Time budgets and foraging of breeding golden plover *Pluvialis apricaria*

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Summary

1. The golden plover *Pluvialis apricaria* is of high conservation concern in Europe. Previous studies have concentrated on how birds utilize moorland. We used radio-telemetry to study their habitat selection and behaviour, during both night and day, in an upland landscape of enclosed fields and moorland in county Durham, UK.

2. During incubation adult golden plover fed principally in enclosed fields 1·1–3·7 km from their moorland nests, but spent less than 5% of their foraging time on moorland. In contrast, birds with broods spent around 85% of their time foraging on moorland.

3. Birds on moorland selected calcareous grassland and avoided old stands of dense tall heather ($> c.$ 12 cm). Younger, shorter ($< c.$ 5–8 cm), sparser heather was used as much as would be expected by chance. Mires of harestail cotton grass *Eriophorum vaginatum*, the dominant community type when heather *Calluna vulgaris* is heavily grazed, was selected on both moorland sites.

4. Only 17 of 85 fields in the study area were used for foraging by breeding golden plover. The number of molehills, a reported indicator of earthworm abundance, was the best single variable explaining field choice. Both field size and distance from road had small but significant effects on field choice.

5. We advocate that groups of enclosed fields regularly used by golden plover during the breeding season be afforded specific protection under conservation schemes (e.g. environmentally sensitive area agreements). Conservationists wishing to locate such fields should look for areas with high earthworm populations, as indicated by molehills, close (< 4 km) to breeding populations of golden plover. Rank heather on flat or gently sloping ground should be kept short by appropriate burning or grazing. Areas of calcareous grassland should be preserved.

6. These data illustrate the value of detailed radio-telemetry in informing equally detailed habitat management for important bird species.

Key-words: activity patterns, habitat choice, moorland management, nocturnal foraging, upland conservation.

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Introduction

Effective conservation relies on detailed knowledge of species' ecological requirements. This paper investigates such requirements for an upland-breeding wader, the golden plover *Pluvialis apricaria* L. By far the majority of the global population breeds in Europe, where it is characteristic of bogs, heaths, upland grassland and tundra (Hagemeijer & Blair 1997; Byrkjedal & Thompson 1998). It breeds throughout Britain's uplands but is declining in both range and numbers (Parr 1992; Gibbons, Reid & Chapman 1993; Stone *et al.* 1997; Hancock & Avery 1998). Britain supports around 25% of the European Union (EU) breeding population and has an international responsibility to take special measures to conserve the species' habitat by virtue of its listing on the Annex 1 of European Union Directive

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79/409/EU on the Conservation of Wild Birds. One of its main breeding habitats, blanket bog, is also of international conservation concern, listed as a priority on Annex 2 of the EU Habitats and Species Directive (92/43/EU).

Discussions between conservationists and colleagues about management of Britain's uplands are long-running (Usher & Thompson 1993). It has been suggested that the extent of heather *Calluna vulgaris* L. moorland, and the area managed for red grouse *Lagopus lagopus* L. in particular, should be encouraged for wildlife and local economic benefit (Hudson 1992). Little is known, however, of the consequences for upland birds. Grazing by sheep and red deer *Cervus elaphus* L. in the Scottish Highlands is recognized as a major influence on upland habitats. However, it is uncertain how changes in grazing pressure would affect upland birds. This study examines the habitat use by golden plover on two moorland areas, one heavily grazed in the past and the other managed for red grouse.

Intensive studies have shown that adult golden plover forage in enclosed agricultural fields adjacent to nesting areas in Britain (Ratcliffe 1976; Parr 1980; O'Connell *et al.* 1996) and in Iceland (Bengtson & Rundgren 1978) during the breeding season. Most studies noted incidental records of breeding birds using fields. O'Connell *et al.* (1996), in contrast, reported extensive use of fields by breeding birds in north-east Sutherland, Scotland. They were found in older, larger, grazed fields, some containing *Juncus* spp. (Byrkjedal & Thompson 1998), although this was only based on a sample of 12 fields and no statistical testing was undertaken (O'Connell *et al.* 1996). Therefore, although the use of fields by moorland nesting golden plover appears widespread in Britain, the relative importance of fields compared with moorland is poorly known. Furthermore, the characteristics of fields chosen by breeding golden plover for foraging and other activities have not been quantified. Such information would influence decisions on the designation of upland nature reserves and wider conservation areas to support golden plover. This study compared the use of fields and moorland by breeding golden plover using radio-telemetry, and identified the characteristics of those fields selected for foraging.

Several previous studies have examined golden plover habitat selection in various parts of Britain at a broad scale, most taking 1-km squares as the sampling units (Ratcliffe 1976; Haworth & Thompson 1990; Brown & Stillman 1993; Stillman & Brown 1994). These studies found that golden plover usually breed between 300 and 460 m above sea level on unenclosed peatlands, grazed or burnt heaths and moorlands dominated by cotton grass *Eriophorum* spp., often showing a strong association with plateaux. In addition, a small number of intensive studies have investigated their habitat prefer-

ences during the breeding season (Ratcliffe 1976; Parr 1980; Byrkjedal 1985, 1989; O'Connell *et al.* 1996). Parr (1980) concurred with wider scale studies when he found a preference for burnt patches of heather by adults. O'Connell *et al.* (1996) found that blanket bog (with many small pools) was the most preferred habitat during the breeding season, although more use was made of grassland when adults had broods. Ratcliffe (1976) noted the highest breeding densities of golden plover anywhere in Britain on limestone grasslands in the Pennines. This study examined the relative use of many of the main habitat types available to golden plover, namely: calcareous grassland, different age stands of heather, blanket bog, grassland and harestail cotton grass *Eriophorum vaginatum* L. mire.

Although well-documented in shorebirds (Goss-Custard 1984; McNeil, Drapeau & Goss-Custard 1992; Mouritsen 1994), there have been few studies of nocturnal foraging in breeding waders (Staine & Burger 1994). Other radio-tagging studies of breeding golden plover did not record activity at night (Byrkjedal 1985; O'Connell *et al.* 1996). When developing conservation strategies it is important to incorporate habitat use at all times as animals can select different habitats at different times (Beyer & Haufler 1994). Therefore we characterized fields used at night, as well as during the day, and over both the incubation and brood-rearing phases.

Our specific objectives and the different data sets used to investigate them were as follows:
1. We aimed to compare the use of moorland and farmland by individually radio-tagged golden plover located once at night and once during the day.
2. We tested for habitat selection on moorland using line-transect data. Radio-tagging was not considered accurate enough to differentiate between the mosaic of moorland habitats.
3. We compared the characteristics of fields used for foraging by breeding golden plover (colour ringed or radio-tagged birds) with a random sample of other fields within a similar distance from the moor.

We conclude by discussing the relevance of our findings to the management of upland areas to sustain/enhance golden plover populations.

Methods

STUDY AREAS

The study was conducted on two upland areas in the northern Pennines of County Durham, UK, from April to July 1992–95. The core of each study site was an area of moorland: 3·7 km² on Chapel Fell (54°43′N, 2°12′W) and 5·1 km² on Widdybank Fell, part of Teesdale National Nature Reserve (54°40′N, 2°16′W). The chosen sites each had reasonably high densities (4–5 pairs km²) of breeding

golden plover and supported a diversity of vegetation types. Chapel Fell was typical of heavily sheep-grazed moorland, dominated by harestail cotton grass with only sparse heather cover. It included many patches of acidic grassland, some dense stands of heather, and several areas of acidic sedge and rush-dominated marsh. Widdybank Fell was a heather moorland managed primarily for red grouse, with a large amount of heather cover and a mosaic of burnt patches of different age. Unusually for upland moorland it also included several patches of limestone grassland and calcareous marshes. The habitats on each study site were classified using the National Vegetation Classification (NVC) system (Rodwell 1991a,b). The stocking rate of sheep on Widdybank during the study was 423 ewes (0·87 ewes ha^{-1}), which was only slightly lower than the 1500 ewes on the Chapel Fell area in 1993 (0·98 ewes ha^{-1}). However, high levels of grazing in the past coincided with declines in heather cover and increases in grasses (L. Waddell, personal communication) and the relationship is known to be causal elsewhere (Thompson, MacDonald & Hudson 1995). Maps of the moorland study sites are described in Whittingham, Percival & Brown (1999a) and Whittingham (1996a).

