

Habitat selection by golden plover *Pluvialis apricaria* chicks

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Abstract

Despite the listing of golden plover *Pluvialis apricaria* on Annex 1 of the European Directive on the Conservation of Wild Birds there is virtually no information on the habitat requirements or diet of their chicks. We used radio telemetry to investigate habitat selection of 22 broods on two upland study sites in northern England. Broods (< 16 days old) avoided old or extensive stands of heather *Calluna vulgaris* but selected small patches of heather mixed with grass. They also selected marshes (mainly soft rush *Juncus effusus*), grassland and *Eriophorum vaginatum* mire. Habitat selection broadly fitted the distribution of their favoured prey (*Tipula* spp. and beetles). We suspect food availability, vegetation structure and cover from predators may partly explain habitat preferences. We suggest moorland could be managed for golden plover broods by managing stocking densities to create patchworks of grass and heather and a heterogeneous mature heather sward and by blocking drainage ditches to create areas of soft rush.

Habitat-Selektion von Goldregenpfeifer-Küken (*Pluvialis apricaria*)

Trotz der Auflistung des Goldregenpfeifers (*Pluvialis apricaria*) in Anhang 1 der „European Directive of the Conservation of Wild Birds“ gibt es kaum Informationen über die Habitatansprüche und die Nahrung der Küken. Wir nutzten die Radio-Telemetrie für die Analyse der Habitat-Selektion von 22 Brutten auf zwei Hochland-Untersuchungsgebieten in Nord-England. Die Brutten (< 16 Tage alt) vermieden alte oder große Heideflächen (*Calluna vulgaris*), selektierten aber kleine Heide-Flecken, die mit Gras gemischt waren. Sie selektierten auch Sümpfe (hauptsächlich mit Binsen, *Juncus effusus*), Grasland und *Eriophorum vaginatum* Morast. Die Habitat-Selektion passte grob zur Verbreitung der bevorzugten Beute (*Tipula* spp und Käfer). Wir vermuten, dass Nahrungsverfügbarkeit, Vegetationsstruktur und Schutz vor Prädatoren zum Teil die Habitat-Präferenzen erklären können. Wir schlagen vor, Moore für die Brut des Goldregenpfeifers zu managen, indem die Boden-deckung gemanagt wird, um Flecken von Gras und Heide sowie einen heterogenen, reifen Heidebestand zu schaffen und die Drainagegräben zu blockieren, um Binsen-Areale zu schaffen.

Key words: food abundance – food availability – golden plover – habitat selection – moorland management – radio telemetry – upland conservation

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Introduction

The habitat requirements of chicks are poorly understood for all of the *Pluvialis* plovers (Johnson & Connors 1996, Byrkjedal & Thompson 1998). Improved knowledge of this phase in the life cycle seems especially important for the golden plover *Pluvialis aprinaria* since this species is listed in Annex 1 of European Union Directive 79/409/EU on the Conservation of Wild Birds and thus requiring special conservation action by European Union member states. Britain supports around 25% of the EU population, and breeding birds are found on upland heaths and moors, upland grasslands and bogs (Hagemeijer & Blair 1997, Byrkjedal & Thompson 1998). Golden plovers breed throughout Britain's uplands but are declining in both range and numbers (Parr 1992, Gibbons et al. 1993, Stone et al. 1997, Hancock & Avery 1998).

The populations of waders, and indeed many other upland birds, in Britain are monitored far less frequently than lowland bird species (e.g. Marchant et al. 1990). Population centres for British waders are often remote from the centres of human populations. To assess our wealth of waders and other upland birds we rely on periodic surveys (e.g. Haworth & Thompson 1990, Brown & Stillman 1993, Stillman & Brown 1994). Studies of lowland bird populations (e.g. farmland birds) have been able to compare population trends with changes in land-use or predators to indicate key parts of the life cycle which may be limiting for British populations (e.g. Thompson et al. 1998, Siriwardena et al. 1999). Determining the key parts of the life cycle which may be limiting populations of upland birds is less easy. There are a number of studies of habitat selection by adults on moorlands (e.g. Parr 1980, Byrkjedal 1985, 1989, O'Connell et al. 1996, Pearce-Higgins 1999), some of which suggest management prescriptions (Whittingham et al. 2000) which may enhance survival or the conditions of adults. In addition, other studies have focussed on enclosed fields where breeding adults often, though not always, feed (O'Connell et al. 1996, Byrkjedal & Thompson 1998, Whittingham et al. 2000). Chick survival may prove to be the key phase where golden plover populations are limited, but we have little information on which to suggest management action (Parr 1980). The best way to safeguard golden plover populations is through providing suitable habitats, among other measures, for both adults and chicks. Our study quantifies habitat selection by golden plover chicks on two study sites in northern England using radio telemetry.

The British uplands are most frequently used for grazing by sheep or the shooting of red grouse *Lagopus lagopus*. Sheep numbers generally increased in

many upland areas during the latter half of the 20th century, with notable increases between the mid-1970s and late 1980s (Anderson & Yalden 1981, Fuller 1996, Fuller & Gough 1999). Sheep grazing is known to reduce heather *Calluna vulgaris* cover and promote the growth of grass (Anderson & Yalden 1981, Thompson et al. 1995a). It has been argued that the extent of heather moorland, and the area managed for grouse, in particular, should be increased to benefit both wildlife and local economies (Hudson 1992). Indeed, the UK Biodiversity Group (1999) seeks to re-create 5000 hectares of upland heath by 2005 and to restore heather cover to a further 50-100 000 hectares of degraded heathland by 2010. However, it is unclear how changes in grazing pressure might affect upland birds. This study (see also Whittingham et al. 2000), compares the use of two contrasting sites by golden plover, one of which is dominated by grasses (probably due to replacement of heather by grass following heavy sheep grazing) and the other dominated by heather and managed principally for red grouse.

As in most waders, golden plover chicks are precocial and feed for themselves within a short time after hatching. It seems likely that food availability within habitats close to the nest may be important for precocial species where adults guide their young from the nest to suitable feeding areas, though there are exceptions [e.g. Greenshanks *Tringa nebularia* which lead their young several kilometres from the nest (Cramp & Simmonds 1983)]. In addition to food availability, habitats should also provide cover from predators and be accessible to chicks (Grant et al. 1992). There have been few studies of foods available to golden plover chicks (Yalden 1991, Pearce-Higgins 1999). We quantified the diet of golden plover chicks and compared the distribution of favoured prey across habitats.

This study had three main aims: first, to describe habitat selection of golden plover chicks on two contrasting study sites; second, to describe the diet of the chicks; and third, to relate habitat selection to food availability and habitat structure. We also compare the survival rates and home range sizes of chicks on the two study sites. We conclude by discussing how uplands could be managed to benefit golden plover broods.

Materials and methods

Study sites

Work was conducted from April to July from 1992 to 1995 on two adjacent moorland areas in the northern Pennines of County Durham, UK. Widdybank Fell, part of Teesdale National Nature Reserve (national

grid reference NY8230), is actively managed for red grouse and comprised a complex mosaic of different age stands of heather and other habitats. It covers an area of 5.12 km² with a stocking density of 0.87 ewes ha⁻¹. In contrast, Chapel Fell (national grid reference NY8535) was formerly managed for red grouse and dominated by heather, but high levels of sheep grazing in the past caused heather to be replaced by narrow-leaved cotton grass *Eriophorum vaginatum*, which is now the dominant vegetation. It covers an area of 3.71 km² and had similar sheep densities (0.98 ewes ha⁻¹) to Widdybank Fell during the study. Habitat maps of the study sites are presented elsewhere (Whittingham 1999a).

