 2004). Conclusions from the previous studies were that in most field conditions, the use of triangulation is no more accurate than the use of twin fixes, that average error for either technique was between 500 and 600 m (which rendered the use of estimated locations invalid for habitat analyses), and that accuracy depended mainly on the angle between the bearings (error was greater when bearings were almost parallel: i.e., when the observers were either facing each other, or pointing in the same direction), but otherwise on variables which are not controllable in the field (maximum bearing error). In analysing data we subsequently eliminated data points based on bearings with angles lower than 45 or higher than 135 degrees. Here we evaluate whether the accuracy of locations determined at Glen App and Galloway Moors in 2004 was similar to that at the other study sites.

METHODS

We used 4 "dummy" tags (i.e., tags glued to the top of a 2 m bamboo canes which were placed in positions unknown to the observers) for the evaluation of error. Telonics TR-4 receivers were used with a 3-element Yagi antenna. Four observers were located at vantage points, from where they tried to locate all the operational dummy tags. GPS were used to identify the locations of observers and tags. Bearings of a given tag were not taken simultaneously (which was not a problem, given that the dummy tags did not change position during the whole test period): observers at a vantage point would locate all possible tags, then move to another vantage point, and locate the same tags from there. Bearings (the estimated direction between the observer and a transmitter) were plotted onto 1:25000 maps, and the point where two bearings crossed was considered as the estimated location of the dummy tag.

Three variables were examined:

- 1. Bearing accuracy, or angle error (defined as the difference between the actual and the estimated direction between the observer and a transmitter).
- The accuracy of estimated locations derived from pairs of bearings. We calculated the distance between the estimated location (the crossing of two bearings) and the actual position of the tag.
- 3. The accuracy of estimated locations derived from triangulation of three bearings. We calculated the distance between the actual position of the tag, and the midpoint of the triangle formed by the intersection of the three bearings.

RESULTS AND DISCUSSION

Average error for the estimated locations (combining estimates from pairs or three bearings) was 651 ± 950 m (n = 30), and this value was higher for estimates arising from twin fixes than for estimates arising from triangulation (749 \pm 1034 m and 160 \pm 45 m respectively), although non significantly so (Oneway ANOVA, $F_{1,28} = 1.58$, P = 0.21). Variables significantly affecting the level of error included maximum bearing error, and the angle between bearings (which had a quadratic relationship with location error, GLM, $F_{1,21} = 24.73$, P = 0.0001 for

bearing error; $F_{1,21} = 13.1$, P = 0.002 for angle between bearings, $F_{1,21} = 8.67$, P = 0.008 for angle²).

When eliminating fixes for which the angle between bearings was lower than 45 or higher than 135, then average error was 206 ± 125 m (n = 19), and there were no significant differences between twin fixes and triangulations (222 ± 140 m vs 160 ± 45 m, $F_{1,17} = 0.91$, $P_{1,17} = 0.91$, $P_{1,17} = 0.91$).

The overall level of error for estimated locations in 2004 was less than half that observed in the two previous years. This was associated with the lower bearing error experienced in Galloway moors: average (absolute) bearing error was 5.5 ± 5 (n = 55) degrees, a figure that was almost half of that observed in Orkney (Arroyo et al. 2004)

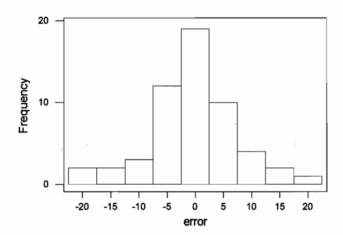


Figure 1. Frequency distribution of bearing errors in Galloway moors.

This may have been related to the different topography of the study areas, with Galloway moors including more rolling landscapes and fewer high peaks and low gullies than either Langholm or Orkney mainland.

Results from 2004 confirm that locations of harriers based on radio-tracking are associated with an error of a few hundred meters, that this error is probably random (i.e., bearing error was not systematically biased to either positive or negative angles), mostly unavoidable, and was minimised by eliminating locations arising from bearings that crossed at angles lower than 45 or higher than 135 degrees.

Real birds are movable and thus potentially fixes on moving targets may be associated with a higher degree of error. However, since fixes on real birds were simultaneous (by coordinating the activity of each observer through a CB), we believe that the error arising from movement was probably much lower than that arising from the other discussed sources.

A2-EVALUATION OF HOME RANGES

We aimed to evaluate the average size of home ranges of breeding harriers, and the maximum hunting distances. In addition, we aimed to test whether home ranges varied between sexes, and whether home ranges overlapped between neighbouring individuals. Finally, we also evaluated whether there was any temporal variation (between the early and the late nestling period) in home range sizes.

METHODS

Breeding harriers were trapped during the nestling period (see Arroyo et al. 2003 and 2004 for details of trapping success in previous years, and Annex 1 for details of trapping success in 2004), and were fitted with 8g tail mounted radio-transmitters, supplied by Biotrack Ltd.

Radio-tags were fitted to four adults in Langholm in 2002 (two females and two males, Arroyo et al. 2003), three adults in Orkney in 2003 (two males and a female, Arroyo et al. 2004), and six adults in Galloway moors in 2004 (two males and four females, this report). One of the males in Langholm and one of the females in Galloway lost their tag a few days after fitting. Data from those birds have not been included in the analyses. Field data from the other birds were used to assess their home ranges. Tracking sessions involved two or three observers in communication through CB radios. When a tag signal was detected, a bearing was taken by as many observers as could do so. Observers maintained radio contact to ensure that the bearings were taken simultaneously. Bearings in 2003 and 2004 were taken every ten to fifteen minutes from the same vantage point for a period of several hours, and repeated every few days. In 2002 the monitoring was less extensive, with one or two bearings per day per bird repeated every few days.

A total of 1146 fixes were obtained (all birds –except the one that lost the tag-combined). We carried out an initial selection of those fixes, eliminating those based on bearings crossing at angles lower than 45 or higher than 135 degrees (see Table 1 for sample sizes). After that selection, the average time between successive fixes on the same bird in Galloway and Orkney was 33 ± 33 min (2-198, Fig. 2). The fact that bearings were sometimes taken at short intervals means that some of the fixes may not have been independent (Kenward 2001). If locations are recorded with short time intervals, individuals will not have had time to travel far, and as a result there may be high spatio-temporal dependence between locations, and more locations will be required to define a home range (Harris et al. 1990). We ran autocorrelation analyses with Ranges VI, and calculated Shoenener's (1981) test of Time to Independence between fixes (Kenward 2001) for each bird. This analysis indicated that locations were independent for all birds but one (a female, 658), for which time to independence was 1100 minutes, a figure much larger than our recording sessions. That particular female did not move much around the nest (Table 1). We therefore included all fixes for this female in further analyses, whils bearing in mind its spatially restricted behaviour.

Home range size was evaluated with Ranges VI, using the selected data points, with a variety of home range estimating methods (Minimum Convex Polygon, Kernel Countours with Fixed Smoothing Multiplier, Kernel Coutours with Least Square Cross Validation Inflection Multiplier, Clusters and Ellipses, all of them with 50, 70 or 90% cores). No consideration was given to the potential effect of the inaccuracy of fixes on the estimation of home range sizes but we assumed that if the error of each location is similar, then the relative differences in

range size among individuals should not be affected. Results for kernel analyses (using the selection of points) were plotted with the Home Range extension of ArcView 3.2.

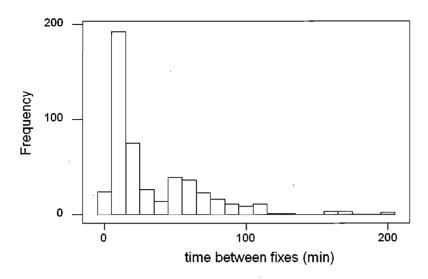


Fig. 2. Frequency distribution of the interval between consecutive fixes for the radio-tracked harriers.

RESULTS

Home range sizes: sexual, geographical and seasonal differences

Average estimations of the 90% of the area male harriers use ranged between 6.5 and 11.8 km², depending on the method of analyses (Table 1). Equivalent figures for females ranged from 2.5 to 3.9 km². For each different estimating method, female home ranges were almost half of those of males. Differences between sexes were most significant for cluster estimates (all P < 0.0004), and least for ellipses (P = 0.08). There was, however, a large variability between individuals, for both sexes (Table 1). In shape, female home ranges were roughly circular around the nest sites (Fig. 4, 6, 7), whereas those of males were not necessarily so, and a preferred foraging direction was apparent in at least three of the monitored males (Figs. 5 and 6).

No marked differences were found in home range sizes between the three study areas (Table 1), although there were insufficient to test this statistically, because of small sample sizes, varying proportions of males and females monitored at each site, and large individual variation in home range size.

In order to evaluate whether home range size varied through the nestling period, we calculated home range sizes (using Kernel methods, which we considered as the most biologically appropriate, see discussion) separately for those fixes obtained in the early nestling period (i.e., the first three weeks after hatching) and thereafter (Table 2). This analysis excluded data points from one female that lost her brood to predators, after nest failure occurred. Results show that average home range sizes increased in the late nestling period, particularly for females, especially when using 90% of the fixes. Estimators for the smaller home range cores differed less. The differences were however not significant even for the larger cores (t-test, t = 0.41, P = 0.6), probably due to large individual differences in the pattern, with some males ranging less far from the nest in the late than the early nestling period (Table 2).

Table 1. Home range size of study harriers according to different calculating methods, areas shown in km^2 . Initial n = sample size (number of fixes) obtained for each bird. Selected n = excludes fixes from bearings crossing at less than 45 or more than 135 degrees

| | | | Minii | num Coi | nvex | | | | | | | | | | | | |
|-----------------|-----------|------------------|-------|----------|-------|-----------|------------|-------|----------|-----------|----------|------|----------|------|------|----------|-------|
| | | Selected | F | oolygons | | Kernel In | flection (| LSCV) | Kernel 1 | Fixed Mul | ltiplier | (| Clusters | |] | Ellipses | |
| ID | Initial n | n | 50 | 70 | 90 | 50 | 70 | 90 | 50 | 70 | 90 | 50 | 70 | 90 | 50 | 70 | 90 |
| Langholm | | | | | | | | | | | | | | | | | |
| Female 225 | 6 | 6 | 0.04 | 0.34 | 0.79 | 0.49 | 0.85 | 1.36 | 0.27 | 0.35 | 0.62 | 0.04 | 0.34 | 0.79 | 1.56 | 2.71 | 5.19 |
| Female 257 | 16 | 13 | 0.62 | 1.31 | 3.07 | 1.71 | 2.52 | 4.63 | 1.01 | 1.7 | 3.35 | 0.36 | 1.19 | 3.07 | 2.21 | 3.83 | 7.34 |
| Male 279 | 14 | 11 | 0.49 | 2.03 | 4.62 | 0.88 | 1.39 | 3.11 | 2.11 | 3.27 | 6.81 | 0.49 | 2.03 | 5.22 | 4.39 | 7.61 | 14.56 |
| Orkney | | | | | | | | | | | | | | | | | |
| Female 115 | 131 | 89 | 1.16 | 2.33 | 5.07 | 1.38 | 2.15 | 4.18 | 2.03 | 3.59 | 5.88 | 0.17 | 1.24 | 4.75 | | | |
| Male 286 | 128 | 80 | 1.14 | 2.31 | 8.00 | 1.68 | 2.41 | 5.23 | 2.33 | 3.66 | 7.40 | 0.29 | 1.71 | 6.52 | | | |
| Male 296 | 109 | 59 | 1.96 | 4 | 5.75 | 2.7 | 3.93 | 6.27 | 2.83 | 4.18 | 6.73 | 0.34 | 2.51 | 4.27 | 3.21 | 5.57 | 10.66 |
| Galloway | | | | | | | | | | | | | | | | | |
| Female 35 | 106 | 61 | 0.77 | 1.89 | 4.42 | 1.02 | 1.71 | 3.11 | 1.39 | 2.23 | 3.93 | 0.18 | 0.76 | 1.54 | 1.78 | 3.08 | 5.89 |
| Female 155 | 98 | 34 | 1.5 | 3.72 | 6.79 | 2.76 | 4.26 | 7.2 | 3.39 | 5.21 | 8.23 | 0.23 | 1.64 | 3.55 | 3.59 | 6.23 | 11.92 |
| Male 233 | 166 | 79 | 2.36 | 5.62 | 25.95 | 4.37 | 6.57 | 12.65 | 9.08 | 15.25 | 27.28 | 1.15 | 2.94 | 9.75 | 9.29 | 16.11 | 30.82 |
| Male 543 | 223 | 116 | 2.95 | 5.32 | 9.55 | 4.49 | 6.59 | 9.49 | 4.87 | 7.43 | 10.93 | 0.73 | 1.65 | 6.86 | 4.21 | 7.3 | 13.97 |
| Female 658 | 131 | 72 | 0.22 | 0.34 | 1.47 | 0.38 | 0.61 | 1.01 | 0.55 | 0.92 | 1.54 | 0.06 | 0.29 | 1.19 | 0.76 | 1.32 | 2.53 |
| Average Males | | Mean Standard | 1.78 | 3.86 | 10.77 | 2.82 | 4.18 | 7.35 | 4.24 | 6.76 | 11.83 | 0.60 | 2.17 | 6.52 | 5.05 | 8.76 | 16.76 |
| | | deviation | 1.05 | 1.73 | 8.63 | 1.53 | 2.25 | 3.74 | 2.86 | 4.96 | 8.92 | 0.31 | 0.50 | 2.65 | 2.41 | 4.18 | 8.01 |
| Average Females | | Mean Standard | 0.72 | 1.66 | 3.60 | 1.29 | 2.02 | 3.58 | 1.44 | 2.33 | 3.93 | 0.17 | 0.91 | 2.48 | 2.08 | 3.61 | 6.91 |
| | | deviation | 0.51 | 1.27 | 2.18 | 0.89 | 1.34 | 2.29 | 1.12 | 1.72 | 2.67 | 0.12 | 0.52 | 1.09 | 0.97 | 1.67 | 3.20 |