Eighty-five 'study fields' surrounding the moorland study areas were selected to investigate golden plover use of enclosed upland farmland, including all fields in which radio-tagged birds were found. To avoid disturbance to birds, which were easily flushed, all parts of fields chosen were viewable from roads or tracks. Many fields could be viewed from vantage points, allowing a spread of fields of varying distance from roads to be sampled. A description of the characteristics of these fields is given below.

ACTIVITY BUDGETS AND LOCATIONS ON FARMLAND AND MOORLAND

Radio-telemetry was used as the prime means of determining the location and activity of adult golden plover. A total of 22 birds was captured on nests using a walk-in trap (eight males and five females in 1994, five males and four females in 1995). Each bird was fitted with a 3·9-g radio-tag incorporating a mercury tilt switch to record activity (Holohil Systems Ltd, Ontario, Canada). Data from one bird whose tag became detached after a day were excluded from the study. The tags were attached between the carpal joints on a bird's back using either Loctite superglue (Henkel Consumer Adhesives, Cheshire, UK) or Saltair Ostomy Adhesive solution (a skin bonding glue supplied by Salt and Son Ltd., Birmingham, UK). The tags did not affect the birds' behaviour significantly (Whittingham 1996b). Only one individual from each nesting pair was tagged to ensure independence of data. Tags

remained attached for an average of 20 days (Whittingham 1996b). Birds were located in individual fields or parts of the moor by triangulation (Kenward 1987).

Initially in 1994, 10 tagged individuals were located every 2 h over a continuous 24-h period. It became apparent that tagged males incubated nests during the day (95% of *ad hoc* records found males on the nest between 06:00 and 20:00 h, $n = 194$) and then flew to fields in adjacent valleys, where they remained (overnight) until shortly before resuming incubation. Inversely, females incubated during the night (99% of *ad hoc* records found females on nest between 19:00 and 06:00 h, $n = 112$) and flew to fields during the day, where they remained until shortly before resuming incubation. In addition, males with broods guarded chicks during the day and sometimes visited the fields at night (again the inverse was true for females). Therefore data were collected from individuals located only once at a random time during daylight hours (06:00–21:00 h) and once at a random time during the night (21:00–05:00 h). This ensured that sample units were independent: each individual made a new choice of location on each occasion. Tag loss and nest predation (*c*. 30% of nests hatched; Whittingham 1996a) meant that most records (79%) came from the incubation period.

An individual sample of radio-tagging data consisted of five consecutive 1-min subsamples. The dominating activity in each 5-min period was used to categorize that sample. Samples were classified as one of the following: foraging, incubating, guarding or other activities. Tags of foraging birds emitted a distinctive pattern of fast and slow pulses caused by the change in position of the mercury within the tag when the bird bent over to peck (Whittingham 1996b). Validation of this technique was carried out by watching tagged birds whilst recording the pulse pattern emitted by their tag. Two independent observers took 1-min samples, one recording actual activity (foraging or not foraging) and the other assigning a category using pulse pattern emission. Ninety-eight per cent of 253 records was classified correctly. In 91% of five consecutive 1-min samples a peck was recorded in at least four of the 1-min periods. Individuals stationary at the nest site during the incubation phase were noted as incubating. This was validated by visiting 26 such birds. An observer flushed an incubating bird from the nest in 25 cases. When the signal indicated that the bird was neither feeding nor incubating, the bird was located by eye to determine if it was guarding. Individuals exhibiting alert behaviour, as defined by Byrkjedal (1989), and/or giving alarm calls close to young, were classified as 'guarding'. Birds that were engaged in none of the three described activities were recorded as engaged in other activities. They included roosting, flying, displaying and other interspecific and intras-

pecific interactions. It was not possible to distinguish guarding from other non-feeding activities at night and so activity of post-hatching adults on the moor could not be distinguished between these two categories. All analysed data were from birds with active nests or broods except when indicated otherwise.

Data analysis

Foraging and other activities were further classified by macrohabitat, resulting in the following six activity/location categories: foraging on moor, foraging in fields, other activities on moor, other activities in fields, incubating on moor (all nests were located on moorland) and guarding on moor (all broods were on moorland). To examine differences in proportion of time spent in each activity/location between sexes and from birds nesting on different moors, with respect to year, logistic regression analyses were performed using GLIM package v.4 (NAG 1993). Models were specified with the number of records of incubating (and each of the other activities/locations used in turn) as the response variable and the total number of records from each individual as the binomial denominator, using a binomial error distribution and a logit link. This both eliminated problems of non-normal and non-constant variance and also weighted the data according to the sample size obtained from each individual (Crawley 1993). The best model was found using stepwise backward selection. The full model was fitted initially with all predictors and the interactions between them. The most complex interactions (i.e. three-way) were then deleted first, followed by the two-way interactions and main effects. An interaction or main effect was only retained in the model if it explained a significant amount of the deviance (Crawley 1993). The statistical significance of including or excluding predictors in the model was assessed by the change in deviance (ΔD) (which approximates to a likelihood ratio test), the results of which were distributed asymptotically as χ^2. The minimum adequate model (MAM) was reached when no predictors could be added or deleted from the model without causing a significant change in deviance. There is no firm theory that predicts the power of the MAM in explaining the variance, i.e. as r^2 does in normal regression (Collett 1991; Crawley 1993). Instead the fit of the model to the data can be assessed approximately by the ratio of the residual deviance divided by the residual degrees of freedom. Ratios close to 1 indicate that the model provides a good fit to the data (Crawley 1993). Ratios of over 2–2·5 indicate that the data are overdispersed and the power of the model in explaining the data is weakened. Ratios found in our models ranged from 0·24 to 1·66 and therefore we felt confident that our models provided a good fit to the data.

USE MADE OF MOORLAND

Moorland study sites were censused for golden plover by walking transects, 100–200 m apart, at least once a week from April to July 1992–94. Censuses were not undertaken during periods of high wind (above force 4/5), heavy precipitation or low cloud. The habitat each individual was using when first observed was recorded. Records of birds giving alarm calls (i.e. those responding to the observer) were discarded. Observers scanned the study area 400 m ahead to minimize the chance that birds were responding to the observer (Percival & Smith 1992). Golden plover have been found to be disturbed by humans at an average of *c*. 200 m (Yalden & Yalden 1989).

Vegetation structure on moorland

The structure of the habitat as well as the species composition is likely to affect decisions by birds on where to forage on moorland. Therefore 10 height and density measurements were taken from eight quadrats randomly distributed within each habitat NVC habitat type. Vegetation density was measured by embedding a 1-m rule with alternate 1-cm colour bands into the earth and recording the amount of 1-cm lines obscured by vegetation from a point 1 m away from the rule. Vegetation height was taken as the highest piece of vegetation touching the rule.

