JOURNAL OF AVIAN BIOLOGY 33: 184–190, 2002

Nest-site selection by golden plover: why do shorebirds avoid nesting on slopes?

Mark J. Whittingham, Stephen M. Percival and Andrew F. Brown

Whittingham, M. J., Percival, S. M. and Brown A. F. 2002. Nest-site selection by golden plover: why do shorebirds avoid nesting on slopes? – J. Avian Biol. 33: 184–190.

It is widely known that many upland-breeding shorebirds tend to nest on plateaus but to date no studies have put forward explanations for this phenomenon. We examined the effect of slope and habitat on the distribution of ground-nesting golden plover *Pluvialis apricaria* at two study sites in County Durham, U.K. Golden plovers showed strong selection for nesting on flat ground. Habitat significantly affected nest-site location on one study site (heather burnt within the past 2 years was favoured and older stands of heather were avoided) but not on the other. Fifty-nine per cent of all nests failed. We attributed 95% of all losses to predation. Seventy-five per cent of nests, in which the predator was identified, were taken by ground predators, mainly stoats *Mustela erminea*. Nests on flat ground had significantly higher rates of survival than those on slopes. Nest survival did not vary significantly with habitat type nor with vegetation height or density around the nest. Neither habitat type, vegetation height nor vegetation density around nests differed between nests on slopes and on flat ground. In addition, individuals that nested on flat ground tended to have less black on their underparts (a suggested indicator of dominance). We suggest that birds nesting on slopes are less efficient at avoiding nest predation than those nesting on the flat. The nature or degree of a bird's response to a predator may be related to the efficiency of individual anti-predator responses and/or to visibility from the nest. This study cannot differentiate between these two explanations. We encourage further work to investigate differences in behaviour between individuals nesting on slopes and those on flat ground.

M. J. Whittingham (correspondence) and S. Percival, Northumbrian Water Ecology Centre, Science Complex, University of Sunderland, Sunderland SR1 3SD, U.K. Present address for Mark J. Whittingham: Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, U.K. E-mail: mark.whittingham@zoo.ox.ac.uk. A. F. Brown, English Nature, Northminster House, Peterborough PE1 1UA, U.K.

Nest predation is the main cause of nest failure in many bird species (Ricklefs 1969, Martin 1993) and nest-predation rates have been shown to vary with nest-site characteristics for a wide range of bird species (Ricklefs 1969, Collias and Collias 1984, Martin 1993). We might expect breeding birds to select nest sites in order to maximise their fitness (Williams 1966). For many species, this objective requires the maximum production of young at the minimum risk of adult predation. Habitat type and nest concealment are two factors widely thought to influence nest predation (Collias and Collias 1984, Martin 1993, Götmark et al. 1995). A number of studies have shown that upland-breeding shorebirds tend to nest on flat or gently sloping ground and avoid more steeply-sloping ground (Ratcliffe 1976, Haworth and Thompson 1990, Brown and Stillman 1993, Galbraith et al. 1993, Stillman and Brown 1994). However, to date no studies have investigated this selection in detail, nor attempted an explanation for the observations. We examine the influence of slope and habitat type on nest-site selection and the influence of these two predictors and concealment on nest survival in golden plover *Pluvialis apricaria*, a ground-nesting shorebird.

Ground-nesting species are particularly vulnerable to predation, especially in grassland shrub habitats (Lack 1968, Martin 1993). The golden plover is one such ground-nesting species with a strong association with flat to gently-sloping ground. It is widespread, nesting in the UK on unenclosed uplands from Dartmoor to Shetland (Gibbons et al. 1993). There have been a number of studies of its ecology (e.g. Ratcliffe 1976, Byrkjedal 1980, 1989, Parr 1980, 1992, Yalden and Yalden 1989a, 1990, Brown 1993, Whittingham et al. 2000a) but none have investigated nest-site selection or survival in relation to slope.

We tested three null hypotheses: first, that golden plovers positioned their nests in proportion to the area of slopes and of habitats available to them; second, that nest survival did not vary with slope, habitat or nest concealment; and third, that plumage characteristics (previously suggested as an indicator of dominance) did not vary with slope.