Table 2. Home range size of study harriers (calculated with Kernel Inflection methods, with LSCV smoothing parameters), according to the time of the nestling period (early nestling = up to three weeks after hatching; late nestling, thereafter). Areas shown in km^2 .

| | _ | E | arly nest | ling | | La | te nestling | g |
|------------|-----------|------|-----------|-------|----|-----------|-------------|-------|
| ID | n | 50 | 70 | 90 | n | 50 | 70 | 90 |
| Langholm | | | | | | · · · · · | | |
| Female 225 | 4 | 0.41 | 0.55 | 0.92 | 2 | 0.19 | 0.20 | 0.21 |
| Female 257 | 0 | | | | 13 | 1.71 | 2.52 | 4.63 |
| Male 279 | 5 | 1.41 | 2.61 | 4.50 | 6 | 3.47 | 5.79 | 9.22 |
| Orkney | | | | | | | | |
| Female 115 | 0 | (*) | | | 89 | 1.38 | 2.15 | 4.18 |
| Male 286 | 35 | 1.42 | 2.11 | 4.31 | 45 | 1.28 | 1.78 | 2.95 |
| Male 296 | 59 | 2.70 | 3.93 | 6.27 | 0 | | 5. | |
| Stair | | | | | | | | |
| Female 35 | 6 | 0.97 | 1.57 | 2.48 | 54 | 0.83 | 1.48 | 2.57 |
| Female 155 | 9 | 0.08 | 0.11 | 0.29 | 25 | 3.40 | 4.99 | 7.73 |
| Male 233 | 26 | 6.53 | 9.34 | 13.08 | 53 | 3.28 | 4.95 | 9.38 |
| Male 543 | 73 | 2.98 | 4.35 | 6.09 | 43 | 5.86 | 9.06 | 13.49 |
| Female 658 | 0 | (91) | • | | 72 | 0.38 | 0.60 | 1.01 |
| Males | Mean | 3.01 | 4.47 | 6.85 | | 3.47 | 5.39 | 8.76 |
| | Standard | | | | | | | |
| | deviation | 2.10 | 2.87 | 3.59 | | 1.87 | 2.99 | 4.35 |
| Females | Mean | 0.49 | 0.74 | 1.23 | | 1.31 | 1.99 | 3.39 |
| | Standard | | | | | | | |
| | deviation | 0.45 | 0.75 | 1.13 | | 1.17 | 1.71 | 2.74 |

Maximum distances from the nest

Most fixes of females (93%, n = 217) were within 2 km (\pm 500m, based on the error associated with fixes) of the nest, and 70% were within 1 km of the nest (Fig. 3). In contrast, 35% (n = 303) of fixes of males were further than 2 km from the nest. The maximum distance from the nest at which a male was recorded was 8.5 km (Fig. 3). All study males were located at least once at 3 km or further from the nest. The frequency distribution of distances to nest was significantly different between both sexes (Kolmogorov-Smirnov, D = 0.40, P < 0.001)

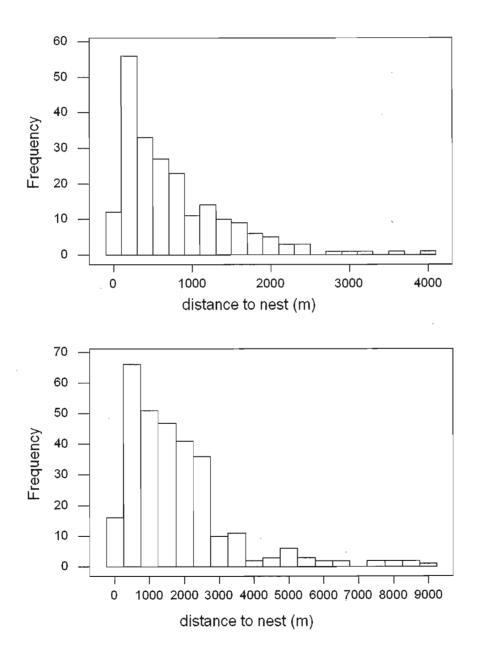


Figure 3. Frequency distribution of the distances to the nest for each fix of the radio-tracked harrier females (above) and males (below).

Relationship between neighbouring birds

Results from Galloway confirmed the findings from previous years (Arroyo et al. 2003, 2004), that home ranges of neighbouring males overlapped extensively (Fig. 4). Home ranges of neighbouring females also overlapped to a certain extent (Fig. 3), although their shape and centering around the nest implied that this overlap was less extensive.

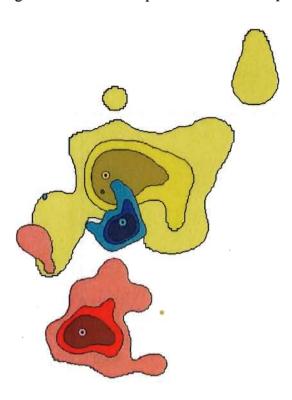


Figure 4. Representation of the home ranges of three females at Galloway. Small circles with the inside dots represent the location of the nests.

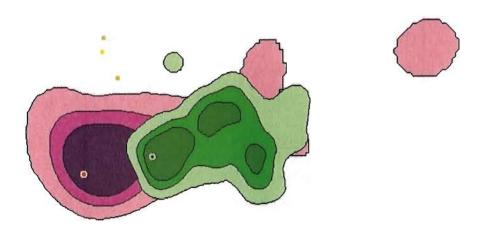
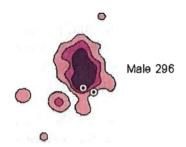


Figure 5. Representation of the home ranges of two males at Galloway. Small circles with the dots inside represent the location of the nests.



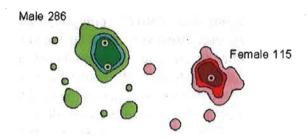


Figure 6. Representation of the home ranges of three tracked birds at Orkney. Small circles with the dots inside represent the location of the nests.

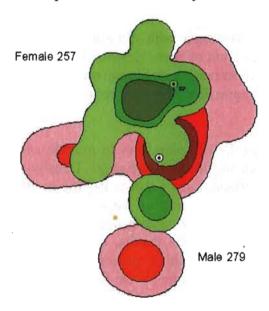


Figure 7. Representation of the home ranges of two tracked birds at Langholm. Small circles with the dots inside represent the location of the nests.

DISCUSSION

Trapping success in 2004 was high (50%, see Annex 1), and similar to that observed in Langholm in 2002 during the nestling period (Arroyo et al. 2003). These results confirm that trapping adult harriers during the nestling period can be efficient, although time consuming (combining data from Orkney in 2003, with low trapping success, and Galloway 2004, with high trapping success, we used ca. 8 observer hours per harrier tagged).

Overall, radio-tracking data provided important information on the sizes of home ranges, the relative overlap between ranges of neighbouring birds, and the maximum distances from the nest visited by each bird.

Estimates of home range sizes varied largely depending on the method used. We evaluated results based on two linkage techniques, and two density techniques.

Linkage techniques are based on forming outlines that encompass locations. The minimum sum of peripheral linkages creates a minimum-area convex polygon that provides comparability between studies due to widespread use. However, outlying locations cause a convex polygon round all the recorded locations to include large unvisited areas. This problem is avoided by excluding from polygons the locations with largest linkage distances, either from a range centre to give mononuclear peeled polygons that estimate single-outline territories, or from nearest-neighbour locations to define high-use areas in multinuclear ranges by cluster analysis (Kenward 1987, Kenward et al. 2001). Cluster analysis is thus particularly good for eliminating outliers and separating range cores, and can identify patchiness in range use, for instance where the study animal forages in several separate areas. Accordingly, the smallest home range values were obtained for clusters (Table 1).

The largest home range estimates were obtained with ellipses (Table 1), which are the simplest density technique for the determination of home ranges. This method does not define range shape well but requires few locations to reach a maximum area estimate and is therefore useful for identifying habitat available to animals that cannot be tracked frequently (Kenward 2001).

More sophisticated density techniques use kernel estimators to provide an indication of the relative frequency of use of different areas within the home range. Density-contouring in this technique confers shape to the estimated home ranges that is lacking in ellipse models, and the use of techniques such as least squares cross validation has potential for providing best-fit results (Seaman & Powell 1996). However, the calculation includes assumptions about the density distribution that can substantially affect the results, and variation in some of the parameters of the estimation, such as the smoothing parameter, may produce different contours (Worton 1995, Kenward 2001, and see Table 1). On the other hand the information they provide may be more biologically meaningful when evaluating frequency of occurrence of a bird in space. Additionally, they may render more reliable estimations of maximum range in certain cases, for example when using small data sets: density contouring can give stable area estimates with only 15-20 fixes (Kenward 2001, and see results in this report), although at least 30 locations are often necessary for smoothing of kernel contour estimates by Least Squares Cross Validation (Seaman et al. 1999). Overall, kernel-based LSCV home-range estimators have been favoured by many authors for analysing home range data with respect to space use patterns (Worton 1989, 1995; Boulanger & White 1990, Boitani & Fuller 2000). This method is the one we chose to adopt although some of our calculations were based in

less than 30 data points, and is the method that we recommend to define the area used by hen harriers in terms of the objectives of the current study.

With any method considered, the home ranges of males were double the size of those of females. Females thus hunted closer to the nests than males. Using Kernel LSCV estimators, average home range of females was 3.6 km², and those of males was 7.3 km². This sexual difference in ranging behaviour is not unexpected. Martin's (1987) study of radio-tracked breeding northern harriers *Circus hudsonius* in southwestern Idaho found that female harriers never ranged further than 2 km from their nest sites, whereas males spent 26% of their time ranging over 2 km from the nest. Longer hunting distances for male than female hen harriers have also been suggested in the UK (Picozzi 1978, Thirgood et al. 2003, Amar 2001) and in Spain (García & Arroyo in press). Additionally, results from this study suggest that female ranges are centred on the nest, whereas males may not use the areas around the nest equally. This may also explain why habitat around the nest affected prey delivery to the nest by females, but not males, at Langholm (Amar et al. 2004).

Geographical variations in home range are expected as a result of differences in habitat and food. However, our results suggest that, at least within the study areas, these differences are not extremely marked. Picozzi (1978) estimated that the foraging range of male harriers in NE Scotland was 14 km², and studies of the closely related northern harrier in the US produced an estimated average male range size of 16 km² (Martin 1987). Both studies used minimum convex polygons to estimate ranges, but those values are larger than the 10 km² found in our study with that method. Differences between studies may reflect that food supply in our study areas and years was higher than in either NE Scotland or the US, or might be due to differences in the sampling protocol or the number of data points.