Data analysis

Chi-square analysis was used to test the null hypothesis that use of habitats by golden plover in each month was in proportion to the habitats available to them. Initially, census data from each year from 1992 to 1994 were analysed separately using chi-square analyses. There were no significant differences in habitat use between years on either Chapel Fell ($\chi^2 = 46\cdot64$, d.f. $= 33$, $P > 0\cdot05$) or Widdybank ($\chi^2 = 60\cdot53$, d.f. $= 48$, $P > 0\cdot10$), so data from each year were pooled for each site. Due to the small amounts of some habitats, some categories were pooled to ensure that expected values were greater than five. The habitat groupings on Chapel Fell and their NVC codes (Rodwell 1991a,b) were acid grassland (U6, U2 and U5); marshes (M6, M3, M7); *Eriophorum vaginatum* mire (M20); and *Eriophorum vaginatum* mire subcommunity *Calluna vulgaris* (M20 with *Calluna vulgaris* covering $> 50\%$ of quadrats; Whittingham 1996a). The groupings on Widdybank were limestone grassland (CG9); old stands of heather (H12); recently burnt stands of heather (< 5 years old) (H12); acid grassland (U5); *Calluna* heath (H9); and marshes (M10, M6 and M20). Expected values were calculated using the proportion of habitat I multiplied by the total number of sightings T (i.e. if $I = 47\%$ and $T = 220$,

expected number of sightings on $I = 103 \cdot 4$). Formal statistical tests between the proportion of records and habitat available within each habitat category were not possible using chi-square analysis, instead relative preferences for a habitat type were assessed descriptively according to the magnitude of preference.

SELECTION OF ENCLOSED FIELDS FOR FORAGING

We measured a number of field characteristics of our study fields in order to investigate relationships between these and field selection by foraging birds. Field area, distances to roads and moorland and slopes were all measured from Ordnance Survey maps. Data on the management, vegetation and topographical features of fields were estimated by eye whilst walking through the fields at the beginning of May and end of July in 1995. Management of fields rarely varied within season, but when it did (e.g. introduction of livestock later in the season) the field use in May was used because all records from foraging birds were in May or in the first half of June. No changes in field use were recorded between years. Frequency of small hills (hummocks) was noted on an ordinal scale from 1 (no hummocks) to 5 (all field covered with hummocks).

The mean area of fields was $5 \cdot 04$ ha $\pm 0 \cdot 41$ (1 SE) (range $0 \cdot 60$–$19 \cdot 4$ ha). The mean distance of the centre of the field to the nearest road was $123 \cdot 8$ m $\pm 10 \cdot 3$ (1 SE) (range 25–425 m). The mean distance from the centre of the field to the nearest unenclosed moorland was $693 \cdot 5$ m $\pm 44 \cdot 4$ (1 SE) (range 50–1700 m). The topography of fields was as follows: 56% were mainly flat with all areas $< 5°$ slope; 35% were predominantly flat with 25% or more of the area $> 5°$; and 8% were mainly found on steep ground with 80% of the area $> 10°$ in slope. Thirty-eight per cent of the fields were managed as meadows for hay production (as part of Ministry of Agriculture Fisheries and Food environmentally sensitive area agreements) and 62% were pasture fields for cattle and/or sheep. Mean vegetation height was < 5 cm high in 46% of the fields and > 5 cm in the remaining 54% (data collected during the first half of May when most fields were used by birds). Twelve per cent of fields had tussocks of vegetation covering $> 50\%$ of the field, while the remaining 88% of fields had $< 50\%$ of the field with tussocks. Seventy-three per cent of fields had $< 10\%$ *Juncus* spp. cover in each field, the remaining fields $> 10\%$. The percentage of scores for each category of hummocks (scale 1–5) were as follows: 78 (1), 18 (2), 4 (3), 1 (4), 0 (5).

In addition, we were interested in determining food availability in study fields. Three-hundred and sixty-eight 1-min focal observations of feeding birds

were made in the study fields in 1994 and 1995. Earthworms were the single most important prey. Fifty-six per cent of successful foraging bouts by adults, before chicks had hatched, were on earthworms (44% prey unknown), compared with 48% after the chicks had hatched (39% unknown, 5% on Coleoptera and 8% *Tipula* spp.). Our findings concurred with a breeding season study of golden plover feeding in fields adjacent to moorland in Iceland. Bengtson & Rundgren (1978) found earthworms constituted about 90% of fresh weight in stomachs. Moles *Talpa europea* L. feed predominantly on earthworms (Macdonald & Barrett 1993) and they leave mounds of earth, 'molehills', where they have been active. Therefore we estimated the number of molehills by eye to give a crude index of earthworm abundance (Micol, Doncaster & Mackinlay 1994; Edwards, Crawley & Heard 1999). The proportion of scores for each category of molehills on a scale of 0 (none) to 10 (abundant in every part of the field) were: $0 \cdot 353$ (0), $0 \cdot 118$ (1), $0 \cdot 176$ (2), $0 \cdot 094$ (3), $0 \cdot 058$ (4), $0 \cdot 105$ (5), $0 \cdot 035$ (6), $0 \cdot 047$ (7), $0 \cdot 012$ (8), $0 \cdot 012$ (9), 0 (10).

Data analysis

Logistic regression analysis, with a binary response variable, was used to predict the likelihood of field use by plover for foraging, based on the environmental predictors collected from each field. A binary response variable was used because only 17 of the 85 fields were used and so data were highly skewed. The modelling procedure used was similar to that described above, using backward deletion and significance testing by likelihood-ratio tests, except all main effects were fitted initially and not the interactions between them. However, interactions between predictors remaining in the minimum adequate model (MAM) were investigated. Stepwise regression can lead to differing predictors remaining in the minimum adequate model (MAM) depending on the method used, particularly so if predictors are highly intercorrelated (James & McCulloch 1990). To test for this, univariate tests were carried out on all predictors excluded from the MAM. We then tested for intercorrelations, using appropriate tests (Siegel & Castellan 1988), between predictors in the MAM and those which were significant with univariate tests.

Fitted values for the probability of occurrence of a golden plover on each field were derived using the equations from the MAM. These values were compared with the observed values using a two-way classification table to investigate the predictive power of the model. The stringency of the threshold values for assigning a field as used or not used from the fitted values was increased to investigate the accuracy of the models.

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Results

ACTIVITY BUDGETS AND LOCATIONS ON FARMLAND AND MOORLAND

Over both incubation and brood periods 78% of records of all off-duty breeding birds in fields during the season were of foraging birds. Conversely, 84% of all records of birds on the moor were of incubating birds. Of the remaining records, only 7% involved foraging birds. However, as noted earlier, these data were heavily biased towards the incubation period.

Incubation period

Both sexes spent *c.* 90% of their time either incubating or foraging in fields (Fig. 1). Males ($n = 12$), but not females ($n = 8$), spent significantly more time incubating than feeding in fields (Fig. 1). Both sexes used fields more than moorland for feeding during the incubation period (Fig. 1). The mean number of records per individual was 19·8 (minimum 3, maximum 52), with less than 10 records collected from only four birds.

Males spent more time incubating than females ($\Delta D = 14·07$, d.f. $= 1$, $P < 0·001$) and less time foraging in fields than females ($\Delta D = 14·57$, d.f. $= 1$, $P < 0·001$). There were no significant differences between the sexes in time spent foraging on moorland or in other activities on moorland or in fields ($P > 0·30$). Both sexes spent more time foraging on Widdybank than on Chapel Fell ($\Delta D = 5·76$, d.f. $= 1$, $P = 0·016$). Study site was not found to affect time spent significantly in any of the other activities/locations (all $P > 0·11$). Differences between years did not explain a significant amount of the variation in any of the five models ($P > 0·06$).

All but one of the radio-tagged birds left the moor to visit nearby fields when not incubating eggs. The exception was a male at Widdybank that stayed within *c.* 300 m of the nest when not incubating. This male spent most of his time feeding on calcareous grassland, which comprised a much larger part of his territory than for any other tagged bird.

Brood period

Data were collected from four females and four males. Two of the males were recorded foraging in fields at night. All other radio-tagged adults were located near their broods on the moor during both night and day. There were insufficient data to investigate differences between the amount of time spent in different activity/location patterns overall or between sexes. The mean proportion of time spent in each activity/location was as follows: guarding (male: 58·8%, female: 29·5%); other activities on moor (male 5·0%, female 10·7%); foraging on moor (male 19·2%, female 53·0%); other activities in fields (males 6·8%, females 3·6%); and foraging in fields (males 10·1%, females 3·2%). Thus, fields were used less frequently and the moorland was used more frequently for foraging during the brood period than during the incubation period.