Radio telemetry

Habitat use by golden plover chicks less than 16 days old can be reliably determined with radio telemetry, the chicks tending to freeze or move only short distances (90% of cases < 4 m, n = 20 broods) when the radio tracker approached (Whittingham et al. 1999a). In a validation exercise on only two occasions (out of 20) would a habitat code have been assigned which did not reflect the habitat in which the chick was originally feeding before the radio-tracker approached (Whittingham et al. 1999a). Therefore we were confident that the habitat recorded when a chick was located was very close to where it had been feeding. Older chicks tend to run from the radio-tracker, or are lured away by the adults, and thus bias habitat recording. Also, large sample sizes are difficult to obtain for older chicks because most chicks are ringed and radio-tagged in the nest but radios subsequently detach or fail, and some individuals die. Therefore, we restricted our investigation to the first 16 days of life, although the fledging period lasts from 25–33 days (Cramp & Simmons 1983).

We used 0.8 g SS-2 button cell transmitters (supplied by Biotrack, Wareham, Dorset) in 1992 and 1993 and 0.9 g BD-2 transmitters (supplied by Holo-hil systems, Ontario, Canada) in 1994 and 1995. Transmitters always weighed 4% or less of the body weight. There were no significant negative effects on survival when radio-tagged chicks were compared with untagged ones (Whittingham et al. 1999a). Attachment techniques are described by Whittingham et al. (1999a). A transmitter was attached usually to one chick in each brood (2 chicks in 8 broods), though data were used from only one tagged chick per brood, selected at random. Therefore the sampling unit was one chick per brood. Generally, transmitters were attached to chicks still in the nest, usually within twenty-four hours of hatching, though some radios were attached to chicks caught by chance away from the

nest. The whole of each study site was searched for nests and for chicks.

Re-location of radio-tagged chicks was aided by locating colour-ringed parents. Radio tagging adults to locate broods was not a viable option because chicks were very hard to find without tags (they are highly cryptic and bury themselves in vegetation) and because adults only indicate the approximate position of the brood (Whittingham et al. 1999a) which was not sufficient to determine habitat selection on the complex mosaic of habitats on the study sites. Searching was limited to one hour each day to minimise disturbance to family groups. To avoid treading on chicks that were buried deep in vegetation, their position was determined by signal strength and triangulation (Kenward 1987). Dense vegetation and uneven ground decreased range and accuracy of radio signal strength. For most tagged chicks only one record was taken from each chick on any one day, but in 1992 and 1995 two records were sometimes taken with 12 hours between records. Each re-location was recorded on vegetation maps. Areas that were obviously not important to the birds, including reservoirs, roads, quarries and cliffs, were excluded when calculating the composition of home ranges. To test for robust patterns of habitat selection two types of home range were plotted: (1) Minimum Convex Polygons (MCPs) were created by joining all outer radio locations with a straight line (White & Garrot 1990). The areas of different habitats covered by the MCPs for the 22 broods are shown in Appendix 2. (2) Potential home ranges were calculated by drawing a circle of radius r around the nest site (r = the greatest distance that each radio tagged chick moved from its own nest). Sometimes the location of the nest site was unknown because chicks were captured after they had left the nest; in such cases the place of capture was used as a surrogate for nest site. The former measure indicated actual areas in which broods were located and the latter showed potential areas that were available to chicks.

Although our sample sizes were relatively small (see Tabs. 1 and 2), it would be difficult to collect more records per day from radio-tagged chicks without sustained disruption and displacement of the brood. Due to the complex nature of habitats and topography on our study sites, neither a hide (Parr 1980, Whittingham et al. 1999a) nor triangulation (Kenward 1987) were viable options to improve sample sizes. Therefore, we collected only one record from each brood on most days (although two records were taken in 1995, one in early morning and one in the evening). Overall, we feel the data were sufficient to illustrate the major patterns of habitat selection. Finer resolution will require more or larger study sites or much higher densities of golden plover.

Table 1. Number of radio relocations of 11 golden plover broods in each of five habitat types on Widdybank Fell compared with the expected number of relocations under a null model based on MCP home ranges (calculated for each brood separately).

Habitat	Number of relocations	Expected no. of relocations	No. broods with habitat in range
Grassland (calcareous and acid)	38 [Calcareous grass 8 records, acid grass 30]	25.7 [Calcareous grass 13 records, acid grass 12.7]	11
Marshes	12	8.9	9
<i>Eriophorum vaginatum</i> mire	19	14.7	6
Heather (including all age stands and <i>Calluna vulgaris</i> heath)	5	45	10
Heather mosaic	42	21.7	10

Table 2. Number of radio relocations of 11 golden plover broods in each of four habitat types on Chapel Fell compared with the expected number of relocations under a null model based on MCP home ranges.

Habitat	Number of relocations	Expected no. of relocations	No. broods with habitat in range
Acid grassland	31	29.4	10
Marshes	25	11.9	9
<i>Eriophorum vaginatum</i> mire	44	52.1	11
<i>Eriophorum vaginatum</i> mire subcommunity <i>Calluna vulgaris</i>	11	17.5	5

Habitat definitions

Although we were initially interested in comparing brood use between subtly different habitat types, insufficient data were collected on tagged broods to allow this. Consequently, the habitat classes used in habitat selection models sometimes comprised groups of habitats with similar National Vegetation Classification (NVC) codes (Rodwell 1991a & 1991b). Grouping habitats served two purposes. First, the proportion of individual habitat groups within home ranges increased. Second, most broods had each of the grouped habitat classes available to them within their home ranges. The habitat classes on Widdybank Fell [with their NVC codes in square brackets] were as follows: **grassland** (*Nardus stricta* [U5] and calcareous grass [CG9]), ***Eriophorum vaginatum* mire** [M20], **marsh** (calcareous marsh [M10] and *Juncus effusus* flush [M6]) and four types of **heather** dominated habitats (*Calluna vulgaris* heath [H9], age stands of < 2 years, 2–5 years and > 5 years [all H12]). In addition,

we also defined **heather mosaics** as any vegetation stand consisting of heather within 10 m of a boundary with grassland or marsh. The habitats on Chapel Fell were as follows: three types of **acid grassland** (*Nardus stricta* [U5], *Deschampsia flexuosa* [U2] and *Festuca ovina/Juncus squarrosus* [U6]), two types of **marsh** (*Juncus effusus* [M6] and *Eriophorum vaginatum* mire subcommunity *Scirpus cespitosus* [M20]), ***Eriophorum vaginatum* mire** [M20] and ***Eriophorum vaginatum* mire subcommunity *Calluna vulgaris*** [M20]. *Eriophorum vaginatum* mire subcommunity *Calluna vulgaris* was distinguished from other M20 habitats by > 50% cover of *Calluna vulgaris* within sward (this community was a remnant of a former heather moorland which had been heavily grazed by sheep). *Eriophorum vaginatum* mire subcommunity *Scirpus cespitosus* was distinguished from other M20 habitats by wetter areas dominated by *Scirpus cespitosus* with few tussocks.

Food availability

We collected 27 faecal samples from eight broods (five on Widdybank Fell and three on Chapel Fell) while handling birds during ringing and radio-tagging work (therefore we treated brood as the level of replication). Different food items tend to be digested differentially and may be under or over-represented in stomach contents and faecal samples. We were able to use conversion factors, as published for the orders found in our study (see Green 1984, Galbraith 1989), to correct for these differences. In addition, we used a conversion rate for eggs of *Tipula* spp. which were commonly found in our samples. These eggs were probably consumed when gravid adult female Tipulidae were captured by chicks. We sampled gravid female *Tipula* spp. and found the average number of eggs contained within a female to be 79 (\pm SE 22, $n = 24$). This is likely to be an underestimate of the true numbers found in gravid females (at least pre-laying) as the numbers of eggs declines rapidly after the first few eggs are laid (Coulson 1962). Coulson (1962) found that before laying female *Tipula subnodicornis* contained a mean of 240 eggs. This species is known to be present in large numbers of our study sites and nearby (Coulson 1962; pers obs), and it therefore seems likely that our method will overestimate the numbers of gravid females eaten.