B. PREDICTING RANGE USE IN BREEDING HEN HARRIERS

Understanding foraging habitat preferences for species of conservation concern such as the hen harrier is important because we may want to manage the habitat within SPAs so that a species has greatest access to its preferred foraging habitats. Alternatively, where harriers may cause economic damage to grouse-shooting interests, we might want to manipulate the environment to discourage a species from hunting in certain areas. Knowledge of the factors which influence where harriers hunt could therefore potentially be useful in designing mitigation measures aimed at reducing this level of predation. Recent research (Amar et al. 2004) has shown that, at Langholm, the habitat around harrier nests can influence the number of grouse chicks brought to nests by females, but not by males.

Further information on harrier foraging behaviour is therefore required in order to manage populations effectively (Madders 2003a). From a conservation perspective, the aim should be to construct a predictive model of ranging behaviour that can be used to evaluate the impacts of different management practices within each area, based on variables that are meaningful to harriers, but also easily gathered (such as remote sensing habitat data, and quantification of the time harriers spend hunting). Such a model of hen harrier ranging behaviour was recently constructed (Madders 2003a), based on data gathered in western Scotland. However, it is possible that habitat preferences vary regionally, and this may affect the accuracy of any predictions.

The most basic way to evaluate habitat selection for foraging is to look at areas with different habitat and quantify whether the frequency at which birds hunt in those areas is dependent on habitat type. A relationship between habitat type and hunting frequency is expected, given that habitat is often a surrogate of prey abundance or availability. For example, a relationship between grouse abundance and heather cover has been found at Langholm (Thirgood et al. 2002), and a relationship between rough-grass and pipit and vole abundance has been found across moorland areas (Redpath & Thirgood 1999; Smith et al. 2001). Similarly, a significant relationship between the abundance of rough-grass and vole and pipit abundance has been found in Orkney (Amar 2001), and a relationship was found in western Scotland between tree cover and field vole abundance, and between upland grass and heather and pipit abundance (Madders 2003b).

However, relatively little empirical data exists on the relationship between habitat and foraging preferences in hen harriers, particularly to identify whether preferences differ between areas or whether there are general patterns which could be reflected in general guidelines for all populations. Additionally, it is important to evaluate whether males and females differ in their foraging patterns, as suggested by previous studies (Thirgood et al. 2003, Amar et al. 2004), and by the fact that males and females may select different prey types. If that was the case, habitat management may be very different depending on the sex targeted for management. However, sexual differences in foraging patterns or preferences may also be confounded by habitat availability when considering that both sexes hunt at different distances from the nest (see above): since hen harriers in Scotland nest in heather moorland (Redpath et al. 1998), the proportion of this habitat within an area is likely to be correlated with its proximity to nest sites. Previous studies on harrier foraging preferences are either based on one single study area (Thirgood et al. 2003, Amar & Redpath 2004), do not separate the relative importance of habitat, prey availability and distance to the nest sites (Thirgood et al. 2003), or do not differentiate between sexes (Madders 2003b). Additionally,

no study has attempted to verify whether habitat selection for foraging changes throughout the breeding period.

Here we examine habitat use by hunting male and female hen harriers at three different sites in Scotland. We watched specific areas for hunting harriers, quantified the habitats in these areas and calculated a nest site proximity index for each of the watch areas. Through this approach we attempted to separate the influence of habitat from the influence of nest site proximity in our analysis, and thereby gain an accurate picture of what factors may influence harrier foraging patterns and whether they differ between the sexes and between breeding areas. Finally, we compared patterns of habitat selection between the incubation and the nestling periods for males only. Females hunt too rarely during the incubation period for a similar analysis to be carried out.

METHODS

Study areas and watch sites

Data on hunting harriers were collected from three SPA study sites: Langholm and the Glen App and Galloway moors (hereafter termed Galloway) in southwest Scotland, and Orkney Mainland in the northern isles of Scotland. Four years of data are available for Langholm and Orkney (in each case including data collected during this study and previous studies), and one year's data for Galloway from the current study. Orkney data were collected between 1998-1999 and 2002-2003, Langholm data between 1994-1996 and in 2002 and Galloway data in 2004. At each site we selected square or roughly squared areas in which to record harrier hunting, measuring between 0.21 km2 - 1.46 km2 (depending on visibility) and located within 5 km of a harrier nest site. The boundaries of some watch areas could be visualised easily on the ground through obvious landscape features such as streams or fences, for others we marked area boundaries on the ground with 4ft high corner flags.

Observations on Orkney were carried out on a total of 26 watch areas, 15 of which were watched in only one year, 10 in two years and 1 area that was watched in three years. At Langholm, observations were carried out on 27 watch areas, 16 of which were watched in only one year, 5 in two years and 6 in three years. The areas watched in Langholm in 1994-1996 were the same as those used in another study (Thirgood et al 2002). At Galloway observations were carried out on 16 areas.

We calculated an average lay date at each study site in each year, using data obtained by regular monitoring and nest visits to all breeding pairs in each year. We defined "incubation period" as the period between the mean lay date (day 0) in each year until the mean hatch date (day 33), and "nestling period" as the period after the mean hatch date (> day 33). Hunting data during the incubation period was available for Langholm in all years, for Orkney in 2003 and for Galloway in 2004; data during the nestling period was collected from all sites in all years, except in 2003 at Orkney.

We also calculated a Nest Site Proximity Index (NPI) for each watch area in each year, as the sum of the reciprocals of the squared distance from the centre of the area to each nest site; this variable has been used to examine foraging of harriers and other species (Madders 2003b, Thirgood et al 2002, Amar & Redpath 2004, Esselstyn et al. 2004). NPI during the nestling period was calculated using only nests with hatched clutches, whereas NPI during the incubation period included all nests that produced clutches.

Quantification of harrier hunting

Watches for hunting harriers occurred between 06.00 hrs and 21.00 hrs. The exact length varied, but most watches lasted between 2 and 3 hours. Each watch area was observed every few days, and these watches were spread out to cover equally all times in the day. We only conducted watches when there was little or no rain. During a watch, quadrats were scanned continuously for hunting harriers using binoculars. When an individual harrier was spotted hunting in a quadrat we recorded the sex of the harrier and the time it spent hunting in the watch area (in seconds). Harriers were classified as hunting if they were flying <10 m above the ground (estimated visually) in the same manner as described by Amar & Redpath (2004) and Madders (2003). As harriers tend to hunt by flying low and quartering across the ground (Schipper et al. 1975), a height of 10 m was chosen to exclude harriers that may not have been actively searching for prey. Behaviour clearly not aimed at capturing or locating prey (eg. perching, territorial behaviours or prey transport) was ignored.

Habitat data

Our original aim was to use Land Cover Map of Great Britain (LCM1990 or LCM2000) data for evaluating the habitat within each watch area, but we needed to consider whether LCM1990 and/or LCM2000 were good habitat descriptors for all sites. In order to estimate the accuracy and relevance of the LCM data in terms of correctly identifying the habitats of interest, we compared the amount of different habitats as identified on the ground with data for the same areas generated from LCM1990 and LCM2000 data (Annex 2). This comparison showed that the fit between estimations of habitat cover by LCM and field data was not very tight, particularly at some study sites. Furthermore, when performing some preliminary comparative analyses for Orkney using both LCM data and habitat data collected in the field, the same models which produced significant relationships between habitat and foraging patterns based on field data failed to find significant effects of habitat on foraging patterns when using LCM data. Because of this, we chose to use only field data for the analyses of hunting behaviour.

Habitat within the watch areas was recorded from habitat surveys. Surveys at Orkney (1998, 1999 and 2004), at Galloway (2004) and Langholm (2002) consisted of 2 or 3 (depending on the size of the area) parallel transects through each watch area. We recorded the dominant vegetation type within 25cm x 25cm quadrats, placed at regular intervals (40 m in Orkney and Galloway; 20 m in Langholm) along these transects. In Orkney and Langholm, we collected 25 or 50 samples from each watch area (depending on the size), and at Galloway moors we had on average 60 samples per watch area. We recorded the dominant vegetation type in each quadrat to species level, except for grasses that were classified categorically as either managed (smooth) or rough unmanaged grass. We defined unmanaged grass by a build-up of dead vegetation forming a mat under the living vegetation, adequate to conceal a moving vole (Amar & Redpath 2004; Hewson 1982). From these data, we calculated the proportion of different habitats (heather, unmanaged grass, managed grass) in each watch area as the proportion of quadrats within each area that had a given vegetation type as dominant. Surveys were slightly different at Langholm in 1994-1996: vegetation was sampled at 50-m intervals along 2 1-km transects placed at right angles through the centre of each watch area, using a 2m X 2-m quadrats, giving a total of 40 vegetation samples per watch area (Thirgood et al. 2002), and only information on the number of quadrats that were dominated by heather (Calluna vulgaris) was available.

At Orkney and Galloway the proportions of the three main vegetation types were correlated with one another, meaning that analyses combining the correlated variables was problematic. Therefore at both sites we constructed a Principal Component Analysis (PCA) with the proportions of the three main vegetation types. The first two axes of these PCA's explained 98% and 96% of the variation in the data for Orkney and Galloway respectively (Table 3). PC1 for Orkney represented a gradient from more heathery areas to areas mainly covered by managed grass and no heather, whereas PC2 represented areas with more rough grass. PC1 for Galloway represented a gradient from more managed areas (covered by managed grass) to more "natural" areas (covered by both heather and rough unmanaged grass), whereas PC2 separated between those "natural" areas that had more grass and less heather, to more heather and less grass (Table 4) At Langholm we only had measures for heather cover, thus no PCA was needed.

Table 3. Results from the Principal Component Analyses of the three main habitat types in two study sites.

| | Orkney | | Gallowa | у | |
|-----------------------|--------|-------|---------|-------|--|
| Vegetation | PC1 | PC2 | PC1 | PC2 | |
| Rough grass | 0.07 | 0.95 | 0.55 | -0.64 | |
| Smooth grass | 0.69 | -0.24 | -0.68 | 0.02 | |
| Heather | -0.71 | -0.13 | 0.47 | 0.77 | |
| Proportional variance | 63 % | 36 % | 67 % | 29 % | |

Statistical analyses

Our original aim was to analyse data using each watch as a separate data unit, controlling for repeated measures for each watch area in a given year by using generalized linear mixed models (GLMM), incorporating watch area, year, and the interaction between watch area and year as random terms in the model. Such an approach would have allowed the use of "date" or "relative date" as a continuous variable, to evaluate temporal patterns in foraging habitat preferences in a more detailed way. However, such an approach led to problems associated with the non-convergence of certain models, and the lack of fit of the response variable to any meaningful distribution (due to the large amount of zeros in the data set).

Therefore, to avoid problems of repeated measures for each watch area in a given year, we calculated a single measure of total observation time and total hunting time for each sex for each watch area in each year and each breeding period (incubation vs nestling). Because some watch areas were watched in several years, and in a given year during both the incubation and the nestling period, we analysed these data using generalized linear mixed models (GLMM), with the watch area as a random term in the model. For areas and periods for which data existed only for one year (ie. Galloway incubation and nestling, and Orkney during the incubation period), and therefore with no repeated data from watch areas, data were analysed using generalised linear models (GLIM). For all analyses, because watch areas varied in both their size and the observation time, we incorporated the log of both these variables as offsets in the model. Therefore, models examined the amount of hunting per hour per km².

Harrier hunting was recorded in seconds. However, due to the highly over-dispersed nature of the data, we finally grouped the amount of observed hunting into minute groups; ie. no hunting recorded = 0 min, 1-60 seconds = 1 min, 61-120 seconds = 2 min, etc. This allowed the data to be analysed using a Poisson error structure and a log link function.

We included NPI in all models as a permanent fixed effect; this was done for two reasons, 1) because previous studies have suggested that the amount of hunting is often dependent on how close an areas is to nest sites, which is likely since the species is a central-place forager during the breeding season and 2) NPI and heather are spatially auto-correlated, as harriers nest in areas with more heather and potentially more rough grass (Redpath et al. 1998; Amar et al. in review). Failing to account for this variable could therefore overemphasise the importance of habitats that are spatially correlated with NPI.