USE OF MOORLAND

The height and density of habitats are presented in Table 1. On Chapel Fell, habitats were utilized approximately in the proportions available to them, except during May and June (Table 2 and Fig. 2a). Only one habitat type, *Eriophorum vaginatum* mire, was utilized consistently more than expected by chance during every month of each year (except April and May in 1994). Acid grassland was avoided
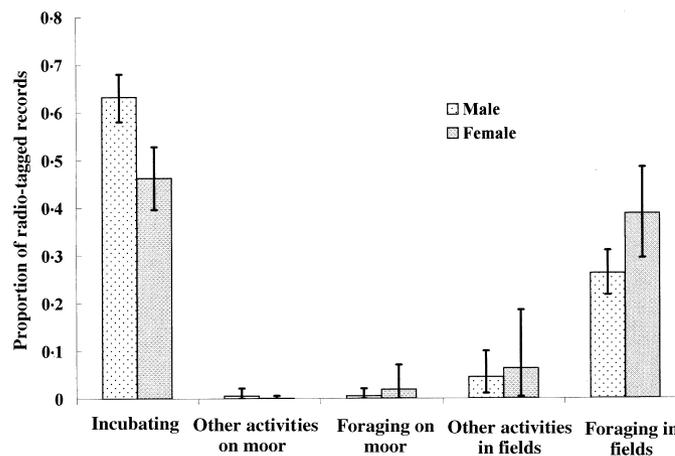
Fig. 1. Activity patterns of adult golden plover with nests. Actual means and back-transformed (arcsine) 95% confidence limits are presented.

Table 1. Vegetation structure and density of habitats

Habitat [National Vegetation Classification code]	Mean height ± SD (cm)	Mean density (no. cm blocks hidden) ± SD
(a) Chapel Fell		
Juncus effusus marsh [M6]	40·6 ± 11·9	24·6 ± 10·9
Juncus squarrosus–Festuca ovina grassland [U6]	3·1 ± 1·3	2·8 ± 1·3
Nardus stricta–Galium saxatile grassland [U5]	8·7 ± 2·4	4·3 ± 2·6
Deschampsia flexuosa grassland – *Vaccinium myrtilis* subcommunity [U2]	5·2 ± 1·9	5·0 ± 2·3
Eriophorum angustifolium pools [M3]	3·0 ± 1·6	0·5 ± 0·2
Carex marshes [M7]	4·3 ± 4·7	0·6 ± 0·8
Eriophorum vaginatum mire–subcommunity *Scirpus cespitosus* [M20]*	8·0 ± 2·2	4·4 ± 2·3
(b) Widdybank		
Eriophorum vaginatum mire [M20]	7·6 ± 2·3	5·0 ± 5·3
Eriophorum vaginatum mire – subcommunity *Calluna vulgaris* [M20]*	8·1 ± 0·7	4·3 ± 1·7
Calcareous grassland [CG9]	4·5 ± 1·0	2·0 ± 1·0
Recently burnt heather (< 2 years old) [H12]	6·2 ± 1·4	4·8 ± 2·3
Medium stands of heather (2–5 years old) [H12]	7·8 ± 0·5	6·5 ± 1·1
Old stands of heather (> 5 years old) [H12]	11·7 ± 2·1	11·4 ± 2·8
Nardus stricta grassland [U5]	8·3 ± 1·4	4·3 ± 1·8
Calluna vulgaris heath [H9]	6·9 ± 0·8	7·7 ± 1·6
Eriophorum heath [M20]	7·6 ± 1·2	6·8 ± 1·2
Calcareous marsh [M10]	2·1 ± 0·4	3·2 ± 1·5
Juncus effusus marsh [M6]	31·0 ± 11·3	21·6 ± 5·5

*Both habitats classified by the authors as distinct from *Eriophorum vaginatum* mire. Subcommunity *Scirpus cespitosus* was distinguished by wetter areas dominated by *Scirpus cespitosus* L. with few tussocks. Subcommunity *Calluna vulgaris* was distinguished by > 50% cover of *Calluna vulgaris* within sward (this community was a remnant of a former heather moorland that had been heavily grazed by sheep).

every year during June and April but patterns varied in May and July. Marshes were selected more than would be expected by chance in every month during 1993, but less than expected by chance in every month in 1992 and 1994. *Eriophorum vaginatum* mire subcommunity *Calluna vulgaris* was generally avoided in each year from May–July, although numbers were slightly higher than would be expected by chance in April in both years where data were available.

On Widdybank non-random use of habitats occurred throughout the breeding season (Table 2

Table 2. Summary table of counts of golden plover from transects on different habitats on Chapel Fell and Widdybank. Chi-square tests for departure from random use of habitats within each month are also shown (*non-random use of habitats: ** $P < 0.01$, *** $P < 0.001$). Proportion of available habitat shown in brackets after each habitat group (rounded to the nearest whole integer)

	April	May	June	July
Chapel Fell				
Acid grass [0·22]	18	24	55	16
Marshes [0·05]	3	6	26	4
Eriophorum vaginatum mire [0·48]	49	118	214	33
Eriophorum vaginatum mire–subcommunity *Calluna vulgaris* [0·26]	33	56	57	7
χ^2 values for testing against random use	2·996 ($n = 103$)	15·497 ($n = 204$)**	38·632 ($n = 352$)***	6·638 ($n = 60$)
Widdybank				
Limestone grassland [0·07]	76	52	87	38
Stands of heather (> 5 years old) [0·35]	0	3	0	2
Stands of heather (< 5 years old) [0·17]	24	54	41	9
Acid grass [0·09]	6	9	27	5
Calluna vulgaris heath [0·26]	1	10	62	19
Marshes and *Eriophorum vaginatum* mire [0·07]	12	22	62	20
χ^2 values for testing against random use	669·264 ($n = 119$)***	296·413 ($n = 150$)***	448·261 ($n = 279$)***	227·687 ($n = 93$)***

*M.J.
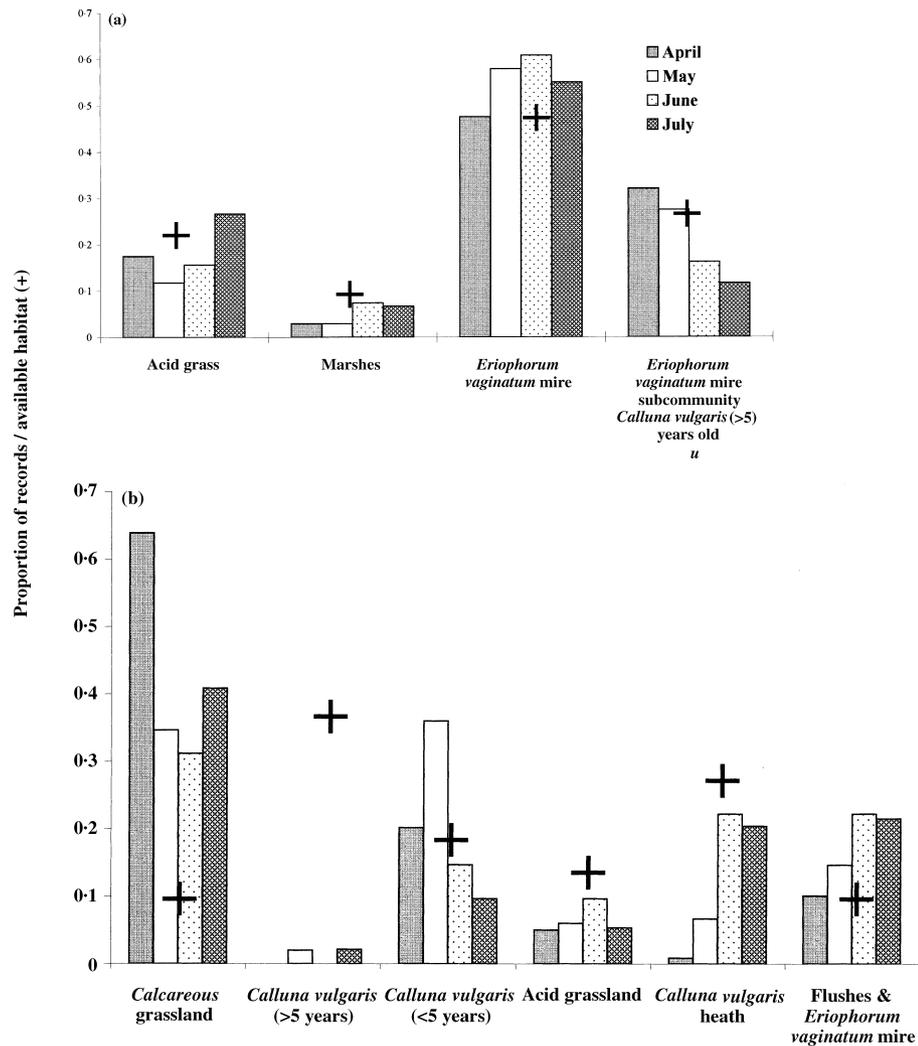Whittingham,
S.M. Percival &
A.F. Brown*