Faecal analysis indicated that coleopterans (beetles) and *Tipula* spp. together constituted nearly all (99%) of the diet of chicks as estimated from the eight broods (see results). Therefore we concentrated on these two orders to assess food availability for chicks. We used pitfall traps to sample beetles. Pitfall traps were preferred to other methods (e.g. blow vacuum

sampling, Whittingham 1996) because of a bias towards active invertebrates, such as beetles, and because they sample at night when chicks (over c.1 week old) are known to be active (Whittingham et al. 1999b). On Chapel Fell (1994) and on Widdybank Fell (1995), 10 beakers (mouth c.6 cm in diameter and a depth of c.10 cm) were placed, with their tops flush with the ground, in a line 5 m apart, in each of the habitat types. To prevent pitfalls being washed out by rain, each one was covered with a tile (15 cm by 15 cm) which was elevated 5 cm over the lip of the trap using small sticks. Pitfall contents were collected every 30 days. We sampled each habitat (as listed above) on each study site, except habitat mosaics on Widdybank Fell and *Eriophorum vaginatum* mire subcommunity *Scirpus cespitosus* on Chapel Fell which was so wet that pitfalls often flooded (this habitat was rarely used by chicks). Sampling began in mid-May and ended in mid-July because all records from tagged broods were made during this period and most plover broods ceased to use the moorland after this time. Pitfall catches were assessed in two ways: with absolute numbers caught and biomass. To calculate biomass individual beetles were weighed separately. Individuals were placed in an oven at 70°C and dried to constant mass. Mass was then plotted against size and a best fit equation derived. These equations were used to derive total biomass. We only included beetles with body lengths of 15 mm or less, because some beetles (e.g. *Carabus problematicus*) were probably too large to be eaten by chicks (particularly those of 15 days old or less as in this study). However, to check this assumption did not bias results we checked and found a similar pattern between habitats when all body lengths were included in the analysis.

We sampled *Tipula* spp. by walking transects (following Galbraith et al. 1993) across the habitat types listed above on both study sites in 1994 and 1995. The observer walked ten paces on each transect, scanning 1 m either side of the route and counting all *Tipula* spp. encountered. Five transects were walked in each habitat every week from April to the end of July. Over the months we varied transect counts between early morning and evening (as *Tipula* spp. are known to have marked emergence and activity patterns, Coulson 1962), though on any one weekly count all habitats were counted at approximately the same time.

Statistical analysis

Brood habitat selection

Whenever broods showed non-random active selection of habitats we compared relative habitat use in order to provide an approximate ranking of habitat

suitability. Data from each study site were analysed separately using GLIM macro procedures supplied by Dr R. E. Green (see Green et al. 2000). This allowed us to test for (a) significant overall variation in habitat use and (b) significant differences in relative use between pairs of habitats (see Appendix).

Chick survival

All chicks were fitted with individual colour ring combinations. We tested the effects of four predictors on chick survival. The daily mortality rates of radio-tagged chicks on the two study sites were compared using logistic regression analysis carried out in GLIM 4.0 (NAG 1993). Two models were constructed. In Model 1, the fate of the chick (survived = 0, dead = 1) was specified as the response variable and the number of days that the chick survived as the binomial denominator, using a binomial error distribution and a logit link. In Model 1 a tagged chick was classified as dead if: (1) it could not be relocated for several days (despite the brood being located) and it was not seen as a fledged chick or in subsequent years, (2) it was found dead. In cases when tags fell off, the chick was classified as surviving for the period that the tag was known to have remained attached. In Model 2, the fate of the tagged brood (at least one chick in the brood survived to fledging = 0, no chicks survived to fledging = 1) was specified as the response variable. In Model 2, the same criteria were used to classify tagged chicks as dead but in addition an untagged chick was classified as dead if it was not seen as a fledged chick or in subsequent years or it was found dead. Three predictors were included in models as continuous variables (hatch date of the brood, MCP home range size after eight records and proportion of MCP home range comprised of grass) and one predictor, site (whether the chick was located on Chapel Fell or Widdybank Fell), was included as a two level factor. MCP home range was calculated for both models using a standard number of records, in this case eight, as those broods with more records were more likely to have had larger home ranges. Broods with fewer than eight records (one from each site) were excluded from the analysis. Model 1 was therefore conducted on a subset of 20 tagged chicks and Model 2 from a subset of 18 broods. Two broods were excluded from Model 2 because they had fewer than eight records and a further two broods were omitted because only the tagged chick was colour ringed and so the fate of the rest of the brood could not be assessed. It is important to note that sampling interval can be equally as important as number of samples (Otis & White 1999). However, we found no difference in the number of days over which eight records

were collected between Widdybank Fell (mean = 9.2 days) and Chapel Fell (mean = 8.6 days) ($T = 0.37$, d.f. = 19, $p = 0.72$). Even so we have probably only compared a sample of the true home range sizes of the chicks as eight records is not likely to be enough to accurately measure home range size (Seaman et al. 1999).

The best model was found using stepwise backward selection. The full model was fitted initially with all predictors. Two-way interactions were then deleted first, followed by main effects. A predictor 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 (Δ) (which approximates to a likelihood ratio test), the results of which are 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. The ratio of residual deviance to residual degrees of freedom was 0.88 for the binomial error model, which indicates a good model fit (Crawley 1993, Whittingham et al. 2000).

Pitfall data

It was not possible to transform the pitfall trapping data to normality and so non-parametric tests were used to analyse the data.

Results

Brood habitat selection

A total of 22 broods were tracked, 11 on each study site. The number of relocations per brood and study site were: five (one brood each site), seven (two broods on Chapel Fell), ten (seven broods on Chapel Fell), 12 (nine broods on Widdybank Fell), and 13–14 (one brood on each site). Total relocations in each habitat along with numbers expected under the null model (based on MCP home ranges) are shown in Tables 1 and 2 for both study sites.

The randomisation test indicated that the probability of obtaining the observed pattern of habitat selection by chance for both the Widdybank Fell and Chapel Fell radio telemetry data was small ($p < 0.001$). Hence radio-tracked broods were positively selecting or avoiding habitats (within MCP home ranges) at both study sites. An almost identical result was found when availability was calculated using potential home ranges.

Golden plover broods avoided extensive stands of heather on Widdybank Fell (which constituted 77% of the area) and preferred to forage in grassland,

marshes and heather mosaics (heather mixed with grassland or marshes) (Tabs. 3a, c). Several broods that were hatched in nests on heather burns moved to patches of grass and marsh and did not return to areas dominated by heather. On Chapel Fell, broods selected marshes and showed no consistent selection of any other habitat (Tabs. 2, 3b, 3d).

Home range size and chick survival

MCP home range size, using eight records to construct the home range, did not differ significantly between Chapel Fell (mean 3.41 ± 0.71 ha, ± 1 se) and Widdybank Fell (mean = 4.61 ± 1.60 ha, ± 1 se) ($t = 0.67$, d.f. = 19, $p = 0.51$). Neither the daily mortality rate of tagged chicks (Model 1) nor the probability of one or more chicks from a tagged brood reaching fledging (Model 2) were significantly associated with any of the four predictors: site, hatch date of the brood, MCP home range size and proportion of MCP home range comprised of grass ($p > 0.19$ in all cases).

Chick diet

The 27 faecal samples were collected between 20th May and 16th June from only eight broods. Using conversion rates we estimated the mean proportion of the diet (treating brood as the unit of replication) were as follows: 41% Coleoptera, 58% adult Diptera (all *Tipula* spp.) and less than 1% for all the other orders (namely: Araneae, Oligochaeta, Hymenoptera, Hemiptera and *Tipula* spp. larvae).

Food availability

Both the numbers and biomass of beetles from pitfall traps placed in the different habitats were non-randomly distributed on Chapel Fell (Kruskall-Wallis $H = 48.3$, d.f. = 3, $p < 0.001$ and $H = 42.5$, d.f. = 3, $p < 0.001$ respectively). The same pattern was found for both numbers (Kruskall-Wallis $H = 42.6$, d.f. = 3, $p < 0.001$) and biomass (Kruskall-Wallis $H = 44.3$, d.f. = 3, $p < 0.001$) on Widdybank Fell (Tab. 4). Beetle biomass and numbers were highest on grassland and marshes at both sites, with the other habitats differing in the amounts of biomass and numbers they supported.