To test for differences in foraging patterns between both sexes, we used only data from the nestling period (when females hunt). We constructed a model for each site, including NPI and habitat variables (PCA Axis or heather measures) as continuous fixed effects, as well as sex and the interaction between sex and the continuous variables. For testing the for seasonal differences in foraging patterns, we used only data from males, including NPI, the habitat variables, period and the interaction between period and the continuous variables in the model. We then removed variables in a stepwise manner (except NPI) until only variables that were significant at the 10% level using type III analysis remained.

All statistical analyses were performed using SAS version 8 (SAS Institute 1999?).

RESULTS

Comparison between male and female foraging patterns during the nestling period

On Orkney, after controlling for sex differences (with observations of hunting females being more frequent than those of males), hunting during the nestling period by both sexes was positively associated with PCA2, representing a preference for areas with larger amounts of rough grass (Table 4). There was also a significant interaction between sex and NPI, with males showing a positive relationship and females showing a negative relationship between the amount of hunting and proximity to nests sites (Table 4). Relationships with NPI were significant when analysing male and female data separately (Males: $F_{1,29}$ =5.07, P=0.03; Females: $F_{1,21}$ =4.62, P=0.04).

At Langholm, after controlling for the significant sex differences (with observations of hunting males being more frequent than those of females), hunting by both sexes was positively associated with NPI, and the lack of significant interaction between sex and NPI implied that this relationship applied equally to both sexes (Table 4). The amount of heather was not a significant explanatory variable in its own right, but this was principally due to the highly significant interaction between sex and heather; this interaction was due to a positive trend between female hunting and heather and a negative relationship between male hunting and heather (Table 4). These relationships (between heather and hunting) were, however, not significant, when male and female data were analysed separately (Males: $F_{1,28}$ =2.73, P=0.66; F=males: $F_{1,14}$ =3.08, P=0.10).

There was insufficient data to examine these relationships at Galloway.

Comparison between incubation and nestling male foraging patterns

At Langholm, hunting by males was recorded more frequently in the incubation period than in the nestling period. After controlling for these differences, no other factors were found to be significant in explaining the variation in the amount of time male harriers were seen hunting in the different areas (Table 5).

At Galloway, hunting by males was again more frequent during the incubation period than the nestling period (Table 5). After controlling for these differences, male hunting was positively associated with PC1, suggesting a positive selection for natural habitat with higher proportions of heather and rough unmanaged grass and avoidance of areas with higher proportions of smooth managed grass habitats.

Significant interactions between period and either NPI or habitat were not found at Langholm or Galloway, which suggests that factors influencing hunting patterns are consistent between the two periods.

On Orkney, during the incubation period neither NPI nor habitat (PC1 nor PC2) were significant explanatory variables for the amount of time males hunted within a given area (Table 5), which appears to be different from results obtained during the nestling period (Table 4). However, lack of data from both periods in the same year meant that we were unable to statistically compare results for the two periods.

Table 4. Hunting by male and female harriers in Orkney and Langholm during the nestling period. Results in bold represent the values of the final model (results not in bold indicate the significant level of the variables before they were removed from the final model)

| Study site | Variable | | Estimate | Df | F | P |
|------------|-------------|--------|----------|------|-------|---------|
| Orkney | Intercept | | -1.1893 | 1,57 | | 0.006 |
| - | NPI | | 0.5386 | 1,59 | 0.16 | 0.69 |
| | Sex | Female | 0.9745 | 1,45 | 4.15 | 0.04 |
| | | Male | 0 | | | |
| | PC1 | | -0.2393 | 1,18 | 1.82 | 0.18 |
| | PC2 | | 0.5487 | 1,19 | 7.15 | 0.01 |
| | Sex*NPI | Female | -1.3416 | 1,45 | 4.75 | 0.03 |
| | | Male | 0 | , | | , |
| • | Sex*PC1 | Female | -0.0607 | 1,46 | 0.04 | 0.84 |
| | | Male | 0 | · | | |
| | Sex*PC2 | Female | -0.0260 | 1,45 | 0.01 | 0.93 |
| | | Male | . 0 | | | |
| Langholm | Intercept | | -1.7824 | 1,27 | | <0.0001 |
| J | NPI | | 0.2476 | 1,14 | 10.70 | 0.005 |
| | Sex | Female | -1.1815 | 1,75 | 1.22 | 0.01 |
| | | Male | 0 | , | | |
| | Heather | | -0.003 | 1,20 | 2.31 | 0.14 |
| | Sex*heather | Female | 0.03292 | 1,75 | 9.98 | 0.002 |
| | | Male | 0 | , | | |
| | Sex*NPI | Female | 0.1192 | 1,75 | 1.22 | 0.27 |
| | | Male | 0 | , | | |

Table 5. Hunting by male harriers in the three study sites during the incubation and nestling period. Results in bold represent the values of the final model (results not in bold indicate the significant level of the variables before they were removed from the final model)

| Study site | Variable | | estimate | Df | F | P |
|-------------------|----------------|------------|----------|------|------|---------|
| Orkney | NPI | | -0.3607 | 1,19 | 2.66 | 0.10 |
| (incubation only) | PC1 | | -0.4048 | 1,18 | 2.86 | 0.10 |
| (mountain emy) | PC2 | | 0.2403 | 1,17 | 0.65 | 0.43 |
| Langholm | Intercept | | -1.6726 | 1,53 | | <0.0001 |
| 8 | NPI . | | 0.1008 | 1,56 | 2.20 | 0.14 |
| | Period | Incubation | 0.5385 | 1,74 | 6.80 | 0.01 |
| | | Nestling | 0 | , | | |
| | Heather | J | 0.0028 | 1,30 | 0.08 | 0.77 |
| | Period*NPI | Incubation | -0.0114 | - | | |
| | | Nestling | 0 | 1,71 | 0.01 | 0.93 |
| | Period*heather | Incubation | -0.0036 | 1.71 | 0.16 | 0.68 |
| | | Nestling | 0 | | | |
| Galloway | Intercept | | -0.7889 | 1,26 | | 0.01 |
| • | NPI . | | 0.0428 | 1,22 | 0.13 | 0.72 |
| | Period | Incubation | 0.6681 | 1,17 | 9.46 | 0.006 |
| | | Nestling | 0 | | | * |
| | PC1 | | 0.4972 | 1,22 | 5.72 | 0.02 |
| | PC2 | | 0.1536 | 1,10 | 0.42 | 0.52 |
| | Period*NPI | Incubation | 0.2836 | 1,12 | 3.12 | 0.10 |
| | | Nestling | 0 | | | |
| | Period*PC1 | Incubation | 0.0657 | 1,11 | 0.05 | 0.82 |
| | | Nestling | 0 | | | |
| | Period*PC2 | Incubation | -0.0817 | 1,11 | 0.13 | 0.72 |
| | | Nestling | 0 | | | |

DISCUSSION

Ground-collected data seemed to be more accurate than LCM to detect differences in use by harriers. However, one of the potential problems of our results lays on whether our ground-collected data is likely to be an adequate descriptor of habitat within the watch areas. Sample units were relatively small, so the number of vegetation points per observation area may have been too small to accurately represent the proportion of each habitat type in each area. Training a satellite image to create a land cover map particularly for our study areas may give a more reliable estimation of the habitat composition in the watch areas (and in the study areas as a whole), and results with those habitat variables may have differed. In the absence of those potentially more accurate habitat estimators, we discuss below the results as they stand with the current data.

If habitat preferences vary regionally, this may affect the accuracy of any predictions from a general predictive model of harrier range use, such as the one developed by Madders (2003a). From our analyses and previous studies, it appears that there is little generality between the study areas in the factors that influence foraging patterns of harriers. Our results showed that harriers tended to hunt close to nests in Langholm, males in Orkney did that too during the nestling period, whereas no relationship was found in Galloway, and females in Orkney hunted preferentially away from the nests. In relation to habitat, harriers of both sexes selected rough grass areas in Orkney, females (but not males) selected areas with heather in

Langholm, and males selected areas with higher proportions of heather and rough unmanaged grass (or avoided smooth grass areas) in Galloway.

The lack of generality in habitat selection can perhaps be explained by differences in the relative abundance (and thus profitability) of various prey types between the study areas. The lack of direct measures of prey abundance between different habitats at the study sites in the years when observations were made may thus be a key issue.

Rough grass was positively selected as a foraging habitat by both sexes during the nestling period in Orkney, which support results obtained previously for spring data (Amar 2001, Amar & Redpath 2004), and also confirm those suggested in a previous analyses for summer data (Amar 2001), although in the latter study results for the effect of rough grass were not quite significant. In Orkney, rough grass is positively associated with vole and pipit abundance, the most important prey items in that area during the nestling period (Amar 2001).

In the current study it was not possible to examine possible associations between rough grass and hunting behaviour at Langholm as data were only available on heather abundance. In this area, a selection for heather was observed, but only by females. A relationship between grouse abundance and heather cover has been found within Langholm (Thirgood et al. 2002), so a preference for heather by females suggest that female harriers in Langholm prey preferentially on grouse when they are available around the nest. This result also coincides with those obtained in another study (Amar et al. 2004), that showed that, in the same study area, the proportion of heather around the nest was associated with the amount of grouse chicks brought to the nest by females, but not by males. Our results also support and complete those of a previous study (Thirgood et al. 2003), which examined habitat use by hunting male and female hen harriers at Langholm over the summer, using a subset of the data analysed in this study. Thirgood et al. found that males tended to hunt closer to nest sites, although that result was not statistically significant. Additionally, and in a similar way to our study, they found that habitat variables did not influence male hunting. In contrast, female hunting was positively associated with NPI, heather cover and grouse abundance. Their analyses, however, could not differentiate the relative importance of those three variables, which were intercorrelated. Our analyses revealed that both heather cover and NPI had some influence on the amount of time an areas was hunted by females: they do not only hunt heather more frequently because it is the most available habitat around the nest, but there seems to be a preference for that habitat even around the nest areas.

In Galloway, there was a selection for "natural" areas (i.e., areas covered by either heather or rough grass), and an avoidance of intensively managed grass, but the analyses failed to detect whether heather or rough grass were preferred. However, the moors at Galloway were, in any case, more mixed (in terms of mixing of heather and rough grass) than either those of Orkney or Langholm, i.e., there were few stands of heather on its own, so the results may simply reflect habitat site characteristics. No data on diet for this area exist, but intensively managed grass holds less prey than either heather or unmanaged grass (Amar & Redpath 2004), so results of this study may also show that harriers in Galloway concentrate on areas with higher prey densities, regardless of the type of prey. Similarly, areas of closed canopy woodland and bracken were avoided in western Scotland, presumably because prey is scarce or difficult to detect and capture (Madders 2000).

In western Scotland, harriers foraged preferentially in young plantation forests (Madders 2000, 2003), which was the habitat associated to higher vole numbers and with higher harrier

hunting success. The moorland vegetation surrounding plantations in this area was generally impoverished due to heavy grazing by sheep, and the young forests therefore had much higher densities of pipits and voles compared to moorland habitats (Madders 2000), but this may not be the case in moors that are less affected by grazing.

Results in our study do not take into account variables potentially important in determining harrier foraging, such as patch size, total perimeter of each habitat type within each area, vegetation structure or height, or the presence of linear habitat and terrain features, such as streams, ditches and tracks. Some of those variables have been found to affect harrier hunting (Martin 1987, Redpath 1992, Madders 1997, Madders 2003b, Amar & Redpath 2004), and may potentially be more important than the actual proportion of different habitats in an area. These variables may affect prey vulnerability, by increasing the probability that harriers approach prey without being detected, thereby increasing the likelihood of successful prey capture. However, the evaluation of the effect of such variables relies on the use of accurate remote sensing data, or else on further data collection in many different study areas. The fact that our analyses suggest that LCM is not accurate enough to be used for analyses of foraging behaviour makes this task complicated.

Overall, it may be concluded based on the current results that it is difficult to predict range use by breeding harriers in a given area, unless there exist previous data on diet, relationships between prey and habitat, and potentially vegetation structure. Even in that case, it is probably safer to assume that quantitative data on hunting should be collected in each separate area in order to identify the best foraging habitats in each breeding site.