Fig. 2. (a) Habitat use by adult golden plover on Chapel Fell (1992–94) and (b) habitat use by adult golden plover on Widdybank (1992–94). Note the percentage area of habitat available indicated by '+'; *n*-values are given in Table 2.

and Fig. 2b). There was strong selection of calcareous grassland and flushes and *Eriophorum vaginatum* mire during every month of each year (except July 1994 when few data were collected) and a strong avoidance of mature areas of *Calluna vulgaris* (> 5 years of age since burning) during every month of each year. *Calluna vulgaris* heath was consistently used less than expected by chance during each month of every year, although it was utilized more strongly in June and July, particularly in 1992. Old stands of heather (> 5 years old) were taller and more dense than any other type of vegetation, with the exception of *Juncus effusus* L. marshes which comprised < 1% of the site (Table 1b). Birds did not avoid younger, shorter and less dense stands of *Calluna vulgaris* (burnt within the previous 5 years) as strongly as older stands.

SELECTION OF ENCLOSED FIELDS FOR FORAGING

Breeding radio-tagged golden plover were clearly not selecting fields at random (a mean of around two fields were selected out of 10 visits per individual) (Table 3). The birds were highly selective, regularly choosing only a small proportion of the fields available to them and flying over many others in order to reach them. All except three of the 17 fields used for feeding were used in both years (1994 and 1995). Seven of the fields were used by both sexes, six fields were used only by males and four fields only by females. During the brood period, only two of the eight tagged birds, both males, continued to forage in fields. Both foraged in the same fields

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*Time budgets and
foraging of golden
plover*

Table 3. Summary of field use by radio-tagged breeding golden plover from two sites. Note: a potential field was classed as any field that lay within a circle of a radius of the maximum distance flown from the nest on that study site to a field (3·13 km of any plover nest found on Chapel Fell or 3·68 km on Widdybank); ranges of distances flown from nest and moor edge were calculated using the mean distance flown by each individual to a field

	Chapel Fell	Widdybank	Total
Number of potential fields available	83	162	245
Number of study fields in adjacent valley	48	37	85
Number of fields used per individual (mean ± SE)	2·00 ± 0·12 (n = 12)	2·22 ± 0·40 (n = 9)	2·10 ± 0·18 (n = 21)
Number of records per individual (mean ± SE)	10·00 ± 2·01 (n = 12)	10·11 ± 2·58 (n = 9)	10·04 ± 1·55 (n = 21)
Range of distance of centre of field from nest in km (mean shown in brackets)	1·96–3·13 km (mean = 2·55 km)	1·15–3·68 km (mean = 2·05 km)	1·15–3·68 km (mean = 2·34 km)
Range of distance of field from edge of moorland block on which bird was nesting	0·43–1·65 km (mean = 0·83 km)	0·32–2·02 km (mean = 0·77 km)	0·32–2·02 km (mean = 0·80 km)

when they were incubating and when they had broods.

Three environmental predictors, the number of molehills, the distance of the field from the nearest road and the score for number of hummocks, had a significant effect on the probability of a field being used for foraging (Table 4a). No other predictors gave a significant increase in the likelihood ratio of the logistic regression model (Table 4a). Overall the model gave a highly significant fit to the data ($\chi^2 = 44\cdot3$, d.f. $= 3$, $P < 0\cdot0001$). The model correctly predicted field use in a minimum of 88% of cases. Univariate tests confirmed that all other predictors, except size of field, did not have a significant effect on field use. Golden plover were more likely to forage in larger fields ($\chi^2 = 8\cdot71$, d.f. $= 1$, $P < 0\cdot005$). Size of field was not significantly correlated with number of molehills (Spearman rank correlation, $r = 0\cdot12$, $P = 0\cdot29$) or number of hummocks (Spearman rank correlation, $r = 0\cdot11$, $P = 0\cdot27$). However, there was a significant positive relationship with distance from nearest road (Spearman rank correlation, $r = 0\cdot57$, $P < 0\cdot0001$). Therefore a second model was developed excluding the predictor 'distance from road'. The MAM for the second model included size of field along with number of molehills and field management (Table 4b) and gave a highly significant fit to the data ($\chi^2 = 46\cdot4$, d.f. $= 3$, $P < 0\cdot0001$). The findings of the first model were further supported by the classification table of observed and predicted values (Table 5). The second model correctly predicted field use in 87% of cases (with a 0·5 cut-off level), and as the stringency of cut-off values increased the model performed in a very similar way to the first model (a maximum of 3% difference in number of fields correctly predicted from all cut-off levels).

Discussion

ACTIVITY BUDGETS AND RELATIVE IMPORTANCE OF MOORLAND AND FARMLAND HABITATS

The main finding of this study is the relative importance to breeding adult golden plover of enclosed fields up to 4 km from the nest and up to 2 km from the moorland boundary. Clearly, the primary function of the moorland was for nesting and the fields were mainly used for foraging during the incubation phase. O'Connell *et al.* (1996) also found birds made substantial use of fields in their study areas in north-east Sutherland. The mean distance flown to fields in their study (2·69 km) was similar to our study but birds did occasionally range much further

Table 4. Logistic regression model predicting the probability that a field will be used for foraging by golden plover

Variable	Amount of deviance explained (χ^2)	Direction of relationship, +(positive), – (negative)	d.f.	Significance
(a) All predictors measured were entered into the model				
Molehill index	24·86	+	1	0·0001
Distance from nearest road	9·40	+	1	0·005
Number of hummocks	5·24	+	1	0·02
Vegetation height	0·09	–	1	0·90
Proportion of *Juncus* spp.	0·98	–	1	0·32
Size of field	1·2	+	1	0·27
Distance from moorland	3·32	–	1	0·07
Proportion of tussocks	0·51	–	1	0·47
Meadow or pasture	2·35	+	1	0·14
Slope	5·87	–	2	0·06
(b) Excluding the effect of distance from road				
Molehill index	35·76	+	1	0·0001
Size of field	10·43	+	1	0·0001
Meadow or pasture	4·68	–	1	0·03
Number of hummocks	2·9	+	1	0·09
Proportion of *Juncus* spp.	1·32	–	1	0·25
Vegetation height	2·55	–	1	0·11
Distance from moorland	0·48	–	1	0·49
Slope	2·07	–	2	0·35
Proportion of tussocks	0·18	–	1	0·67

(up to 10 km). During the chick-rearing phase moorland was used for foraging by both chicks and adults, while fields were used for foraging by some males at night. O'Connell *et al.* (1996) found 56% of off-duty radio-telemetry fixes were from birds in fields, of which 55% were assigned to feeding. However, during the post-hatching phase only 3% of fixes were from birds in fields. The increased use of fields shown in our study (74% of all off-duty fixes were to fields) compared with that in north-east Sutherland (O'Connell *et al.* 1996) may be due to lower food availability on our moorland study areas.