The numbers of *Tipula* spp. counted on transects in different habitats in 1994 and 1995 on the two study sites are presented in Figures 1 a–d. Numbers were generally low on grassland on both sites in both years. Marshes and *Eriophorum vaginatum* mire typically supported high numbers of *Tipula* spp., and Heather showed mixed results.

Table 3a–d. The density of radio relocations of golden plover broods in habitats listed at the left of each table relative to the density in those listed across the top. Relative densities were calculated from log-linear models fitted to a subset of data from broods in whose home ranges both of a pair of habitats were present. The number of brood ranges contributing to each calculation is given in brackets. The two-tailed statistical significance of the difference between the estimated relative density and 1 (i.e. density equal in the two habitats) was determined by a randomisation test (see Appendix 1) and is indicated by: * $p < 0.05$, ** $p < 0.01$. Relative densities with no asterisks were not different from 1 at $P < 0.05$. Thus in table 3a the relative density of use of heather mosaic was 1.16 times that of grassland. Habitats were assigned a ranking score by adding the number of times a habitat was significantly selected over another habitat (+s) and taking away the number of times that habitat was avoided relative to another habitat (-s).

3a. Widdybank Fell with MCP home ranges

	Grassland	Heather mosaic	Heather	Marshes	Score
Grassland					+1
Heather mosaic	1.16 (10)				+1
Heather	0.06** (10)	0.05** (10)			-3
Marshes	0.60 (9)	0.90 (8)	11.68** (8)		+1
<i>Eriophorum vaginatum</i> mire	0.76 (6)	1.27 (5)	41.01 (5)	0.14 (5)	0

3b. Chapel Fell with MCP home ranges

	Acid grassland	Marshes	<i>Eriophorum vaginatum</i> mire	Score
Acid grassland				-1
Marshes	3.04*(8)			+1
<i>Eriophorum vaginatum</i> mire	0.61 (10)	0.37 (9)		0
<i>Eriophorum vaginatum</i> mire subcommunity	1.00 (4)	0.26 (4)	0.46 (5)	0
<i>Calluna vulgaris</i>				

3c. Widdybank Fell with potential home ranges

	Grassland	Heather mosaic	Heather	Marshes	Score
Grassland					+1
Heather mosaic	1.45 (11)				+1
Heather	0.03** (11)	0.02** (11)			-4
Marshes	0.95 (11)	0.66 (11)	35.29** (11)		+2
<i>Eriophorum vaginatum</i> mire	0.36 (6)	0.75 (6)	40.77* (6)	0.13* (6)	0

3d. Chapel Fell with potential home ranges

	Acid grassland	Marshes	<i>Eriophorum vaginatum</i> mire	Score
Acid grassland				0
Marshes	1.78 (11)			+1
<i>Eriophorum vaginatum</i> mire	0.39 (11)	0.22 (11)		0
<i>Eriophorum vaginatum</i> mire subcommunity	0.17 (11)	0.10** (11)	0.45 (11)	-1
<i>Calluna vulgaris</i>				

Table 4. Numbers and biomass of coleopterans (up to 15 mm in length) caught per pitfall in different habitats on Widdybank Fell in 1995 and on Chapel Fell in 1994.

Widdybank Fell		
Habitat (number of pitfalls shown in brackets)	Median number of beetles caught per pitfall (upper Q3 and lower Q1 quartiles)	Median biomass (g) of beetles caught per pitfall (upper Q3 and lower Q1 quartiles)
Grass (40)	4.50 (1.25–10.75)	0.10 (0.02–0.27)
Marsh (40)	4.00 (1.00–5.75)	0.04 (0.02–0.13)
<i>Eriophorum vaginatum</i> mire (20)	0 (0–0)	0 (0–0)
Heather (80)	1.00 (0–3.00)	0.01 (0–0.06)
Chapel Fell		
Grass (60)	5.00 (2.00–9.00)	0.08 (0.02–0.20)
Marsh (20)	6.00 (2.50–19.00)	0.13 (0.04–0.74)
<i>Eriophorum vaginatum</i> mire (20)	4.00 (1.00–7.75)	0.07 (0.01–0.19)
Heather (20)	1.00 (0–3.00)	0.01 (0–0.04)

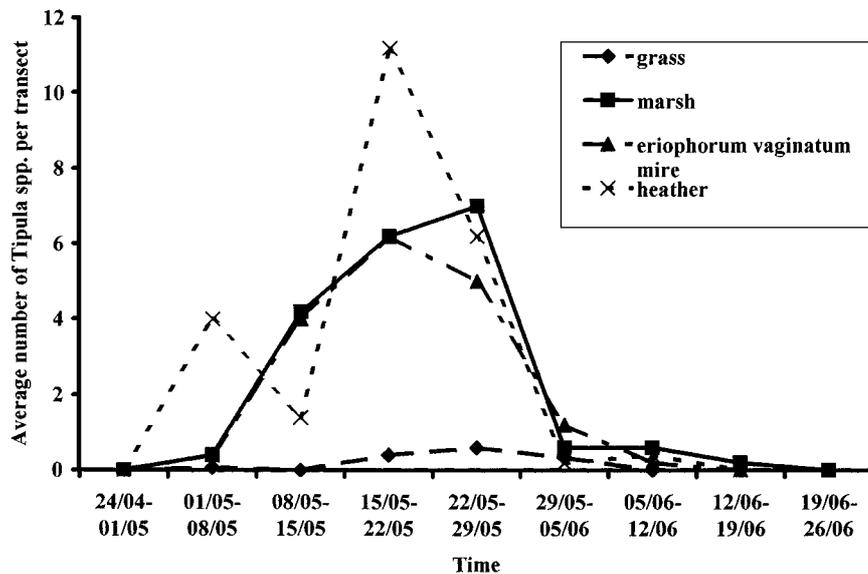
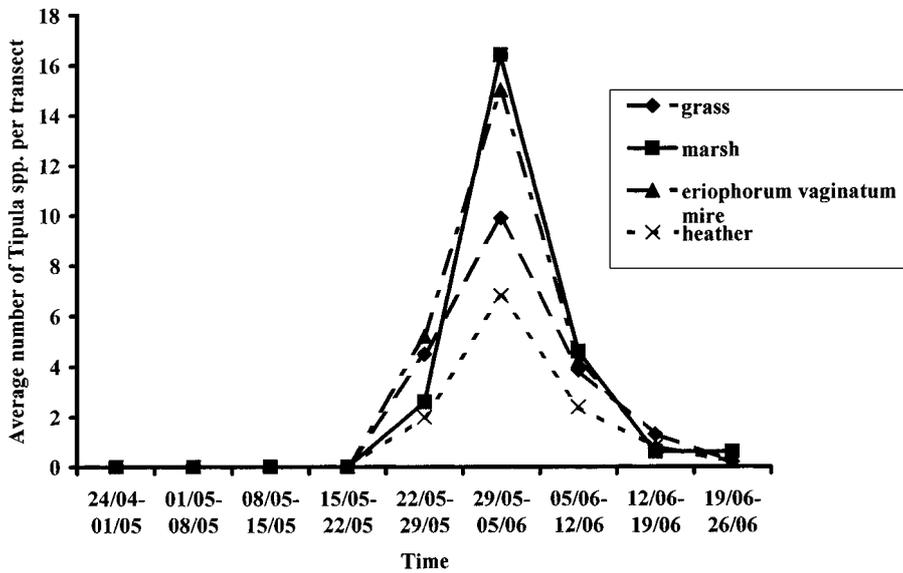


Fig. 1a. The numbers of *Tipula* spp. recorded on weekly transects through different habitats on Chapel Fell from April to July 1994. Note: additional weekly transects were also carried out in the last week of June to the end of July but no *Tipula* spp. were recorded.

Fig. 1b. The numbers of *Tipula* spp. recorded on weekly transects through different habitats on Chapel Fell from April to July 1995. Note: additional weekly transects were also carried out in the last week of June to the end of July but no *Tipula* spp. were recorded.