The lack of generality in the influence of the proximity of a watch area to nest sites found in our analyses is puzzling. A positive relationship between NPI and harrier foraging has been found in most of the previous studies (Madders 2003b, Thirgood et al. 2003, Amar & Redpath 2004), although not for males in Orkney during the late nestling period (Amar 2001). The negative relationship between NPI and female hunting in Orkney during the nestling period found in our analyses contradicts results for the same area based on a subset of the data set (Amar 2001), but may be explained by the fact that, in that area, failure rate is extremely high (Amar et al. 2003), so there is a possibility that observations of females in that area at that time corresponded mainly to non-breeders, which would preferentially hunt away from occupied and active nest areas, given the strong territorial behaviour around the nest of breeding females at that time of the year (García & Arroyo 2002). The lack of relationship between NPI and male hunting observed in Galloway is more difficult to explain, but corresponds to the data obtained through radio-tracking in the same year (see above). In general, observational and radio-tracking results suggest that proximity to nests is more important in explaining female foraging patterns than male foraging patterns, but patterns varied across study areas. This also means that predictions of range use based on general models may be flawed, unless there exist data on hunting ranges for each site of interest.

C- HABITAT AND HARRIER NEST DISTRIBUTION

Effective habitat management for hen harriers on moorland Special Protection Areas (SPAs) under Natural Care Schemes requires knowledge of preferred nesting habitats. Identifying habitats selected by breeding harriers and evaluating how habitat can explain harrier nest distribution and breeding success is critical in terms of management. To increas our understanding of the habitat requirements of harriers the present project aimed to evaluate any relationships between habitat and harrier distribution using data from harrier SPAs with long-term data sets for nesting hen harriers. There is often considerable variation in harrier density between areas, as well as in the distribution of harrier nests within each area. We aimed to investigate whether any of this variation can be explained through variations in habitat availability. Given that nest areas are not necessarily used every year (among other things, because breeding density can also vary between years), it is also important to evaluate whether habitat can also explain the likelihood of a given area being used more regularly. This exercise should increase our understanding of the potential gains in harrier breeding density and/or success that may be possible through habitat management and, therefore, the Natural Care programme.

Additionally, understanding how habitat variables influences harrier distribution may have strong impacts on management in non-protected areas: where there are perceived conflicts between harrier conservation and the maintenance of grouse shooting, habitat management could be implemented to minimise the impact of harrier predation on grouse, by manipulating habitat in order to either reduce harrier density to a non-impacting level, or else to segregate as much as possible the spatial distribution of grouse and harriers.

The aim of this study was therefore to evaluate aspects of habitat that explain harrier breeding in Scottish SPAs/protected areas, and to test whether habitat-related relationships apply across all sites or whether they are site specific. These relationships may be used to identify which habitat characteristics should be the focus of management recommendations and, ideally, to quantify the extent to which that management should be implemented, and whether those management guidelines may be general across all sites or whether they need to be site-specific.

We present here final results on this aspect of the work, involving data from six different study areas. This part of the report is based on an MSc Project carried out by Jude Hamilton (University of St. Andrews), and completed with further analyses.

METHODS

Harrier distribution data

Long-term data sets of harrier nest locations were obtained for six areas located throughout Scotland (Figure 7). Data were collated by the Royal Society for the Protection of Birds (RSPB), Scottish Raptor Study Groups, and Scottish Natural Heritage (SNH). Five of these sites (Arran, Clunie, Glen App, Langholm and Orkney) have been classified as Special Protection Area (SPAs) as they support some of the species' largest and densest breeding populations in Scotland. A sixth site, Ladder Hills, is currently listed as a potential SPA. Collectively, these sites provide a good sample of the most suitable habitat for hen harriers in Scotland, supporting about of 27% of the UK population.

The time period over which nest data was collected varied from 7 to 11 years between sites: Arran (1994-2001), 7 years; Langholm (1993-2000), 8 years; Glen App (1994-2003), 9 years; Orkney (1989-1997), 9 years; Clunie (1988-1997), 11 years and Ladder Hills (1991-2002), 11 years. Each nest site location was recorded using a six-figure grid reference using 1:50,000 Ordnance Survey maps. Some site locations were recorded using GPS, but others were not.

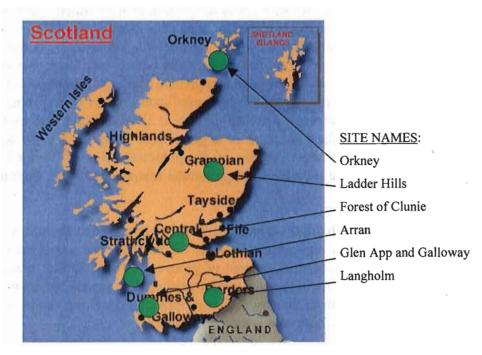


Figure 7. Map of Scotland with green circles indicating location of study sites. Site names given in order from north to south and west to east.

Habitat variables

All habitat data were derived from the Land Cover Map of Great Britain 1990 (LCM1990) (Fuller et al. 1994a) and incorporated into ArcView GIS 3.2 (ESRI, Redlands, CA). Analyses were conducted using ArcView Spatial Analyst 2.0a. We superimposed a grid with cells measuring 1km2 onto each of the study sites. This grid size was chosen as an appropriate scale at which to assess the long-term suitability of breeding habitat at the landscape level, as nest locations moved on average 521m (\pm SD = 271m), between consecutive years (Hamilton 2004). Overall, it was considered that $1km^2$ grid cells were biologically meaningful for hen harriers, and provided enough variability within each site to allow for statistical analyses.

For the purposes of this study, we were mainly interested in broad habitat categories such as heather, woodland, rough (unmanaged) grass, or smooth (improved) grassland. Within LCM1990, four separate cover types denoted 'heather' habitat. These were open shrub moor and heath (categories 10 and 25) and dense shrub moor and heath (categories 11 and 13). Three vegetation types represented 'rough grass' habitat; these were grass heath, marsh grass and moorland grass (categories 5, 8 and 9, respectively). Both 'smooth grass' habitat and 'forest' habitat were represented by two cover type categories. These were improved pasture and managed grassland (categories 6 and 7) and deciduous and coniferous woodland (categories 15 and 16) (see Annex 3). To ensure the relevance and accuracy of the LCM data for use in this current context (in terms of correctly identifying the habitats of interest), ground-truthing field surveys were conducted in three of the study sites (Annex 2). The fit

between field and satellite data was not tight, particularly for some study areas (see also the discussion in the previous section); however, it was better for LCM1990 than for LCM2000, and we used LCM1990 as an estimator of habitat variability among grid cells, despite the associated error.

As habitat descriptors for this study, we calculated the total percentage cover of each of the main habitat types in each cell as the surface covered by each habitat type (calculated as the sum of values for the LCM cover types as specified above, divided by total cell surface after excluding areas covered by unclassified habitat). Habitat variables described in this way are not necessarily independent, as the proportion of area covered by one habitat type is constrained by the proportion of area covered by different habitat types. There is, therefore, the possibility of habitat variables showing collinearity, so their inclusion in the same model may lead to spurious results. To avoid potential problems arising from this fact, and in order to avoid over-parameterisation, an a priori decision was made to incorporate only habitat predictors directly related to the biology of the species (Jegnathan et al. 2004), thus facilitating the production of more ecologically meaningful models. Heather and rough grass are two habitat types previously identified as being most important for harrier breeding and foraging, respectively (Redpath & Thirgood, 1997; Redpath et al. 1998; Madders, 2000; Amar & Redpath 2004). The overall correlation between these two habitat types was low $(R^2 =$ 17%). Those cells that contained zero heather coverage were eliminated from the analyses, as harrier nests are located in heather in almost all cases (Redpath et al. 1998).

In addition, to explore the effect of the spatial configuration of available habitat on the distribution of harriers, three variables indicative of the degree of fragmentation of heather and rough grass habitats were selected. These were the number of patches of each habitat type, average patch size, and total perimeter of each habitat type within each grid cell. These three variables are correlated to each other, and also to the amount of habitat cover (Table 6). To test the relative effects of habitat cover, habitat fragmentation and their interaction effect, principal component analyses (PCAs) were carried out for both heather and rough grass using the procedure PRINCOMP in SAS version 8.0. The first principal components were associated primarily with an increase in patch number and perimeter, and a decrease in mean patch size (Table 7a). PCA1 thus represented a fragmentation index, with higher values indicating a higher degree of fragmentation in both habitat types. Both indices were significantly correlated with each other $(r = 0.635, R^2 = 40\%)$, with more rough grass fragmentation in those areas with higher heather fragmentation, and viceversa. Therefore, we calculated another PCA with all six habitat variables (Table 7b), and used the first principal component of that relationship as a measure of overall fragmentation.

Table 6. Pearson product-moment correlation coefficients indicating the correlation between indices of heather and rough grass fragmentation. All relationships are highly significant

| | No. patches | Total perimeter | Cover |
|---------------------|-------------|-----------------|--------|
| Heather indices | • | | |
| Mean patch size | -0.509 | -0.219 | 0.738 |
| No. patches | | 0.441 | -0.536 |
| Total perimeter | | | 0.229 |
| Rough grass Indices | | | |
| Mean patch size | -0.167 | 0.204 | 0.558 |
| No. patches | | 0.647 | 0.207 |
| Total perimeter | | | 0.816 |

Table 7. Principal component loadings for the three indices of fragmentation for heather and rough grass (above) or for the six indices of fragmentation combined (below)

| | Heather | r | Rough gra | ass |
|-----------------------|---------|-------|-----------|-------|
| Indices | PC1 | PC2 | PC1 | PC2 |
| Number of patches | 0.64 | -0.05 | 0.70 | -0.27 |
| Mean patch size | -0.51 | 0.63 | 0.04 | 0.94 |
| Total perimeter | 0.52 | 0.77 | 0.71 | 0.20 |
| Proportional variance | 60% | 85% | 56% | 91% |

| Indices | PC1 | PC2 | |
|-------------------------------|---------------|-------|--|
| Number of patches heather | 0.45 | -0.26 | |
| Number of patches rough grass | 0.46 | 0.09 | |
| Patch size heather | -0.4 1 | -0.26 | |
| Patch size rough grass | 0.02 | 0.83 | |
| Perimeter heather | 0.50 | 0.17 | |
| Perimeter rough grass | 0.39 | -0.35 | |
| Proportional variance | 47% | 67% | |

Other variables: breeding and altitude

Each nest location was assigned to a grid cell using its six-figure grid reference. Any nest that fell directly on the boundary between two cells was randomly assigned to one of the adjoining cells. We calculated two variables to describe harrier breeding within each grid cell. First, presence and absence of harriers was determined for each grid cell where 'presence' was defined as any cell that had been occupied by a harrier nest in at least one of the years of study. Secondly, we determined how many years that particular cell had been occupied. Given that the length of study period differed between sites, for analyses we used the proportion of years that a given grid cell had been occupied, which was comparable between sites.

A measure of maximum harrier nest density was calculated for each study site by dividing the maximum number of nests found in any one year, by the total number of grid cells with at least some heather.

Altitude data was provided by the RSPB. For each grid cell, we calculated minimum and maximum altitude, standard deviation of altitude, maximum and minimum slope, and standard deviation of slope.

Statistical Analyses

Neighbouring grid cells may violate the assumption of independence between observations as they are more likely to contain similar habitat types and experience similar environmental conditions than those located greater distances from each other. Furthermore, the probability of occurrence of harriers in one cell might not be independent of whether harriers occur in an adjacent cell, which could also generate spatial autocorrelation of data. To investigate if spatial autocorrelation was present in our data, we computed a semivariogram of the deviance residuals from the model explaining harrier distribution (see below and results). A semivariogram plots the difference in residuals of two grid cells in relation to the pairwise

distance between the grid cells. If spatial autocorrelation exists, one should expect the residual differences to be lower in those cells that are closer to each other. This was performed with the procedure Variogram in SAS version 8.0. Given that the comparison between grid cells in different study areas is likely to be meaningless, we excluded pairs of points beyond the maximum distance found between grid cells within each study area. For that, we used the options Lagdistance and Maxlags in the variogram procedure, fixing Lagdistance at 1000m to classify all pairs of points into intervals of 1000m according to their pairwise distances, and limiting the number of lags (intervals) to 14. The semivariograms showed that some spatial auto-correlation existed for at least four of the study sites, although the effect seemed to be relatively small (Hamilton 2004). However, and in order to control for potential effects of this factor, we incorporated spatial relationships in the model, by including a repeated-measures statement in the model, based on the coordinates of each grid cell, using the GLIMMIX procedure in SAS version 8.0 (SAS Institute, 1999).