One likely explanation of why birds leave the moor in order to feed and roost when off-duty is that fields provide better foraging sites. Upland grasslands tend to be earthworm-rich relative to other upland habitats and therefore densities in enclosed fields enriched by the addition of organic fertilizer are likely to be far in excess of those on moorlands (Coulson 1988). Birds might also leave the moor to minimize the chance of attracting predators to the nest or to engage in social interactions with other individuals. The activity of a single male with a nest on Widdybank is instructive in these respects. Unusually amongst the territories studied, the area close to the territory contained a large amount of calcareous grassland (this habitat comprised only 7% of the Widdybank study area). Calcareous grassland is known to support high densities of earthworms relative to other moorland habitats (Coulson 1988). Whilst breeding, the bird was never

recorded away from the moor and, when off-duty, he fed predominantly on earthworms taken from the calcareous grassland near the nest. Perhaps relatively poor moorland sites for foraging may result in a heavier reliance of fields by breeding golden plover.

After the chicks hatched there was a marked switch by foraging adults from fields to moorland. Young need almost constant attention from their parents in the form of vigilance against predators, at least for the first 10 days after hatching (Byrkjedal 1985), and chicks in our study remained on the moor. Adults thus needed to forage on the moor. In addition, there is a sudden increase in prey availability on the moor when most chicks hatch (Whittingham 1996a), in the form of *Tipula* spp. These form a staple food item of chicks. Forty-four per cent of remains from faecal samples from eight broods were *Tipula* spp. after applying a correction formula for each group (Whittingham 1996a; Byrkjedal & Thompson 1998). They were also eaten extensively by adults (Whittingham 1996a). If the food resources on the moor were much less than those in fields then some adults might have moved their chicks off the moor and into enclosed fields. However, there were no records of any adults moving their broods to enclosed fields despite some broods being moved considerable distances (one brood moved over 1 km in 4 h) and one brood was even moved adjacent to a field boundary but continued to feed on the moorland (Whittingham 1996a). This may suggest that resources on the moorland, possi-

Table 5. Accuracy of the model for predicting field use by foraging breeding golden plover derived from minimum adequate model from Table 4a. Fields were classified as either used or not-used based on their predicted values from the equation generated from the binary logistic regression model $[-7.93 + (0.86 \times$ score for no. molehills) $+ (0.013 \times$ distance from nearest road) $+ (1.36 \times$ score for number of hummocks)]. Note: to use this formula each datum (x) must be back-transformed using the equation: $1/[1 + (1/\mathrm{EXP}x)]$. The cut-off levels for predicted values are shown in the top left corner of (a–e). If the derived probability of occurrence of a bird in a field was 0.58 and the observed value was 1, i.e. bird present in field, then it was classified in the part of (a) shown with (y). However, this field would be excluded from (b–e) because it fell outside the cut-off values for those parts

Observed	Predicted Unused	Used	Total number of fields	% correct in each class	Overall % correct
(a) 0–0·49 : 0·50–1					
Unused	64	4	85	94·1	88
Used	6	11 (y)		64·7	
(b) 0–0·39 : 0·60–1					
Unused	64	2	81	94·1	91
Used	5	10		64·7	
(c) 0–0·29 : 0·70–1					
Unused	63	1	72	98·4	94
Used	3	9		75	
(d) 0–0·19 : 0·8–1					
Unused	60	0	70	100	97
Used	2	8		80	
(e) 0–0·09 : 0·9–1					
Unused	50	0	59	100	97
Used	2	7		77·7	

bly including cover from predators, are favourable in comparison with enclosed fields during the summer after broods have hatched.

All golden plover nests were found on unenclosed moorland areas. Yet if fields offer such rich feeding then why do birds not nest there? Ratcliffe (1976) suggested that golden plover depended on camouflage to avoid nest predation. Unlike the closely related lapwing *Vanellus vanellus* L., it nests at comparatively low densities and therefore is not able to form flocks to mob potential nest predators. Predation rates of artificial lapwing nests (using black-headed gull *Larus ridibundus* L. eggs) in enclosed fields have been found to be very high: after 7 days, 36% of eggs were taken on intensified pastures compared with 100% of eggs taken on intensified pastures not used by breeding lapwing over the same time period (Baines 1990). In comparison, of 30 artificial golden plover nests (using quail *Coturnix coturnix* L. eggs) put out on three different moorland habitats (two favoured for nesting by golden plover and one avoided), only 13% of the eggs they contained were taken in the same time period (Whittingham 1996a). There are two plausible hypotheses that could explain this pattern. First, golden plover do not nest in fields because fields do not provide appropriate cover to conceal nests or incubating adults; and secondly, the density of nest predators may be much lower on moorland than farmland.

Our study provides the first evidence that breeding golden plover frequently feed at night, although both golden plover (Barnard & Thompson 1985) and pacific golden plover *Pluvialis fulva* L. (Rohweder & Baverstock 1996) have been recorded feeding at night during the non-breeding season. Golden plover have large eyes in relation to those of many other shorebirds and this is likely to be an adaptation for foraging at night (Dugan 1981 in McNeil, Drapeau & Goss-Custard 1992). The closely related grey plover *Pluvialis squatarola* L. has a retinal structure suited for nocturnal visual foraging (Rojas de Azuaje 1991; McNeil, Drapeau & Goss-Custard 1992) and it is likely that the golden plover has similar structural adaptations.

Differences between behaviour of males and females

In common with other studies (Byrkjedal 1985; Byrkjedal & Thompson 1998) we found males spent more time incubating and brood guarding than females. During the day lone mothers were often encountered at some distance from their brood whilst their mate guarded chicks. Overall our study suggests males take a greater role in caring for eggs and young than females, although we were unable to distinguish caring from other activities at night and females have been recorded brooding young at night (Whittingham, Percival & Brown 1999b). One

possible explanation for the difference in caring between the sexes could be that females are in poor condition after egg-laying (Byrkjedal 1985). There may be a cost for males associated with increased caring (and the consequent loss of time available for foraging) because male body condition deteriorates as the breeding season progresses although that of the females does not (Byrkjedal & Thompson 1998). This slight imbalance between caring efforts of the sexes may still benefit the male as at least some mate with the same female in consecutive years (M. J. Whittingham, personal observation).

We found that males incubated during the day and females at night, and this has been shown in other studies (Parr 1980; O'Connell *et al.* 1996). Contra to this, other workers have found males incubating during the night or off-duty during the day (Nethersole-Thompson & Nethersole-Thompson 1961; Holt & Whitfield 1996). The reasons why males have been consistently reported incubating at night in some areas and by day in others is not clear.

USE OF MOORLAND

Data from radio-tagged birds indicated that moorland is crucial for foraging by adults with broods. We recorded non-random use of habitats on both moorland study sites using census data. However, there was some pseudoreplication of data in the chi-square analysis caused by the summation of data from all individuals. This was because not all birds on study sites were colour marked, and it was not always possible to see colour rings on those that were from observations on transects. We minimized the effects of pseudoreplication by analysing our data by month, the same bird potentially being surveyed up to a maximum of four times per month.

On Chapel Fell habitats were used by birds approximately in the proportion available to them. There was consistent marginal selection of only one habitat: *Eriophorum vaginatum* mire. This habitat is known to result from heavy grazing (Thompson, MacDonald & Hudson 1995). Golden plover densities on Chapel Fell ($3.7–4.3 \, \mathrm{km}^{-2}$) were similar to those on Widdybank ($3.9–4.3 \, \mathrm{km}^{-2}$), where numbers have been stable for over 20 years (I. Finlay, personal communication). Therefore *Eriophorum vaginatum* mire resulting from heavy grazing appears capable of supporting at least equal densities of golden plover as heather-dominated grouse moorland. Widdybank was perhaps better suited to golden plover than other sites lacking calcareous grassland, suggesting that, in our study at least, *Eriophorum vaginatum*-dominated moorland is a good quality habitat for golden plover. Density is not necessarily an indicator of habitat quality but no significant differences were found between nest survival rates or numbers of fledged young per pair

between the two sites, suggesting they were of similar benefit for breeding golden plover (Whittingham 1996a). However, this may only be the case when enclosed farmland is nearby (Widdybank was used more for foraging than Chapel Fell).