Discussion

Habitat preferences could result from a number of influences such as food availability, cover from predators and the ease with which chicks are able to move through and forage within habitats as determined by the physical structure of the vegetation. Below we consider the effects of prey abundance and vegetation structure on habitat choice.

Beetle catches were high on grasslands on both sites, though *Tipula* spp. numbers were low. Densities of both *Tipula* spp. and beetles have been found to be higher on upland grassland sites elsewhere in northern England compared to blanket bog, dry heaths and lowland mires at comparable altitudes to our study sites (Coulson & Butterfield 1985, Coulson 1988).

Grassland patches were selected by broods on Widdybank Fell, but not on Chapel Fell (where beetle catches were slightly lower relative to other habitats when compared with Widdybank). Marshes were selected on both study sites and held high numbers of both beetles and *Tipula* spp. Large stands of heather of all ages were strongly avoided on Widdybank Fell and beetle catches here were low, though *Tipula* spp. numbers were occasionally high. Therefore, the general pattern of habitat selection by broods appears to match the distribution of food. Several studies of gamebirds and wildfowl indicate that broods of precocial species often select habitats with highest prey densities (e.g. Green 1984, Hill 1985, Galbraith 1988, Sjoberg et al. 2000), though this is not always the case (Grant et al. 1992).

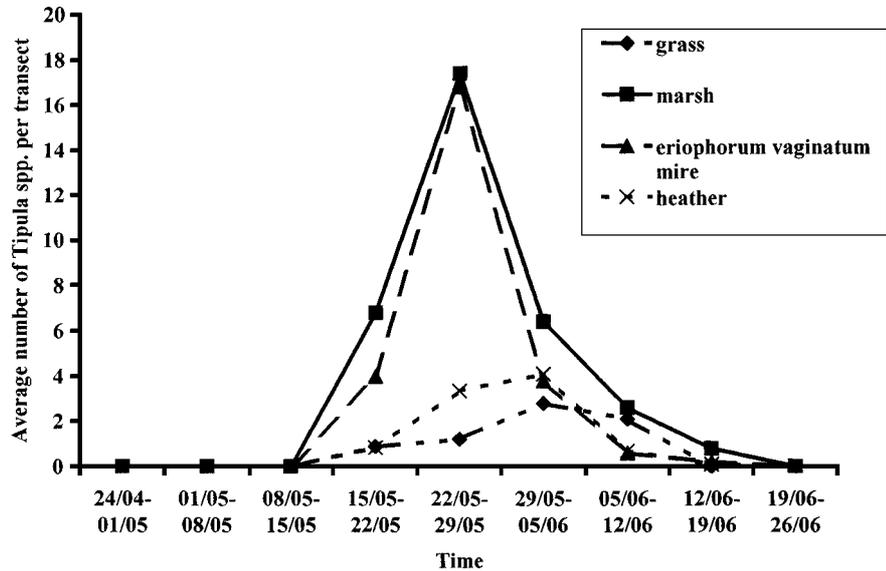


Fig. 1c. The numbers of *Tipula* spp. recorded on weekly transects through different habitats on Widdybank Fell from April to July 1994. Note: additional weekly transects were also carried out in the last week of June to the end of July but no *Tipula* spp. were recorded.

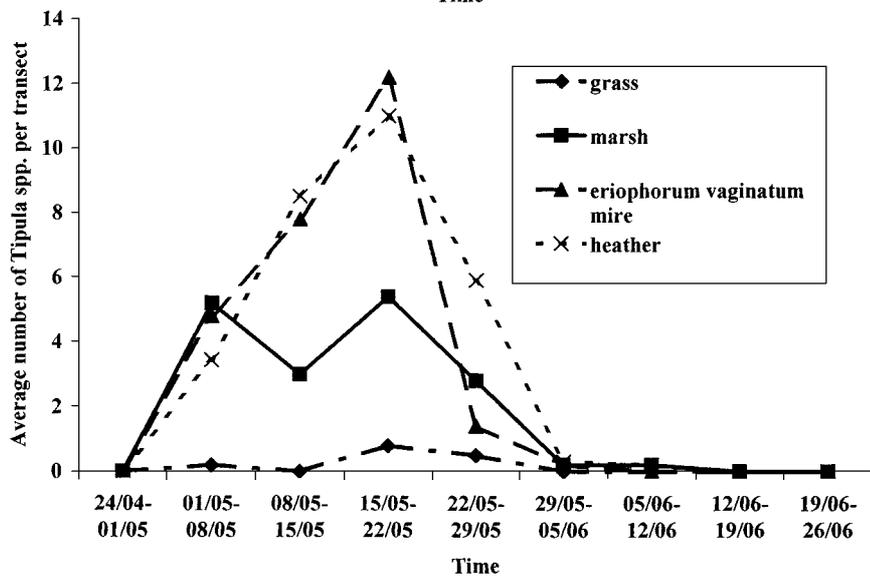


Fig. 1d. The numbers of *Tipula* spp. recorded on weekly transects through different habitats on Widdybank Fell from April to July 1995. Note: additional weekly transects were also carried out in the last week of June to the end of July but no *Tipula* spp. were recorded.

Chick habitat selection may also be influenced by vegetation structure. Different habitats could provide differing amounts of concealment from predators and chicks may be unable to utilise some habitats because the structure of the vegetation impedes their movement or access to food. Information on vegetation height and density in the habitats on both the study sites is presented elsewhere (Whittingham et al. 2000). The selection of heather mosaics (heather mixed with grass or marsh) on Widdybank Fell and the avoidance of extensive stands, particularly older, thicker vegetation, suggests heather may have impeded the movement of chicks (particularly younger chicks). However, marshes with patches of *Juncus effusus* were used more frequently by broods than expected, despite these being the tallest and most dense of all habitats present on both study sites. Some very open habitats with short-cropped grass and high invertebrate densities, such as calcareous grass, were used rarely where present on the moor in large patches. The pattern of habitat selection is not readily explained solely by reference to vegetation structure.

We suspect that the observed pattern of habitat use by chicks can be explained by a combination of prey abundance and vegetation structure. On several occasions we observed that chicks that were feeding in grassland ran towards patches of *Juncus effusus* or heather when threatened. This could explain why broken ground consisting of a mosaic of heather with grass or marshes was selected – grassland for foraging and heather or *Juncus* patches within marshes for concealment. The central parts of large patches of *Juncus effusus* were never used (though such areas were rare) and it was only the edges of larger patches or small clumps that were used. Marshes were frequently found adjacent to grassland patches on both study sites.

We found *Tipula* spp. formed a mean of 58% of the diet of the eight broods that we sampled. The average hatch date for our radio tagged broods was the 3rd June (\pm 2.6 days, 1se). Whittingham (1996) found that 61% (22/36) of nests found on Chapel Fell and 64% (18/28) of nest found on Widdybank Fell from 1992–1995 hatched in the second half of May, the remaining nests hatching from early June through to early August. *Tipula* spp. numbers peaked in the second half of May on both our study sites in both years studied (Figs. 1a–d). It is possible that golden plovers time the hatching of their nests to co-incide with the peak of *Tipula* spp. emergence. This supports the findings from the faecal analysis which suggest that *Tipula* spp. are a key component of the diet of golden plover chicks.

We found no relationship between the size of the chicks' home range or hatch date and the probability

of survival of either the individual tagged bird or the brood as a whole. This result is in contrast to studies on the chicks of the pheasant *Phasianus colchicus* and red-legged partridge *Alectoris rufa*, where broods with smaller home ranges tended to have higher survival rates (Green 1984, Hill 1985). However, in these latter two studies it was not clear why the broods were moving. Riley et al. (1998) found that pheasant broods hatching later in the season were more likely to perish. Golden plover broods often moved from one apparently suitable area (e.g. marshes or patches of grassland near clumps of heather) to another suitable area. This could allow chicks to avoid predators, to maximise food intake between patches or to avoid disturbance from humans. Two chance observations are of interest here. One brood moved 400 m in three hours after being disturbed by a stoat *Mustela erminea* (the radio tagged chick weighed 25 g). Another brood moved 700 m in 24 hours the day fence construction began adjacent to their initial location (the radio tagged chick weighed 28 g). Broods are thus clearly able to move quite large distances, even when the chicks are small, to avoid predators or human disturbance. Human disturbance has previously been shown to affect the behaviour of golden plover broods and has even been associated with population decline in the Peak District (Yalden & Yalden 1989, 1990), although this was later been found to be erroneous (Brown 1993, Yalden & Pearce-Higgins 1997). Our observations suggest that in some circumstances disturbance may be an important factor in determining habitat use by golden plover chicks (see Yalden & Yalden 1990), though recent studies have found this is not always the case (Pearce-Higgins 1999).