Methods

Study areas

The study was conducted on two moorlands in the north Pennines, County Durham, UK from 1992 to 1996. Both areas comprised a mix of blanket bog-dominated plateaus and slopes, although a greater proportion of the area of Chapel Fell was sloping. Widdybank Fell (54°40′N, 2°16′W) forms part of Teesdale National Nature Reserve and is a heather-dominated moorland primarily managed as a red grouse *Lagopus lagopus* moor. Chapel Fell (54°43′N, 2°12′W) site is used primarily for sheep grazing, with a mosaic of heather *Calluna vulgaris* and grassland, high sheep densities and no heather burning. The two sites provide a range of nesting habitats for golden plover.

Nest finding and monitoring

Golden plover nests were located by systematically traversing the study areas on foot, locating birds as they flushed from the nest (Ratcliffe 1976). When nests were located, the length, breadth and weight of all the eggs were measured to estimate hatching date (Drent 1970, Yalden and Yalden 1989b, Whittingham 1996). Nests were visited at 3–4 day intervals and their contents recorded until they either hatched or failed. Visit frequency was increased as hatching approached to check whether the nest was successful (the chicks remained in the nest for approximately 24 hours). Nests were classified as depredated if one egg, or more, was taken by a predator or disappeared. We were able to identify the predators of some nests from the egg remains (Green et al. 1987). Nests that were deserted were treated as successful up until the day the adult birds deserted the nest (the midpoint from the last time the nest was active and when the nest was found to be deserted). Depredated nests were treated as failed and all other nests as successful (except deserted nests which were treated as successful up to desertion) in all nest survival models (see below).

Slope and habitat measurements

Nest-site selection was initially investigated by comparing the characteristics of nest sites with those of the habitats available on the study sites. Availability was measured from habitat maps of each study site (Whittingham et al. 1999, 2000b). Habitat maps of the study sites, to National Vegetation Classification (NVC) standard (Rodwell 1991a, b), were constructed using a combination of aerial photographs, a base map of Widdybank Fell constructed by Jones (1973), data collected by Percival and Smith (1992) and ground surveys.

The observer (MJW) measured the slope between the nest itself and a point 10 m distant using a clinometer. Slope was recorded from 55 nest scrapes. The five nests for which slope was not recorded were all used in 1992 and the nests could not be located during the following year. We compared the slopes of nests with 100 random slope measurements, 50 on each study site. Random points to make slope measurements were chosen by overlaying a 10×10 cell grid on each 1 km square of the map of each study site and randomly selecting 50 numbers from the total number of cells, each cell being allocated a different number. Any random point which landed on a cell comprising an unsuitable area for nesting golden plover (i.e. cliff, road or quarry) was ignored and another cell chosen. We therefore only considered slopes from areas that could potentially be occupied by golden plover nests.

We measured nest concealment in two ways: vegetation density and vegetation height. Vegetation density was measured by embedding a 1 m rule with alternate 1 cm colour bands into the earth immediately next to the nest scrape and recording the number of 1 cm lines obscured by vegetation from a point 1 m away from the rule. Vegetation height at the nest was taken as the mean from four measurements (from north, south, east and west) taken at the nest. Each measurement was taken as the highest piece of vegetation touching a rule placed touching the side of the nest scrape.

Plumage

Differences in nest survival rates may result from differences in the 'quality' of individual birds. The extent of black on the underparts has been suggested as an indicator of dominance and dark males have been shown to pair with dark females (Parr 1980, Edwards 1982). Male and female birds were each separately assigned a plumage score from 1 (lightest) to 7 (darkest) using the grading system illustrated in Parr (1980).

Statistical analyses

We located a total of 66 nest scrapes. We sampled nests on the same sites for five years. We avoided problems of pseudoreplication, in part at least, by excluding the following: nests located in the same nest scrape as in a previous year (6 nests); and nests found where one, or both, of the parents were previously known (from colour ringing) to have had a nest found previously during the study (11 nests). This reduced the size of the dataset to 49 nests. At least one of the parents from 31 of the 49 nests was colour-ringed. Therefore the same individuals may have tended more than one nest even in the reduced dataset of 49 nests.