On Widdybank, habitats were selected non-randomly across the breeding season. Calcareous grassland was the most strongly favoured habitat throughout each month of every year (at least four times the numbers of plover expected were observed). Calcareous grassland is somewhat atypical of many moorland areas in Britain and it is known to support very high populations of golden plover (Ratcliffe 1976). Its selection is not surprising given the high densities of earthworms it supports. Heather (> 5 years old) was almost entirely avoided, with only one-tenth of the records expected. Rank heather is tall and dense and may impede movement and limit foraging. More use was made of younger stands of heather than older stands. The records of adults on recent heather burns (< 5 years old) in April and May is probably a consequence of the high density of nests found in these areas (Whittingham 1996a). The relatively few records on recent burns in June and July could be a consequence of avoidance of these areas by broods (Whittingham 1996a). *Eriophorum vaginatum* mire and marshes were selected throughout the season but they were used more in June and July, when they were favoured by chicks (Whittingham 1996a).

SELECTION OF ENCLOSED FIELDS FOR FORAGING

Golden plover selected specific types of fields for foraging, where they fed mainly on earthworms. There is a strong positive correlation between number of molehills and earthworms (Micol, Doncaster & Mackinlay 1994; Edwards, Crawley & Heard 1999). The number of molehills was the most important variable in predicting field use by foraging golden plover. This is consistent with our previous argument that fields are selected on the basis of food availability. One positive correlate of earthworm abundance, not measured by this study, is age of field (Barnard & Thompson 1985; Edwards & Lofty 1993; Byrkjedal & Thompson 1998). The decline in older fields has been suggested as a contributory factor in golden plover population declines (Byrkjedal & Thompson 1998).

The effects of distance from roads and size of fields were confounded in our study. Separate models were developed that excluded each predictor in turn which showed that they were interchangeable in the final model. Therefore we cannot be certain what effect each had on field choice by plover. Other studies have suggested field size is an important variable in field choice (O'Connell *et al.* 1996). The results shown by O'Connell *et al.* (1996) were

backed up by field observations showing that birds avoided the edges of fields. Although we did not study selection within fields, casual observations indicated that birds mainly used areas away from field edges (although edges were utilized for feeding particularly when the flock size was greater). Therefore we suspect that field choice may be the causal factor.

Two other predictors, an increase in the number of small hills in a field and grazed fields (compared with hay meadows), also increased the probability of field use. However, evidence for both was fairly weak and was not consistent between the two models (Table 4).

Both logistic regression models provided a highly significant fit to the data and successfully predicted field use by golden plover in at least 88% and 87% of cases, respectively. However, the models were more accurate when predicting unused fields, suggesting that some other criteria may be important in conjunction with those already defined. Given the site fidelity to particular fields both within and between years by individuals and populations from particular breeding areas (O'Connell *et al.* 1996; Whittingham 1996a), birds may remain site-faithful despite changes in food resources or physical characteristics of fields. These findings need to be tested in other areas and on a wider scale to identify the relative importance of different types of upland farmland for golden plover in the breeding season. Study of changes in the characteristics of fields in areas of population decline may prove valuable in explaining those declines.

IMPLICATIONS FOR CONSERVATION MANAGEMENT

Our findings suggest that the ecological requirements of golden plover during the breeding season are more complex than hitherto appreciated. Not only do birds associate strongly with unenclosed moorlands for nesting and chick rearing, but also adults make frequent use of intensified enclosed fields, particularly during the incubation period. Management of both unenclosed moorland and enclosed fields may be crucial to retaining populations of breeding golden plover, at least in this part of the British Isles. Information is presented elsewhere on prescriptions for moorland management that might favour breeding birds (Backshall 1988) and we concur with these. However, our study suggests a number of specific management prescriptions the application of which might further safeguard golden plover populations in the uplands:

1. Where action is being taken to protect populations of breeding golden plover, the groups of fields regularly selected for feeding by the target birds should be identified (e.g. those with high earthworm populations as indicated by large numbers of mole-

hills) and afforded specific protection. Environmental land management schemes (e.g. wildlife enhancement scheme, environmentally sensitive area) should seek to retain such fields within the farming landscape.

2. Where heather becomes rank (on flat to gently sloping ground) an appropriate burning or grazing regime should be adopted to prevent it becoming too dense and long.

3. Areas of calcareous grassland on, or near, moorland should be retained.

Both management for red grouse and grazing by sheep (at the levels recorded during this study) appear to be beneficial or neutral to golden plover in our study areas. Management for red grouse provides younger patches of heather that are avoided less by golden plover than the rank heather which they replace. Grazing of moorland, allowing encroachment by *Eriophorum vaginatum* mire, with some *Calluna vulgaris* persistent within the sward, still enables healthy populations of golden plover to persist. However, this may only be so when enclosed fields suitable for feeding are also present within a few kilometres of the moor. It is worth noting that lower levels of sheep stocking are necessary to cause heather to become highly fragmented, within mixed grass/heather areas, on sloping as opposed to flat ground (Hester *et al.* 1999). This is linked to our second management suggestion above.

Our study has enhanced our understanding of management regimes within the English upland landscape that provide suitable habitats for breeding golden plover. Presently it is unclear how to provide guidelines for increasing earthworm numbers (e.g. increasing the input of organic fertilizer, installing underground drainage and sward re-seeding) without causing negative impacts on other breeding waders (Baines 1988). Planning at the whole farm level may enable suitable habitats to persist for both needs. Future research may benefit from exploring field selection at different times of year (e.g. pre- and post-breeding) and by investigating past management histories of fields (McCracken & Bignal 1998).

References

Backshall, J. (1988) *The Upland Management Handbook.* English Nature, Peterborough, UK.

Baines, D. (1988) The effects of improvement of upland marginal grasslands on the distribution and density of breeding wading birds (*Charadriiformes*) in northern England. *Biological Conservation*, **45**, 221–236.

Baines, D. (1990) The roles of predation, food and agricultural practice in determining the breeding success of the lapwing *Vanellus vanellus* on upland grasslands. *Journal of Animal Ecology*, **59**, 915–929.

Barnard, C. & Thompson, D.B.A. (1985) *Gulls and Plovers.* Croom-Helm, London, UK.

Bengtson, S.A. & Rundgren, S. (1978) Selective predation on lumbricids by golden plover *Pluvialis apricaria*. *Oikos*, **31**, 164–168.

Beyer, D.E. Jr & Haufler, J.B. (1994) Diurnal versus 24-hour sampling of habitat use. *Journal of Wildlife Management*, **58**, 178–180.

Brown, A.F. & Stillman, R.A. (1993) Bird–habitat associations in the Eastern Highlands of Scotland. *Journal of Applied Ecology*, **30**, 31–42.

Byrkjedal, I. (1985) Time–activity budget for breeding greater golden plovers *Pluvialis apricaria* in Norwegian mountains. *Wilson Bulletin*, **97**, 486–501.

Byrkjedal, I. (1989) Habitat use and resource overlap by breeding golden plovers and dotterels (*Pluvialis apricaria, Charadrius morinellus*). *Journal of Ornithology*, **130**, 197–206.

Byrkjedal, I. & Thompson, D.B.A. (1998) *Tundra Plovers: The Eurasian, Pacific and American Golden Plovers and Grey Plover.* T & A.D. Poyser, London, UK.

Collett, D. (1991) *Modelling Binary Data.* Chapman & Hall, London, UK.

Coulson, J.C. (1988) The structure and importance of invertebrate communities on peatlands and moorlands, and effects of environmental and management changes. *Ecological Change in the Uplands* (eds M.B. Usher & D.B.A. Thompson), pp. 365–380. Blackwell Scientific Publications, Oxford, UK.