The broods from the two study sites had similar survival rates and home range sizes. This supports the argument proposed by Whittingham et al. (2000) that moorland sites, where heather cover has been largely replaced by grasses, such as Chapel Fell, are of comparable quality, in terms of golden plover breeding habitat, to grouse moorland, such as Widdybank Fell.

The preference of chicks for feeding in grassland shown in this study suggests that recent increased levels of grazing in the uplands, and the resultant break up of extensive heather swards, should benefit golden plover broods at least within the range of heather/grass mosaics found within our study (Fuller & Gough 1999). However, recent increases in drainage may have reduced the amount of marsh on moorland and hence had negative effects on the survival of young golden plover. The reported declines in golden plover populations during recent decades (e.g. Parr 1992, Gibbons et al. 1993, Stone et al. 1997, Hancock & Avery 1998) may therefore have been caused by increases in land drainage or excessive graz-

ing (which we did not investigate in this study). However, it should be noted that there are at least three other plausible suggestions to explain declines in golden plover populations: winter weather (Yalden & Pearce-Higgins 1997), changes in management of upland fields that are important for foraging adults (Whittingham et al. 2000) and management of lowland fields where the birds winter.

Conservation recommendations

Chick survival and home range size (as shown in this study), the numbers of fledged young per pair, nest survival and the density of pairs did not differ between our two study sites (Whittingham 1996, Whittingham et al. 2000). Therefore the degree of encroachment of grasses observed in our study seems to have had little effect on reproductive output or chick survival. It is important to note that we are not advocating grazing beyond the bounds of that observed in our study, as we do not know the consequences of such grazing for golden plover. However, there are large losses of biodiversity for many other species (including birds and invertebrates) as a result of heavy grazing levels, beyond those observed in our study, which ultimately result in communities wholly dominated by grass (Usher & Thompson 1993, Thompson et al. 1995b, Gardner et al. 1997). The results of our study suggest that, within the levels of grass encroachment observed, upland habitats could be managed to maximise feeding opportunities for golden plover chicks in two ways.

1) There should be sufficient grazing to break up extensive heather swards thus allowing grasses to invade. We suggest this management be targeted towards heaths where heather is dominant, such as Widdybank, and not on blanket bogs where heather is nearly always co-dominant with other vegetation such as grasses. This will provide feeding opportunities while retaining cover from predators. We also encourage grazing to create structural variation of mature heather stands that will benefit beetles (a major food source for golden plover chicks) (Gardner et al. 1997). The grazing levels necessary to achieve these aims are likely to differ between individual sites and in different parts of the UK (Thompson et al. 1995b). Utilisation of heather by sheep, and red deer, is strongly related to distance from grass and so the scale at which patchworks of heather and grass are maintained are likely to have impacts on the time-scales at which rotations of livestock are necessary to prevent total heather loss (Hester & Baillie 1998). Grazing to promote encroachment of grass to uni-

form heather swards and to create structural variation of mature heather may best be incorporated into moorland management as part of a range of techniques designed to maximise biodiversity, including short rotation burning for red grouse and the encouragement of tall heather on slopes to encourage use by nesting raptors.

2) Create marshy areas by blocking drainage ditches. This will encourage rushes and damp grass and the associated communities of beetles and *Tipula* spp. upon which golden plover chicks feed. Creating such areas near to patches of grassland so offering tall cover, within which chicks can hide from predators, is likely to maximise their value.

Potential effects of conservation proposals on other species

We think it likely that a number of other species will benefit from the management we suggest. Extensive grazing will prevent the colonisation of moorland areas by trees, thus retaining open habitat for such open country species as red grouse. Increasing the patchiness of uniform heather stands by promoting the development of grassy patches may well facilitate breeding by higher densities of other waders such as curlew *Numenius arquata* (Robson et al. 1994) and lapwing and is likely to increase the numbers of passerines such as meadow pipit *Anthus pratensis* and skylark *Alauda arvensis* which are abundant in grassy areas (Gibbons et al. 1993, Brown & Stillman 1993, Smith et al. 2000). These in turn, may attract more foraging (and, as a consequence, perhaps nesting) birds of prey such as merlin *Falco columbarius* and hen harriers *Circus cyaneus* which both feed on small passerines, particularly meadow pipits, amongst other prey (Cramp & Simmonds 1980, Redpath & Thirgood 1999).

Such management, however, may not be popular with those who manage heathland to maximise the numbers of red grouse available for shooting in autumn, as raptors such as hen harriers, and mammalian predators such as foxes *Vulpes vulpes* attracted by the abundance of such prey as meadow pipits and field voles *Microtus agrestis* (Redpath & Thirgood 1999, Smith et al. 2000), may also reduce the numbers of red grouse available for shooting by direct predation. Some of these losses could be offset by the legal control of predators. Although some studies have suggested that heather cover explains much variation in the territory size and nesting density of red grouse (e.g. Miller & Watson 1978), intimate mosaics of heather and grass (as opposed to the wholesale replacement of heather with grass) are unlikely to support fewer red grouse than uniform stands of heather of similar area (Smith et al. 2000). We can

think of no other avian species that might be disadvantaged. Amongst other taxa, management of the type we advocate, that is extensive livestock management, would increase plant diversity that is suffocated by tall heather swards which develop when grazing is limited (Gimingham 1978, Welch & Scott 1995). Invertebrate biodiversity is adversely affected by heavy grazing pressure that results in the total loss of heather. However, a heterogeneous heather sward, which could result from either burning or grazing, such as we suggest, would provide good conditions for both carabid and lepidopteran spp. (Gardner et al. 1997, Haysom & Coulson 1998).

Our recommendations concerning the (re-) provision of wet areas is also likely to increase the diversity of other taxa and by affecting the relative abundance of some species, may make more food available to other heathland species such as red and black grouse *Tetrao tetrix*, and curlew, whose chicks, at least, all select wet feeding areas (Savory 1977, Parr & Watson 1988, Robson et al. 1994).

Our two management options are likely to have minimal impacts on use of moorland for foraging by adult golden plovers and they should be used in conjunction with the suggestions given by Whittingham et al. (2000) in order to manage uplands beneficially for breeding golden plovers.

Our study does not indicate the proportions of heather and grass or in what patch sizes or configurations they are best suited for golden plover chicks. We encourage further work that provides answers to these questions. We also encourage further research into the understanding of grazing on vegetation in the uplands which will enable individual sites to be managed to provide specific conditions (see Armstrong et al. 1997a & b). Future work on golden plovers should concentrate on the relationship between food abundance and availability and on the habitat requirements of older chicks.

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Appendix 1

For both models (a) and (b), a log-linear model with a Poisson error distribution and log link function was used, with the number of times that a tagged chick was recorded in each habitat specified as the response variable. Habitat type and brood were treated as factors. \log_e (area) of habitat, calculated as either MCP or potential home range, was declared as an offset variable. Hereafter, this model will be referred to as model 'A'. All modelling was carried out using GLIM, release 4 (NAG 1993). This method was preferred to compositional analysis for two reasons. First, compositional analysis uses proportions and the data from the 23 broods had a variable number of records (5 to 14). Log-linear models allowed us to weight data according to the observed sample sizes. Second, the measure of overall variation (V score – see below) allowed habitats to be weighted according to their availability. These weights reduced the influence of habitats that covered a small area (such as marshes).