To evaluate whether habitat availability had an influence on harrier presence in a grid cell, the habitat variables extracted from the GIS were used as explanatory variables in the GLIMMIX model. Presence or absence of a harrier nest was modelled as a binary response variable with a binomial error structure and a logit link function. For those grid cells that had been used by breeding harriers at least once, analyses were performed to evaluate whether habitat availability influenced how regularly an area was used for breeding. For that, we tested the influence of habitat on the proportion of study years in which a given cell had been used. Models were again fitted with a binomial error structure and a logit link function with the response being number of years used/length of study period.

The initial model included site, heather, rough grass and site*habitat interactions, because we were interested to test whether the relationships with habitat were site-dependent or general across sites. Secondly, and in order to explain site differences, we included further variables in the general model, such as altitude or density, as well as the habitat heterogeneity index. Differences in deviance were used to compare the predictive performance of models. Type III analyses were used, except when otherwise stated.

RESULTS

Influence of habitat availability on harrier occupancy

For all study sites combined, the percentage of available rough grass, when considered alone, did not explain the likelihood of a cell being occupied by harriers. In comparison, occupied cells contained significantly more heather and significantly less smooth grass and forest cover than unoccupied cells (Table 8). After controlling for the availability of heather (the critical habitat for breeding, Redpath et al. 1998), however, rough grass was found to account for the greatest amount of variation in the data (as compared to models adding smooth grass, or forest cover). This confirmed the a priori decision to focus model development of harrier distribution in relation to those habitats considered of greatest importance to harriers in terms of breeding and foraging.

Table 8. Results of four univariate analyses testing for the effects of percentage of available habitat type present in a grid cell, on the probability of that cell being occupied by harriers (all study sites combined). Sign indicates the sign of the parameter estimate for significant variables.

| Response variable | d.f. | F | P | sign | |
|-------------------|------|---------------|----------|------|--|
| Rough grass | 1 | 0.63 | 0.42 | | |
| Smooth grass | 1 | 66.95 | < 0.0001 | - | |
| Heather | 1 | 11 8.6 | < 0.0001 | + | |
| Forest | 1 | 25.07 | < 0.0001 | - | |

After controlling for the amount of heather, a positive trend was found to exist between rough grass and harrier presence (Table 9). This indicated that for a given amount of heather in a grid cell, the probability of that cell being occupied increased as the amount of rough grass covering the remaining surface of the cell increased. However, the relative importance of this vegetation type to breeding harriers was found to vary significantly between sites (Table 9). Additionally, and although increased availability of heather had a positive influence on harrier presence at all sites investigated, highly significant differences in this relationship were found to exist between sites (Table 9).

Table 9. Results of the type III analyses testing for effects of availability of habitat types on the probability of that cell being occupied by harriers. Sign indicates the sign of the parameter estimate for continuous variables.

| Response variable | d.f. | F | P | sign |
|-------------------|------|-------|----------|------|
| Site | 5 | 4.76 | 0.0003 | • |
| Heather | 1 | 34.24 | < 0.0001 | + |
| Rough grass | 1 | 3.84 | 0.050 | + |
| Site*heather | 5 | 8.82 | < 0.0001 | • . |
| Site*rough grass | 5 | 4.48 | 0.0005 | |

As heather availability had a positive influence on harrier presence in all sites and a positive trend was found to exist between harrier presence and rough grass availability, we examined the possibility of there being an optimal ratio of rough grass to heather, as an increase in one would be expected to have a limiting effect on the other. If that were the case, one would expect to find that the relationship between heather and harrier occupancy would be better explained by a quadratic, rather than a linear relationship. To examine this, a quadratic term for heather was included in the model, and it significantly improved model fit (change in deviance = 16.22, df = 1, P < 0.01). The significance levels of the other variables (except rough grass alone) did not change (Table 10).

Table 10. Results of the type III analyses testing f for effects of availability of habitat types on the probability of that cell being occupied by harriers.

| Response variable | d.f. | F | p-value | sign |
|-------------------|------|-------|----------|------|
| Site | 5 | 5.25 | < 0.0001 | • |
| Heather | 1 | 45.80 | < 0.0001 | + |
| Heather*heather | 1 | 18.11 | < 0.0001 | • |
| Rough grass | 1 | 2.25 | 0.13 | |
| Site*heather | 5 | 6.84 | < 0.0001 | |
| Site*rough grass | 5 | 5.58 | < 0.0001 | |

The quadratic effect of heather on occupancy was particularly marked in Arran and Glen App (Fig. 8). In Arran, areas with 70-80% heather coverage were predicted to have the highest likelihood of being occupied by breeding harriers. In Glen App, areas with 80-90% heather coverage were predicted to have the greatest chance of being occupied by harriers. For the remaining sites, harriers were predicted to preferentially select those cells that had complete heather coverage (Fig. 8). Overall, the greatest effects of heather availability on harrier presence were thus predicted to occur in those sites where heather was most scarce (Table 11).

When the amount of rough grass and heather available at a site were considered simultaneously, then the relative importance of rough grass at some sites was highly noticeable (Figure 8). In Glen App, Langholm and Orkney, harriers were predicted to occur with equal if not greater probability in cells that contained upwards of 40% heather coverage and the remainder rough grass, compared with cells that were completely covered by heather only. In Ladder Hills, rough grass was predicted to have a positive influence on harrier presence only in those cells that contained in excess of 70% heather. Rough grass had a negligible effect on harrier presence in Clunie (the slope for the relationship of rough grass was not significantly different from 0) and Arran was the only site in which rough grass had a negative influence on harrier occupancy.

Table 11. Overall proportions of habitat types present within usable cells in each study site presented in order of ascending heather coverage. Other habitat types include all other categories combined including smooth grass, bracken, etc. Also shown are maximum harrier density values for each site and heather dominance values (proportion of grid cells that contained in excess of 50% heather coverage).

| Site | Heather | Rough grass | Other habitat types | Ratio of rough grass:heather | Maximum Density/km ² | Heather Dominance |
|-------------|---------|----------------|---------------------|------------------------------|------------------------------------|----------------------|
| Glen App | 0.17 | 0.32 | 0.51 | 1.88 | 0.11 | 0.03 |
| Langholm | 0.20 | 0.52 | 0.28 | 2.60 | 0.17 | 0.16 |
| Orkney | 0.38 | 0.10 | 0.52 | 0.26 | 0.24 | 0.35 |
| Clunie | 0.52 | 0.15 | 0.34 | 0.29 | 0.04 | 0.52 |
| Arran | 0.54 | 0.10 | 0.36 | 0.18 | 0.07 | 0.62 |
| Ladderhills | 0.81 | 0.05 | 0.14 | 0.06 | 0.08 | 0.84 |

Finally, there were significant differences among sites in the likelihood of occupancy, even when taking into account the site-related differences in the influence of habitat. Therefore the probability of an area being occupied by harriers varied to some extent between sites due to factors unaccounted-for by differences in habitat availability. In an attempt to understand the factors that may have contributed to these site differences, two additional variables were included in the model; these were maximum nest density observed at each site, and also a measure of the overall prevalence of heather at each site which will be referred to as 'heather dominance' (calculated as the proportion of grid cells for which heather cover was higher than 50%). As both these variables were strongly confounded with site, use of type III analysis was deemed unsuitable. Results of a type I analysis showed that if included in the model preceding site and habitat types, maximum nest density and heather dominance did account for some of the variance formerly explained by site. Maximum density explained more of the variation in the data than heather dominance (Table 12). No further reduction in deviance was observed with this model when compared with the model shown in Table 10. Site remained a significant predictor even after inclusion of these additional variables.

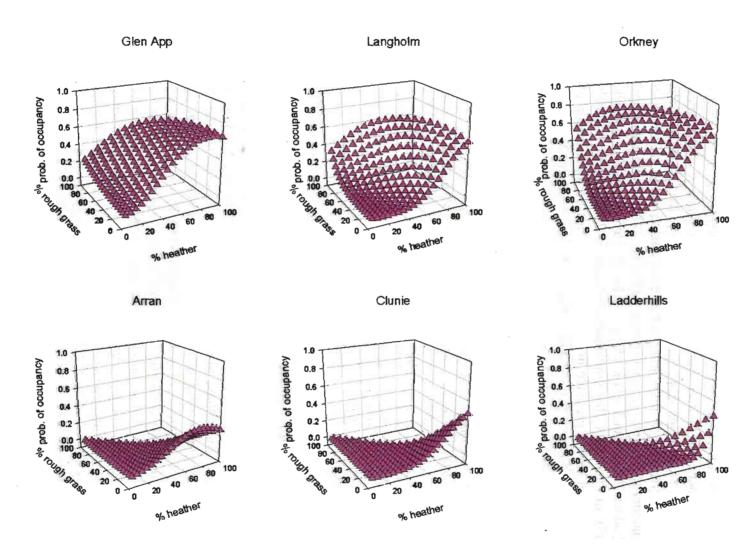


Figure 8. Predicted probabilities of harrier occurrence when the effects of both heather and rough grass habitat were considered simultaneously. Rough grass has a negative effect on the probability of occupancy by harriers in Arran, a negligible effect in Clunie and a positive effect elsewhere.

Table 12. Results of type I analysis showing the relative effects of variables (in order of inclusion) on the probability of that cell being occupied by harriers. Maximum density was calculated as the maximum number of harrier nests in a site in any one of the study years, divided by the total number of grid cells at that site. Heather dominance values as the proportion of grid cells that contained in excess of 50% heather coverage.

| Variable | d.f. | F | P | Sign |
|-------------------|------|-------|----------|------|
| Maximum density | 1 | 21.80 | < 0.0001 | - |
| Heather dominance | 1 | 4.06 | 0.044 | + |
| Site | 5 | 9.14 | < 0.0001 | |
| Heather | 1 | 118.7 | < 0.0001 | + |
| Heather*heather | 1 | 6.59 | 0.010 | - |
| Rough grass | 1 | 5.94 | 0.015 | + |
| Site*heather | 5 | 6.37 | < 0.0001 | |
| Site*rough grass | 5 | 5.58 | < 0.0001 | |

Another potential explanation for differences between sites lies in differences in altitude, since that is a variable potentially affecting harrier distribution. In order to test that, we included altitude variables for each grid cell to the model in Table 10. Altitude significantly explained probability of occurrence of breeding harriers (F = 17.84, P < 0.0001), with the probability of occurrence decreasing at grid cells with higher altitude, but site differences remained significant even when taking altitude into account.

Influence of habitat heterogeneity on harrier occupancy

In order to test the influence of habitat heterogeneity on the probability of harrier occurrence in a grid cell, we incorporated the values of the first axis of the PCA of habitat variables (Table 7) to the model in Table 10. This variable significantly explained probability of occurrence, once controlling for all other ones (F = 8.41, P = 0.0038), and the relationship was negative: the more the habitat was fragmented, the lower the probability that harriers occupied the cell for breeding.

Influence of habitat on regularity of use

The most parsimonious model explaining regularity of use had only site and heather availability as explanatory variables (Table 13). In other words, for those grid cells that had been occupied at least once throughout the study, regularity of use increased with heather availability, although there were also site differences in the overall frequency of use (maximum proportion of years used) of grid cells.

Harriers therefore occurred with greatest regularity in those areas that contained the highest levels of heather coverage. This relationship followed a linear trend, evident in all six study sites (Fig. 9). In sites where heather was relatively scarce, even those cells that contained very low levels of heather cover were used with greater regularity when compared to cells containing the same percentage of heather cover in heather-dominated sites.