Crawley, M.J. (1993) *Methods in Ecology: GLIM for Ecologists.* Blackwell Scientific Publications, Oxford, UK.

Dugan, P.J. (1981) The importance of nocturnal foraging in shorebirds: a consequence of increased invertebrate prey activity. *Feeding and Survival Strategies of Estuarine Organisms* (eds N.V. Jones & W.J. Wolff), pp. 251–260. Plenum Press, New York, NY.

Edwards, C.A. & Lofty, J.R. (1993) *Biology of Earthworms.* Chapman & Hall, London, UK.

Edwards, G.R., Crawley, M.J. & Heard, M.S. (1999) Factors influencing molehill distribution in grassland: implications for controlling the damage caused by molehills. *Journal of Applied Ecology*, **36**, 434–442.

Gibbons, D.W., Reid, J.B. & Chapman, R.A. (1993) *The New Atlas of Breeding Birds in Britain and Ireland: 1988–1991.* T. & A.D. Poyser, London, UK.

Goss-Custard, J.D. (1984) Intake rates and food supply in migrating and wintering shorebirds. *Behaviour of Marine Animals, Vol. 6* (eds J. Burger & B. Olla), pp. 233–270. Plenum Press, New York, NY.

Hagemeijer, W.J.M. & Blair, M.J. (1997) *The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance.* T. & A.D. Poyser, London, UK.

Hancock, M. & Avery, M. (1998) Changes in breeding bird populations in north-east Sutherland and Caithness between 1988 and 1995. *Scottish Birds*, **19**, 195–205.

Haworth, P.F. & Thompson, D.B.A. (1990) Factors associated with the breeding distribution of upland birds in the South Pennines, England. *Journal of Applied Ecology*, **27**, 562–577.

Hester, A.J., Gordon, I.J., Baillie, G.J. & Tappin, E. (1999) Foraging behaviour of sheep and red deer within natural heather/grass mosaics. *Journal of Applied Ecology*, **36**, 133–146.

Holt, S. & Whitfield, D.P. (1996) *Montane Ecology Project Site Report.* Research and Advisory Services Directorate Reports. Scottish Natural Heritage, Edinburgh, UK.

Hudson, P.J. (1992) *Grouse in Space and Time.* Game Conservancy Trust, Fordingbridge, UK.

James, F.C. & McCulloch, C.E. (1990) Multivariate analysis in ecology and systematics: panacea or Pandora's box? *Annual Revue of Ecology and Systematics*, **21**, 129–166.

Kenward, R.E. (1987) *Wildlife Radio Tagging: Equipment, Field Techniques and Data Analysis.* Academic Press Limited, London, UK.

McCracken, D.I. & Bignal, E.M. (1998) Applying the results of ecological studies to land-use policies and practices. *Journal of Applied Ecology*, **35**, 961–967.

Macdonald, D.W. & Barrett, P. (1993) *Mammals of Britain and Europe.* HarperCollins, London, UK.

McNeil, R., Drapeau, P. & Goss-Custard, J.D. (1992) The occurrence and adaptive significance of nocturnal habits in waterfowl. *Biological Review*, **67**, 381–419.

Micol, T., Doncaster, C.P. & Mackinlay, L.A. (1994) Correlates of local variation in the abundance of hedgehogs *Erinaceus europaeus*. *Journal of Animal Ecology*, **63**, 851–860.

Mouritsen, K.N. (1994) Day and night feeding in dunlins *Calidris alpina*: choice of habitat, foraging technique and prey. *Journal of Avian Biology*, **25**, 55–62.

NAG (1993) *General Linear Interactive Modelling.* The Numberical Algorithms Group Ltd, Oxford, UK.

Nethersole-Thompson, D. & Nethersole-Thompson, C. (1961) The breeding behaviour of the British golden plover. *The Birds of the British Isles, Vol. 10* (ed. D.A. Bannerman), pp. 206–214. Oliver & Boyd, Edinburgh, UK.

O'Connell, M.J., Thomas, C.J., Twiss, S.D., Downie, I.S., Evans, P.R. & Whitfield, D.P. (1996) *Functional Ecology of Peatland Animals in the Flow Country of Northern Scotland. I. Habitat Requirements of Breeding Waders (Charadrii).* Research and Advisory Services Directorate Report. Scottish Natural Heritage, Edinburgh, UK.

Parr, R. (1980) Population study of golden plover *Pluvialis apricaria*, using marked birds. *Ornis Scandinavica*, **11**, 179–189.

Parr, R. (1992) The decline to extinction of a population of golden plover in north-east Scotland. *Ornis Scandinavica*, **11**, 179–189.

Percival, S.M. & Smith, C. (1992) *Habitat Requirements of Golden Plover: A Pilot Study.* English Nature Research Report No. 1. English Nature, Peterborough, UK.

Ratcliffe, D.A. (1976) Observations on the breeding of the golden plover in Great Britain. *Bird Study*, **23**, 63–116.

Rodwell, J. (1991a) *British Plant Communities. Vol. 2. Mires and Heaths.* Cambridge University Press, Cambridge, UK.

Rodwell, J. (1991b) *British Plant Communities. Vol. 3. Grasslands and Montane Communities.* Cambridge University Press, Cambridge, UK.

Rohweder, D.A. & Baverstock, P.R. (1996) Preliminary investigation of nocturnal habitat use by migratory waders (Order Charadriiformes) in northern New South Wales. *Wildlife Research*, **23**, 169–184.

Rojas de Azuaje, L.M. (1991) Proporcion de cones y bastones en la retina de tres especies de aves limicolas y la relación entre visión y estrategis alimenticia. MSc Thesis. Universidad de Oriente, Cumaná, Venezuela.

Siegel, S. & Castellan, N.J. (1988) *Nonparametric Statistics for the Behavioural Sciences*. McGraw-Hill, Singapore.

Staine, K.J. & Burger, J. (1994) Nocturnal foraging behaviour of breeding piping plovers *Charadrius melodus* in New Jersey. *Auk*, **111**, 579–587.

Stillman, R.A. & Brown, A.F. (1994) Population sizes and habitat associations of upland breeding birds in the South Pennines, England. *Biological Conservation*, **69**, 307–314.

Stone, B.H., Sears, J., Cranswick, P.A., Gregory, R.D., Gibbons, D.W., Rehfisch, M.M., Aebischer, N.J. & Reid, J.B. (1997) Population estimates of birds in Britain and in the United Kingdom. *British Birds*, **90**, 1–22.

Thompson, D.B.A., MacDonald, A.J. & Hudson, P.J. (1995) Upland moors and heaths. *Managing Habitats for Conservation* (eds W.J. Sutherland & D.A. Hill), pp. 84–99. Cambridge University Press, Cambridge, UK.

Usher, M.B. & Thompson, D.B.A. (1993) Variation in the upland heathlands of Great Britain: conservation importance. *Biological Conservation*, **66**, 69–81.

Whittingham, M.J. (1996a) *Habitat requirements of golden plover* Pluvialis apricaria. PhD Thesis. University of Sunderland, Sunderland, UK.

Whittingham, M.J. (1996b) The use of radio telemetry to measure the feeding behaviour of breeding European golden plovers *Pluvialis apricaria. Journal of Field Ornithology*, **67**, 463–470.

Whittingham, M.J., Percival, S.M. & Brown, A.F. (1999a) Evaluation of radio telemetry methods in measuring habitat choice by young golden plover *Pluvialis apricaria. Bird Study*, **46**, 363–368.

Whittingham, M.J., Percival, S.M. & Brown, A.F. (1999b) Notes on night-time activity of golden plover *Pluvialis apricaria* chicks in the north Pennines. *Wader Study Group Bulletin*, **90**, 56–58.

Yalden, D.W. & Yalden, P.E. (1989) The sensitivity of breeding golden plovers *Pluvialis apricaria* to human intruders. *Bird Study*, **36**, 49–55.