(a) Testing for overall variation in habitat use

Model 'A' was constructed to derive maximum-likelihood estimates of 'habitat use densities' (number of brood records in a habitat per unit area of that habitat) in each habitat relative to one reference habitat (where the foraging density coefficient for reference habitat $b_1 = 1$). These habitat use coefficients were then used to derive a measure of overall variation (V) in habitat use between all habitat types, using the formula:

$$V = \frac{\sum_i(w_i \cdot b_i) - \left[\frac{\sum_i(w_i \cdot b_i)^2}{\sum_i(w_i)} \right]}{\sum_i(w_i)}$$

where b^i is the \log_e habitat use density coefficient from model 'A' (described above) for habitat i and w^i is either the total number of observed records or the expected number of records based on available area (whichever is the greater) to habitat i from all nests. Summation \sum_i is across all habitats. The weights (*expected* w^i scores) were used to reduce the influence of coefficients for those habitats which either covered a very small area or were only present in territories in which few visits were observed, or both. The derived (*expected*) values were calculated using the formula:

$$w^i = \sum_n \frac{a^i F}{A}$$

where a^i is the area of habitat i within a home range, A is the total area within that home range and F is the total number of records from that brood. Summation

Σ_n is across all broods. The statistical significance of V was tested by performing a randomisation procedure. The labels of the habitats within each territory were shuffled randomly and model 'A' was fitted to derive V from the randomised data, which was then compared with the score from the actual data. This procedure was performed 1000 times and the number of occasions on which the randomly derived V score exceeded or was equal to the actual V score was obtained. This value, when divided by 1000, gives the probability that non-random habitat selection had taken place.

(b) Testing for significant differences in density of use between pairs of habitats

In pairwise habitat tests, model 'A' was used to derive maximum-likelihood estimates of habitat use density (*observed*) in one habitat relative to the second habitat, but only for those broods with both habitats present within their home range. A randomisation procedure

was then performed to test the statistical significance of the *observed* relative foraging density by deriving a *randomised* maximum-likelihood estimate of relative foraging density. This was achieved by randomly shuffling the labels of the pair of habitats being tested for each brood where both habitats were present (the other habitat labels were left unaltered) and re-fitting model 'A'. This procedure was performed 1000 times and the number of occasions on which the *randomised* relative habitat use density was equal to or exceeded the value for the *observed* relative foraging density was obtained. This value was divided by 1000 to obtain the probability that the foraging density was significantly different between the two habitats. This procedure was repeated for all pair combinations of habitats.

Habitats were assigned an approximate ranking score by adding together the number of times a habitat was significantly selected over another habitat (pluses) and taking away the number of times that habitat was avoided relative to another habitat (minuses).

Appendix 2

Areas (in hectares) of each habitat type within the Minimum Convex polygon (MCP) home range for 22 broods used in the habitat selection analysis. A dash indicates the habitat was not present within that home range. * A tagged chick was classified as dead if: (1) it could not be relocated for several days (despite the brood being located) and it was not seen as a fledged chick or in subsequent years, (2) it was found dead.

Brood number (WD = Widdybank, CF = Chapel Fell)	Grassland	Marsh	<i>Eriophorum vaginatum</i> mire	Heather	Heather mosaics	MCP total size (ha)	Fate of radio tagged chick* (0 = survived, 1 = died). ^T = tag fell off.
WD1	1.8	0.04	3.08	1.8	0.56	7.28	1
WD2	2.56	0.04	0.28	1.2	0.24	4.32	0
WD3	0.04	0.36	-	0.72	1.32	2.44	0
WD4	0.12	0.28	-	0.84	0.64	1.88	1 ^T
WD5	1.64	0.12	2.56	11.72	2.76	18.8	1 ^T
WD6	0.08	0.12	1.2	0.64	0.28	2.32	1
WD7	0.68	0.96	-	1.44	0.76	3.84	1
WD8	0.32	-	0.72	2.08	0.72	3.84	1
WD9	0.6	0.92	-	2.24	1	4.76	1
WD10	8.8	0.12	3.2	-	-	12.12	1
WD11	0.28	-	-	1.12	0.36	1.76	1
CF1	3.24	1.88	0.92	-	-	6.04	1
CF2	5.4	0.04	4.08	0.28	-	9.8	1
CF3	0.68	0.4	3.04	-	-	4.12	1 ^T
CF4	0.4	0.32	3.12	-	-	3.84	1 ^T
CF5	-	0.44	2.08	3.2	-	5.72	1 ^T
CF6	0.8	-	3.32	6.04	-	10.16	1 ^T
CF7	1.2	0.16	2.16	-	-	3.52	0 ^T
CF8	1.04	-	0.6	-	-	1.64	1
CF9	0.5	1.68	3.88	0.36	-	6.42	1
CF10	1.88	0.2	2.36	2.84	-	7.28	1
CF11	0.24	0.2	0.96	-	-	1.4	1 ^T

References

- Anderson P, Yalden DW (1981) Increased sheep numbers and the loss of heather moorland in the Peak District, England. *Biological Conservation* 20: 195–213.
- Armstrong HM, Gordon IJ, Grant SA, Hutchings NJ, Milne JA, Sibbald AR (1997a) A model of the grazing of hill vegetation by sheep in the UK. I. The prediction of vegetation biomass. *Journal of Applied Ecology* 34: 166–185.
- Armstrong HM, Gordon IJ, Hutchings NJ, Illius AW, Milne JA, Sibbald AR (1997b) A model of the grazing of hill vegetation by sheep in the UK. II. The prediction of off-take by sheep. *Journal of Applied Ecology* 34: 186–207.
- Brown AF (1993) The status of golden plovers *Pluvialis apricaria* in the south Pennines. *Bird Study* 40: 196–202.
- Brown AF, Stillman RA (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 DBA (1998) Tundra plovers: the eurasian, pacific and american golden plovers and grey plover. T & A.D. Poyser, London.
- Coulson JC (1962) The biology of *Tipula subnodicornis* Z., with comparative observations on *Tipula paludosa* M. *Journal of Animal Ecology* 31: 1–21.
- Coulson JC, Butterfield JEL (1985) The invertebrate communities of peat and upland grasslands in the north of England and some conservation implications. *Biological Conservation* 34: 197–225.
- Coulson JC (1988) The structure and importance of invertebrate communities on peatlands and moorlands, and effects of environmental and management changes. In: Usher MB, Thompson DBA (eds) *Ecological change in the uplands*. Blackwell Scientific Publications, Oxford, pp 365–380.
- Cramp S, Simmons KEL (eds) (1980) *The Birds of the Western Palearctic*. Vol. II. Oxford University Press, Oxford.
- Cramp S, Simmons KEL (eds) (1983) *The Birds of the Western Palearctic*. Vol. III. Oxford University Press, Oxford.
- Crawley MJ (1993) *Methods in Ecology: GLIM for Ecologists*. Blackwell Scientific Publications, Oxford.
- Fuller RJ (1996) Relationships between grazing and birds with particular reference to sheep in the British uplands. British Trust for Ornithology research report No. 164, Norfolk.
- Fuller RJ, Gough SJ (1999) Changes in sheep numbers in Britain: implications for bird populations. *Biological Conservation* 91: 73–89.
- Galbraith H (1988) Effects of agriculture on the breeding ecology of lapwings *Vanellus vanellus*. *Journal of Applied Ecology* 25: 487–504.
- Galbraith H (1989) The diet of lapwing *Vanellus vanellus* chicks on Scottish farmland. *Ibis* 131: 80–84.
- Galbraith H, Murray S, Duncan K, Smith R, Whitfield DP, Thompson DBA (1993) Diet and habitat use of the dotterel *Charadrius morinellus* in Scotland. *Ibis* 135: 148–155.
- Gardner SM, Hartley SE, Davies A, Palmer SCF (1997) Carabid communities on heather moorlands in northeast Scotland: the consequences of grazing pressure for community diversity. *Biological Conservation* 81: 275–286.
- Gibbons DW, Reid JB, Chapman RA (1993) *The new atlas of breeding birds in Britain and Ireland: 1988–1991*. T & AD Poyser, London.
- Gimingham CH (1978) *Calluna* and its associated species: some aspects of co-existence in communities. *Vegetatio* 36: 179–186.
- Grant MC, Chambers RE, Evans PR (1992) The effects of re-seeding heathland on breeding whimbrel *Numenius phaeopus* in Shetland. III. Habitat use by broods. *Journal of Applied Ecology* 29: 516–523.
- Green RE (1984) The feeding ecology and survival of partridge chicks (*Alectoris rufa* and *Perdix perdix*) on arable farmland in East Anglia. *Journal of Applied Ecology* 21: 817–830.
- Green RE, Tyler GA, Bowden CGR (2000) Habitat selection, ranging behaviour and diet of stone curlews *Burhinus oedicnemus* in southern England. *Journal of Zoology* 250: 161–185.
- Hagemeijer WJM, Blair MJ (1997) *The EBCC atlas of European breeding birds: their distribution and abundance*. T & A.D. Poyser, London.
- 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 PF, Thompson DBA (1990) Factors associated with the breeding distribution of upland birds in the South Pennines, England. *Journal of Applied Ecology* 27: 562–577.
- Haysom KA, Coulson JC (1998) The Lepidoptera fauna associated with *Calluna vulgaris*: effects of plant architecture on abundance and diversity. *Ecological Entomology* 23: 377–385.
- Hester AJ, Baillie GJ (1998) Spatial and temporal patterns of heather use by sheep and red deer within natural heather/grass mosaics. *Journal of Applied Ecology* 35: 772–784.
- Hill DA (1985) The feeding ecology and survival of pheasant *Phasianus colchicus* chicks on arable farmland. *Journal of Applied Ecology* 22: 645–654.
- Hudson PJ (1992) *Grouse in space and time*. Game Conservancy Trust, Fordingbridge.
- Johnson OW, Connors PG (1996) American Golden-Plover *Pluvialis dominica*, Pacific Golden-Plover *Pluvialis fulva*. In: Poole A, Gill F (eds) *The Birds of North America*, No. 201–202. The Academy of Natural Sciences, Philadelphia and The American Ornithologists' Union, Washington, D.C.
- Kenward RE (1987) *Wildlife Radio Tagging: equipment, field techniques and data analysis*. Academic Press Limited, London.
- Marchant JH, Hudson R, Carter SP, Whittington P (1990) Population trends in British breeding birds. British Trust for Ornithology, Tring.