Table 13. Results of the type III analyses testing for the effects of habitat on the regularity of use of a grid cell. Non-significant results are given at the point at which they were removed from the model in the backward elimination procedure.

| Response variable | d.f. | F | P | sign |
|-------------------|------|-------|----------|------|
| Site | 5 | 7.60 | < 0.0001 | |
| Heather | 1 | 22.37 | < 0.0001 | + |
| Rough grass | 1 | 0.09 | 0.77 | n.s |
| Heather*heather | 1 | 1.92 | 0.16 | n.s |
| Site*heather | 5 | 1.54 | 0.17 | n.s |
| Site*rough grass | 5 | 1.45 | 0.21 | n.s |

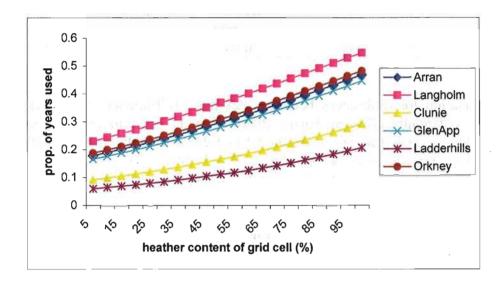


Figure 9. Predicted values of the GLM explaining the proportion of study period during which a grid cell was occupied in relation to the availability of heather in each cell. No significant differences in this relationship were found between sites.

DISCUSSION

Results from this study should be taken with caution given the possible error associated with LCM data as an estimator of habitat composition in upland habitats. As in the previous section, the creation of a land cover map based on a trained satellite image may give a more reliable estimation of the habitat composition in the study areas, and results with those habitat variables may have differed. We discuss below the results as they stand with the current data.

This study confirms that the availability of heather in an area has the greatest influence in determining the distribution of breeding hen harriers in Scottish SPAs (Redpath & Thirgood 1997; Redpath et al. 1998). The presence of nesting harriers was positively associated with the proportion of heather at all six of the study sites, although the strength of this relationship was observed to vary between sites. Nesting harriers were also observed to occur with greatest regularity in areas that contained the greatest coverage of heather.

In addition, when amount of heather was controlled for, the availability of rough grass in the proximity of a nest site was also found to have a positive influence on harrier presence, although the extent of this relationship also varied between sites, and was non-significant or negative in two of the six study sites. Both Glen App and Langholm had high overall ratios of rough grass to heather. In contrast, the ratio of rough grass to heather in Orkney was much

lower and comparable to levels found in Clunie and Arran, although not as low as that found in heather-dominated Ladder Hills (Table 11). Despite the low quantity of rough grass available, the relationship between harrier presence and habitat type in Orkney was more similar to that seen in the grass-prevalent sites (Glen App and Langholm) compared to the heather-prevalent sites (Ladder Hills, Clunie and Arran). Furthermore, the highest densities of harriers observed in this study were located in Orkney, Langholm and Glen App (Table 11). With the exception of Orkney, these results are in accordance with previous findings, which conclude that maximum densities of harriers are found in those sites that have a high ratio of rough grass to heather (Smith et al. 1999), which encourages high densities of field voles (Microtus agrestis) and meadow pipits (Anthus pratensis). Intensive studies have shown that pipits (an important prey for Harriers) are found in the highest numbers in areas containing a mosaic of heather and grass (Smith et al. 2001; Vanhinsbergh & Chamberlain 2001, Pearce-Higgins & Grant 2002). In these studies, maximum pipit abundance was found to occur when hill grass covered between 40% and 60% of a grid square which is very much in accordance with the results of this study wherein the greatest influence of rough grass was found in cells containing upwards of 40% rough grass in Glen App, Langholm and Orkney.

Nevertheless, the study also showed that there were significant and important differences between sites in the relationship between habitat and occupancy, which makes quantitative predictions about the effect of habitat management on harrier distribution difficult (or even impossible) at a general level.

The site differences in the relationships between harrier occupancy and habitat may be attributed to the influence of several factors. They may be partially attributed to the differences in the overall proportion of habitat types available within each site as a whole. For example, heather availability was observed to have greatest effect in those sites where heather was least abundant. Other environmental factors may also affect the regional distribution of harriers and thus probability of occupancy in a given area. Vegetation height is important for harrier nest site selection (Redpath et al. 1998), and may explain some of the differences. Climatic variables such as precipitation and temperature could also provide additional information on the distribution of harriers (Redpath et al. 2002) as has been shown for other raptor species (Seoane et al. 2003). Additionally, site differences (particularly differences in the relative effect of rough grass) may be due to the use of habitat as a surrogate for more subtle cues such as prey abundance, which may also vary between sites. In this study, the original habitat variables used in the development of the models were included because of their likely biological significance as a surrogate for more subtle cues such as prey abundance. the data for which is more difficult to quantify and much more labour-intensive and costly to obtain. Amount of rough grass is known to correlate with the abundance of many of the important prey species including meadow pipits (Vanhinsbergh & Chamberlain, 2001) and field voles (Gorman & Reynolds, 1993; Amar, 2001; Madders, 2003b). However, there may be differences between sites in the overall density of these prey species within rough grass. and also on the relative importance of these prey versus other alternative prey species in the harrier diet. Additionally, differences in the condition or height of vegetation between sites may have an influence on individuals when exploiting different prey types (Preston 1990; Madders 2000). The site differences observed in this present study may thus also reflect variations in foraging profitability of different prey (the ease with which prey are captured). Overall, therefore, variation in habitat composition and prey density between the study areas is most likely to contribute to the site differences in the relationships between harrier occupancy and habitat type found.

We also attempted to evaluate whether habitat heterogeneity (in terms of patch sizes and overall mosaic of heather and rough grass) influenced harrier distribution. It could be hypothesized that harriers would preferentially select nest-sites in a highly fragmented landscape to fulfil their requirements for both nesting and foraging habitat. Furthermore, increased heterogeneity of habitat may increase prey abundance as boundary length between rough grass and heather patches has been shown to be a zone of high prey availability for raptors (Austin et al. 1996). Our results showed, in contrast, that habitat fragmentation had a negative influence on the probability of occurrence. This may suggest that harriers prefer large continuous areas of heather to settle.

Overall, while it was possible to produce a model that predicts the areas where harriers are most likely to place their nests in the landscape, some caution needs to be taken in making ecological inferences from such a model; especially regarding specific quantitative predictions of the relative amounts of each habitat that would be best for harriers. Our results are useful in identifying which of the habitat variables are of highest value to breeding harriers and therefore which should be the focus of conservation measures, in a way that has not been possible previously. For example, it was possible to prove that creation of rough grass adjacent to heather areas is likely to be beneficial in most cases. Such a scheme has already been implemented in Orkney (SNH, 2003). Our results also show that management of rough grass is likely to be beneficial for hen harriers even in areas where this habitat type is more abundant, such as Langholm or Glen App.

However, an important finding of this study is that the optimal heather-grass composition for harriers is likely to vary across SPAs, and thus that management recommendations for each site are likely to be contingent on the initial conditions of each site, since there were significant interactions with site for both the effect of heather and the effect of rough grass and also due to the effects of site per se. Habitat management guidelines should thus be developed on a site-by-site basis. Results in this study suggest that in sites where heather is in low abundance, an increase in heather availability would be likely to increase the probability of harrier occupancy. In contrast, in heather dominated sites it may be more advantageous to break up some of the continuous coverage of heather with patches of rough grass. The effect of heather availability on regularity of use must also be taken into consideration as heather was observed to be the most important influence in determining regularity of occurrence, therefore large quantities of heather must remain.

To determine the best management recommendations for individual SPAs, more detailed measurement of habitat variables measured on the ground would be desirable to aid development of a second model at site level. Additionally, these results show that it may be possible to infer which habitat types are likely to increase the likelihood of an area to be occupied by breeding harriers, but it would be difficult to predict how much that increase is going to be, given the overall site differences (unaccounted for by variables measured in this study) found in probability of occurrence. The findings of this study may be used to suggest management recommendations regarding heather and rough grass, however continued monitoring of the effects of these procedures would be required at each site, to allow modification of these procedures in time, where necessary.

ASSESSMENT OF PROGRESS TOWARDS PROJECT OBJECTIVES

Three years of fieldwork have now been completed – at Langholm in the spring and summer of 2002 (pilot study, Arroyo et al. 2003), Orkney Mainland Moors in 2003 (Arroyo et al. 2004) and Glen App and Galloway Moors in 2004 (this report). This section considers progress to date against the project objectives:

1. To investigate the ranging behaviour and habitat use of breeding hen harriers on three representative SPAs where Natural Care Schemes have or will be implemented.

The original aim was to achieve this through either radio-tracking or observations of individually recognisable wing-tagged hen harriers. A pilot study (Arroyo et al. 2003) showed that the feasibility of observing and identifying wing-tagged harriers while foraging was extremely low. Further observations in Orkney in 2003 showed the same results (Arroyo et al. 2004). Radio-tracking was therefore considered as the primary method to achieve this objective.

Large difficulties were encountered in terms of capturing birds to attach radio-tags early in the breeding season (pre-laying and incubation periods) so we only obtained data in relation to the nestling period, but it is likely that home ranges in that period are likely to be the largest (since energy requirements are largest at that time). In addition issues related to the accuracy of pinpointing radio-tagged birds (associated error of about 200-500m) indicate that radio-tracking data cannot be used with confidence to identify preferred foraging habitats and to relate ranging behaviour of tagged birds to habitat use (those objectives have to be addressed through observation of hunting harriers, see section 2 below).

Nevertheless, data from radio-tracked birds has provided critical information related to the size of home range, the relative overlap in the home range between neighbouring birds, and the maximum distances visited from the nest for each bird. The combined results from 2002-2004 prove that males range over much larger areas than females (almost double); that geographical differences in home range are (apparently) less marked than individual differences, at least in the areas studied; that ranges of neighbouring males do overlap to a large extent; and that there is a trend for home ranges to increase with increasing age of nestlings, although these differences are particularly marked for females, not so much for males. Average range size for males was ca 7.3 km², and for females 3.5 km². Females spent most of the time within 2 km from the nest, whereas males spend a significant amount of time outside that radius. Maximum distances recorded from nest sites were respectively 3900 and 8900 m.

Overall, we consider that results so far answer (as far as possible) the questions stated in the proposal.

2. To develop a model that predicts range use in breeding hen harriers.

The original aim was to base this aspect of the work on the model developed by Dr Mike Madders (Madders 2003) which predicts the relative probability of use of areas by breeding hen harriers based on habitat characteristics. However, the development of a model which can be applied to all areas of breeding habitat was dependant on an absence of strong geographical differences between harrier foraging preferences.

Our analyses suggest that there is little generality across the areas included in this study and thus, that it is impossible to predict range use by breeding harriers in a given area, unless previous data on diet, relationships between prey and habitat, and potentially vegetation structure are available for that area. Even in that case, it is probably safer to assume that quantitative data on hunting should be collected in each area in order to identify the best foraging habitats at each breeding site. Our data also show that nest proximity is probably more important in determining the ranging behaviour of females than males, which confirm data based on radio-tracked individuals.

A further issue is whether our ground-collected data is likely to be an adequate descriptor of habitat within the watch areas, and that the errors associated with LCM are such that the land cover data is not useful in terms of the analyses of hen harrier foraging data. The latter further complicates the possibility of preparing predictive models of range use for unmonitored areas. Training a satellite image to create a land cover map particularly for our study areas may give a more reliable estimation of the habitat composition in the watch areas, and would allow creating predictive models in further areas. In 2005 we will aim to create this new land cover map, and repeat the analyses with the new habitat variables.

3. To produce a set of criteria on which to assess and monitor the success of Natural Care management prescriptions on moorland SPAs for hen harriers.

As specified before, no work was carried out in 2004 in relation to this objective. Data should be prepared for initiating population viability analyses (PVA). This will require compiling all data on population parameters from the SPAs or the RSPB wing-tag data sets. This will be done during 2005, provided that there is enough time once the other objectives have been completed. Alternatively, simpler criteria based not on PVA but on harrier densities and habitat use will be created.

4. To produce a set of management recommendations for every Scottish SPA for breeding hen harriers to inform effective and cost-efficient management prescriptions.

Our current results show that management recommendations cannot be applied generally across SPA sites in Scotland, since there were significant interactions with site for both the effect of heather and the effect of rough grass and also due to the effects of site per se. Habitat management guidelines must be developed on a site-by-site basis.