- Miller GR, Watson A (1978) Territories and the food plant of individual red grouse – I. Territory size, number of mates and brood size compared with the abundance, production and diversity of heather. *Journal of Animal Ecology* 47: 293–305.
- NAG (1993) General linear interactive modelling. Oxford, UK: The Numerical Algorithms Group Ltd.
- O'Connell MJ, Thomas CJ, Twiss SD, Downie IS, Evans PR, Whitfield DP (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.
- Otis DL, White GC (1999) Autocorrelation of location estimates and the analysis of radiotracking data. *Journal of Wildlife Management* 63: 1039–1044.
- 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.
- Parr R, Watson A (1988) Habitat preferences of black grouse on moorland-dominated ground in north-east Scotland. *Ardea* 76: 175–180.
- Pearce-Higgins JW (1999) The ecology of golden plovers *Pluvialis apricaria* in the Peak District. Unpublished PhD thesis, University of Manchester.
- Redpath SM, Thirgood SJ (1999) Numerical and functional responses in a generalist predator: hen harriers and peregrines on Scottish grouse moors. *Journal of Animal Ecology* 68: 879–892.
- Riley TZ, Clark WR, Ewing DE, Vohs PA (1998) Survival of ring-necked pheasant chicks during brood rearing. *Journal of Wildlife Management* 62: 36–44.
- Robson G, Percival SM, Brown AF (1994) The breeding ecology of curlew: a pilot study. English Nature Research Report No. 127, Peterborough.
- Rodwell J (1991a) *British Plant Communities, Volume 2: Mires and Heaths*. Cambridge University Press, Cambridge.
- Rodwell J (1991b) *British Plant Communities, Volume 3: Grasslands and Montane Communities*. Cambridge University Press, Cambridge.
- Savory CJ (1977) The food of red grouse chicks *Lagopus lagopus scoticus*. *Ibis* 119: 1–8.
- Seaman DE, Millsbaugh JJ, Kernohan BJ, Brundige GC, Raedeke KJ, Gitzen RA (1999) Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63: 739–747.
- Siriwardena GM, Baillie SR, Wilson JD (1999) Temporal variation in the annual survival rates of six granivorous birds with contrasting population trends. *Ibis* 141: 621–636.
- Sjoberg K, Poysa H, Elmberg J, Nummi P (2000) Response of mallard ducklings to variation in habitat quality: an experiment of food limitation. *Ecology* 81: 329–335.
- Smith A, Redpath S, Campbell S (2000) The influence of moorland management on grouse and their predators. Department of the Environment, Transport and the Regions, Bristol.
- Stillman RA, Brown AF (1994) Population sizes and habitat associations of upland breeding birds in the South Pennines, England. *Biological Conservation* 69: 307–314.
- Stone BH, Sears J, Cranswick PA, Gregory RD, Gibbons DW, Rehfish MM, Aebischer NJ, Reid JB (1997) Population estimates of birds in Britain and in the United Kingdom. *British Birds* 90: 1–22.
- Thompson DBA, MacDonald AJ, Hudson PJ (1995a) Upland Moors and Heaths. In: Sutherland WJ, Hill DA (eds) *Managing Habitats for Conservation*, Cambridge University Press, Cambridge, pp 84–99.
- Thompson DBA, MacDonald AJ, Marsden JH, Galbraith CA (1995b) Upland heather moorland in Great Britain: a review of international importance, vegetation change and some objectives for nature conservation. *Biological Conservation* 71: 163–178.
- Thomson DL, Green RE, Gregory RD, Baillie SR (1998) The widespread declines of songbirds in rural Britain do not correlate with the spread of their avian predators. *Proceedings of the Royal Society London. B* 265: 2057–2062.
- UK Biodiversity Group (1999) Tranche 2 action plans. Volume 6 – terrestrial and freshwater species and habitats. English Nature, Peterborough.
- Usher MB, Thompson DBA (1993) Variation in the upland heathlands of Great Britain: conservation importance. *Biological Conservation* 66: 69–81.
- Welch D, Scott D (1995) Studies in the grazing of heather moorland in north-east Scotland. VI. 20 year trends in botanical composition. *Journal of Applied Ecology* 32: 596–611.
- White GC, Garrott RA (1990) *Analysis of wildlife radiotracking data*. Academic Press Ltd., London.
- Whittingham MJ (1996) Habitat requirements of Golden Plover *Pluvialis apricaria*. PhD thesis, University of Sunderland.
- Whittingham MJ, Percival SM, Brown AF (1999a) Evaluation of radio telemetry methods in measuring habitat choice by young golden plover *Pluvialis apricaria* chicks. *Bird Study* 46: 363–368.
- Whittingham MJ, Percival SM, Brown AF (1999b) Notes on night-time activity of golden plover *Pluvialis apricaria* chicks in the North Pennines. *Wader Study Group Bulletin* 90: 56–58.
- Whittingham MJ, Percival SM, Brown AF (2000) Time budgets and foraging of breeding golden plover *Pluvialis apricaria*. *Journal of Applied Ecology* 37: 632–646.
- Yalden DW, Yalden PE (1989) The sensitivity of breeding golden plovers *Pluvialis apricaria* to human intruders. *Bird Study* 36: 49–55.
- Yalden DW, Yalden PE (1990) Recreational disturbance of breeding golden plovers *Pluvialis apricaria*. *Biological Conservation* 51: 243–262.
- Yalden DW (1991) Radio-tracking of golden plover *Pluvialis apricaria* chicks. *Wader Study Group Bulletin* 63: 41–44.
- Yalden DW, Pearce-Higgins JW (1997) Density-dependence and winter weather as factors affecting the size of a population of golden plovers *Pluvialis apricaria*. *Bird Study* 44: 1–18.