However, and as for section 2 above, the validity of LCM as a habitat descriptor is an issue, and there remains some doubt about whether site differences reflect "real" ecological differences between sites, or else are a byproduct of habitat data quality differing between sites. As for section 2, in 2005 we will aim to create a new land cover map (based on a trained satellite image), and repeat the analyses with the new habitat variables. In any case, management guidelines for the SPAs which have been involved in the current study will be prepared in 2005.

Once final models have been produced, work in 2005 will also to explore different scenarios of how hen harrier nesting and feeding distributions will respond to changes in habitat. Finally, analyses in 2005 should also concentrate on the relationship between habitat and breeding success for those sites for which data is available (Clunie, Langholm, others?), to complete those analyses carried out for Orkney.

ACKNOWLEDGEMENTS

This work is a partnership project between Royal Society for the Protection of Birds (RSPB), Scottish Natural Heritage (SNH), Game Conservancy Trust (GCT) and Centre for Ecology and Hydrology (CEH). We are very grateful to Genevieve Jones, Winks Emmerson, Darren Edwards, Charlie Parks, Ricky Gladwell and Geoff Sheppard for assistance with fieldwork in 2004, and to landowners and tenants for allowing us access for observations and trapping. Thanks are due to Helen Riley, Blair Urquhart and Bruce Anderson for compiling the information on harrier locations for Orkney and Galloway, Arran and Forest of Clunie (respectively). Data in all those areas were gathered by numerous people, including members of Raptor Study Groups, and RSPB staff. Thanks also to Steve Palmer and Sue Wallis for providing LCM data, to Dave Elston for statistical advice, to Graeme Buchannan for help with spatial correlation analyses, to Ellen Wilson for compiling altitude data, and to Helen Riley and Jeremy Wilson for constructive comments on the report.

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ANNEX 0. CLASSIFIED/DESIGNATED HEN HARRIER SPAS IN THE UK.

| site name | Local authority | Season | Importance |
|------------------------------------|---|--------|--|
| Arran Moors | North Ayrshire | В | 4% of JNCC defined GB population (breeding) |
| Caithness and Sutherland Peatlands | Highland | В | 2.2% of JNCC defined GB population (breeding) |
| Forest of Clunie | Perth and Kinross | В | 4.0% of JNCC defined GB population (breeding) |
| Glen App and Galloway Moors | Dumfries and Galloway; South Ayrshire | В | 2% of JNCC defined GB population (breeding) |
| Glen Tanar | Aberdeenshire | В | 0.5% of JNCC defined GB population (breeding) |
| Langholm - Newcastleton Hills | Dumfries and Galloway; Scottish Borders | В | 2.7% of JNCC defined GB population (breeding) |
| Loch of Inch and Torrs Warren | Dumfries and Galloway | W | 1.1% of JNCC defined GB population (wintering) |
| Muirkirk and North Lowther Uplands | Dumfries and Galloway; East Ayrshire; South Lanarkshire | W | 2.0% of JNCC defined GB population (wintering) |
| Muirkirk and North Lowther Uplands | Dumfries and Galloway; East Ayrshire; South Lanarkshire | В | 6% of JNCC defined GB population (breeding) |
| Orkney Mainland Moors | Orkney Islands | В | 5% of JNCC defined GB population (breeding) |
| Orkney Mainland Moors | Orkney Islands | W | 2% of Great Britain (Wintering) |
| Rinns of Islay | Argyll and Bute | В | 1.1% of JNCC defined GB/population (breeding) |
| River Spey – Insh Marshes | Highland | W | 1.5% of JNCC defined GB population (wintering) |

Source JNCC website SPA/GIS data 2004

B – breeding W - wintering

ANNEX 1. TRAPPING ATTEMPTS IN GALLOWAY IN 2004

Trapping success this year was high (54%), and similar to that observed in 2002 at the same period (Arroyo et al. 2003). As in previous years, no detrimental effects of trapping and handling were observed in trapped harriers. Overall, results from this year confirm that trapping breeding harriers during the nestling period may be efficient and is innocuous to the birds, although it is relatively time consuming.

Trapping attempts and their outcome on Galloway in 2004; Sex = sex of harrier present after detection of decoy.

| Date | Stage | Location | Decoy | Trap | Sex | Success | Comments |
|--------|----------|------------------|--------------|----------------|--------|---------|--|
| | | , | | | | | female left nest of own accord, swooped decoy a couple of times, eventually knocking |
| 9-Jun | nestling | Pools 1 | male | net | both | 0 | it. Male came in with food, dropped at nest and flew away. |
| | | | | | | | replaced male decoy with owl after 3 hours, female again came off nest, saw owl and |
| 9-Jun | nestling | Pools 1 | owl | net | female | 1 | went directly into net. |
| | | | | | | | Male flew over owl and net a few times but no alarming. Then perched. Female up for food pass and start alarming, male flew over net a few times then perched on hill across |
| 11-Jun | nestling | Pools 1 | owl | net | both | 0 | gully. Abandoned after 30 mins. |
| 18-Jun | nestling | Kirklatchie Burn | owl | net | both | 1 | male arrived with food, went directly into net |
| 18-Jun | nestling | Kirklatchie Burn | owl | net | both | 1 | female directly into net after coming up to alarm |
| 20-Jun | nestling | Balker Moor | owl | net | male | 1 | male appeared with food, alarming and circling over owl, clawed at net a few times. Then perched and ate food. Started attacks again, then looped back into net. |
| 20-Jun | nestling | Braid Fell | owl | net | both | 0 | initial set up too far from nest, ignored by both birds during food pass. Moved in closer, but male didn't return. |
| 4-Jul | nestling | Braid Fell | owl and male | net | both | | at start owl at net male decoy off to side. Ignored by male who brought prey in to female. Female yickered and flew at both decoys, swooping more at male until hit it, avoiding net on way in. Moved male into net and removed owl. Female returned and went straight for male and into net, but escaped. Large hole, but also too windy. |
| 6-Jul | nestling | Braid Fell | male | net | both | 1 | female took food from male, then she yickered, flew about, flew over net then into it. |
| 7-Jul | | Pools 2 | | net and nooses | both | , | male in with food, yickered and went away to perch, ate food. Put out male decoy and nooses too. Male back yickering, female up, swoop at male decoy, male swoop at owl from all over direction!. Female into nooses on male decoy. |
| /-Jui | nestling | Pools 2 | owi and male | net and nooses | bom | 1 | male in with food, yickering, another male about too, no calls, swooped once over owl |
| | | | 1 . | | | | while Pools 2 male called. Other male left, this male carrries on yickering from a |
| | | | | | | | distance with prey. Went away. Reappeared minus prey, swoop on owl and hit it, not |
| | | | | | | | caught, swoop lots more on owl. Also swoop on male decoy, and hit it, then away to |
| | | | | | | | perch on fence. Male yickered from above us on hill, swoop over decoys and over hide |
| 8-Jul | nestling | Pools 2 | owl and male | nooses | male | 0 | too. Abandoned eventually. |

ANNEX 2. CALIBRATION OF LCM DATA (1990 AND 2000) WITH FIELD DATA

In order to estimate the accuracy and relevance of the LCM data in terms of correctly identifying the habitats of interest, we compared the amount of different habitats as identified on the ground from three different study areas, with data for the same areas generated from LCM1990 and LCM2000 data.

In Orkney habitat surveys were carried out in 18 1km squares. Ground data from these squares were collected in summer (July-August) 1998 and spring (February-March) 1999. The dominant vegetation type was recorded in each of fifty 25cm^2 quadrats which were placed every 40 m along two parallel 1km transects, placed 250m and 750m away from one of the sides of the square (for further details on these methods see Amar 2001 – chapter 3). LCM Data came from satellite images, which were taken during summer and winter and 88% of areas were classified using a combination of images taken over these two time periods (Fuller et al. 1994b). Therefore, we also averaged the habitat data collected from transects during spring and summer to make the comparisons with the LCM data more realistic.

In Langholm, three sources of ground data were used. First, ground data was taken in summer 2002 from 23 quadrats 0.25 km² (those used for the observations of hunting harriers). Within each of these quadrats, the dominant vegetation type was recorded in each of fifty 25 cm² quadrats which were placed every 20 m along 4 parallel lines within each quadrat. Additionally, percentage of heather cover (but not other habitat variables) was evaluated on the ground in 16 areas in 1996 (Thirgood et al. 2003), also used for the observations of hunting harriers. Finally, there was data available for 74 quadrats 0.25 km², which had been used to evaluate the relationship between habitat and pipit abundance (Smith et al. 2001).

In Galloway moors, we collected ground data from 18 areas in 2004 (each area being either 0.5 or 1 km² large).

We compared the proportion of heather, rough (unmananged) grass or smooth (improved) grass dominated quadrats within each square, with the proportion of those habitats as calculated from the LCM data, or combinations of different habitat measures. We compared the R² of the relationships for LCM1990 and LCM2000, to see which one provides a better fit for the ground data.

Overall, relationships were better (R² were higher) with LCM1990 than with LCM2000 (see Table below), except for heather data obtained in Langholm in 2002 and in Galloway in 2004, where R² values were overall low for both LCM data sets. In any case, the relationship between ground data and LCM data was considered to be poor, except for Orkney. Reasons for this are unexplained, but the most likely reason is that LCM data does not actually provide a good enough picture of small-scale variations in habitat in areas where the distribution of heather and current occurrence of grassy areas at Langholm.

We conclude that, if LCM data is probably valid for identifying large-scale variation in habitat, such as that needed to evaluate the importance of habitat in harrier distribution and between-area differences, since for those analyses the difference between occupied and unoccupied areas is probably bold. In those cases, we chose to use LCM1990 (instead of LCM2000) as the best estimator of habitat availability in the study areas. In contrast, the use of LCM data for analysing variation in hunting effort is probably worthless, and we consider it more prudent to use ground data for those analyses.

Table X. R^2 of the regressions between ground data and estimators of habitat using LCM1990 and LCM2000.

| Site | Heather | Rg | Sg | Rg and sg |
|-----------------|---------|------------|--------------|-----------|
| Orkney | | | | |
| Lcm 1990 | 0.90 | 0.63 | 0.98 | |
| Lcm 2000 | 0.41 | 0.48 | 0.95 | |
| Langholm | | | - | |
| Hunting sqs | | • | | |
| Lcm 1990 | 0.39 | 0.13 | 0.03 | 0.56 |
| Lcm 2000 | 0.45 | 0.03 | 0.08 | 0.17 |
| Thirgood et al. | | | | |
| Lcm 1990 | 0.68 | | | |
| Lcm 2000 | 0.58 | | | |
| Smith et al. | | | | |
| Lcm 1990 | 0.68 | 0.46 (MOL) | | |
| Lcm 2000 | 0.51 | 0.26 | | |
| Galloway | | | | |
| Lcm 1990 | 0.01 | 0.23 | 0.76 | |
| Lcm 2000 | 0.03 | 0.08 | 0.74 | |

ANNEX 3: COVER TYPES IDENTIFIED BY LCM1990

| TARGET CLASSES (25 class system) | | | | |
|----------------------------------|-------------------------------|--|--|--|
| 1 ^a | Sea / Estuary | | | |
| 2 | Inland Water | | | |
| 3 | Beach and Coastal Bare | | | |
| 4 | Saltmarsh | | | |
| 5 | Grass Heath | | | |
| 9 | Moorland Grass | | | |
| 6 | Mown / Grazed Turf | | | |
| 7 | Meadow / Verge / Semi-natural | | | |
| 19 | Ruderal Weed | | | |
| 23 | Felled Forest | | | |
| 8 | Rough / Marsh Grass | | | |
| 25 | Open Shrub Heath | | | |
| 10 | Open Shrub Moor | | | |
| 13 | Dense Shrub Heath | | | |
| 11 | Dense Shrub Moor | | | |
| 12 | Bracken | | | |
| 14 | Scrub / Orchard | | | |
| 15 | Deciduous Woodland | | | |
| 16 | Coniferous Woodland | | | |
| 24 | Lowland Bog | | | |
| 17 | Upland Bog | | | |
| 18 | Tilled Land | | | |
| 20 | Suburban / Rural Development | | | |
| 21 | Continuous Urban | | | |
| 22 | Inland Bare Ground | | | |
| 0 | Unclassified | | | |

 $^{^{\}rm a}$ label value within the 25 'target' cover-type 25 x 25 metre data.