Nest-site selection

We tested the null hypothesis that the 49 nests were distributed at random with respect to habitat on the two study sites using Chi-square goodness of fit tests. Study sites were tested independently because different habitats were available on each site. Due to small sample sizes, the nests found were lumped into a smaller number of categories. This reduced expected values to greater than 5 in all but one case where it was 4.56. We therefore used Yates correction. These categories, along with their National Vegetation Classes (Rodwell 1991a, b) shown in parentheses, are detailed below for Chapel Fell: grass & marsh dominated (U6, U2, U5, M6, M3 and M7); cotton grass *Eriophorum vaginatum* dominated (M20); and mature heather dominated (M20 subcommunity *Calluna vulgaris*, heather covering $>50\%$ of quadrats, Whittingham 1996). The groupings on Widdybank were: grass & marsh dominated (CG9, U5, M10, M6 and M20); recently burnt (within past two years) heather dominated and cotton grass dominated (H12 and M20); and mature heather dominated (burnt more than two years ago) (H12).

Nest survival

Logistic regression was used to model daily nest-predation rates. We used a binomial error structure and a logit link function, with nest fate (one or more eggs depredated = 1, no eggs depredated = 0) as the binomial response variable, and the number of days that the nest was exposed to the risk of failure after it had been found ('exposure days') as the binomial denominator (Aebischer 1999). The number of exposure days was taken to be the number of days from nest discovery to estimated failure date (Mayfield 1961, 1975). The date of failure was estimated as the mid-point between the date when the nest was last known to be active and the date on which it was found to have failed (Mayfield 1975). This method assumes that the daily nest-survival probability remains constant during the nesting period.

In the nest analysis the backward deletion method described by Crawley (1993) was used to identify those variables that accounted for a significant amount of the variation in the response variable. The full model was fitted initially with all variables included. The statistical significance of each variable in the model was assessed by the change of deviance (ΔD) recorded by removing it or then adding it back to the model. This change in deviance is distributed asymptotically as χ^2. The variable whose exclusion caused the smallest change in deviance was deleted from the model provided that this change was not significant at $P = 0.05$. The Minimum Adequate Model (MAM) was reached when no variables could be either deleted or added to the model without causing a significant change in deviance. Linear and quadratic relationships were explored by fitting simple linear terms and squared terms. Modelling was carried out using GLIM 4.0 (NAG 1993).

We were interested in investigating the effects of habitat, slope and concealment on golden plover nest survival. We constructed three models using different subsets of data to investigate the effect of each of these three predictors on nest survival. Model 1 (habitat) investigated the relative effects of habitat (habitat classes as defined in 'Nest site selection' section above but with recently burnt heather as a separate category), whilst also controlling for other nuisance variables (namely study site, hatch date and year), on nest survival rate in 48 nests. Model 2 (slope) investigated the effect of slope, in addition to the predictors included in Model 1, on the probability of nest survival. Model 2 was applied to a reduced dataset of 43 nests for which we had slope data (data on slope were not recorded for some nest sites during 1992). Model 3 (concealment) investigated the effect of the two measures of concealment, in addition to the predictors included in Model 2, on nest survival. Model 3 was applied to a reduced dataset of 31 nests for which we possessed density and height measures (data on vegetation structure of nests were not collected for 10 nests in 1992, one in 1993, one in 1995 and all nests in 1996). Data from one nest were omitted from all three models because hatch date was not known. The inclusion of this information in models 1–3 did not alter any of the conclusions drawn.

As nest survival might vary with the age of the nest when found and this may have influenced model construction (because nest survival was assumed to be constant), we tested for associations, using appropriate tests (Siegel and Castellan 1988), between age when nest was found and all the predictors in the three models. The probability values for each association were all non-significant ($P > 0.10$ in all cases).

It is possible that slope was related to habitat type and therefore results of nest survival models may have reflected this association. We tested the association between slope and habitat in two ways. First, we classified habitat in two groups as either grass-dominated (U6, U2, U5, M20 and CG9) or heather-dominated (M20 Subcommunity *Calluna vulgaris* and H12). Second, we classified habitat as either dark (H12 < 2 years old and > 5 years old, M20 Subcommunity *Calluna vulgaris*) or light (U6, U2, U5, CG9, H12 2–5 years old).

Plumage

We investigated the relationship between slope on which the nest was found and the plumage of the owner. Data were only used from one individual per pair as birds are known to pair assortatively by plumage, lighter birds being found together (Parr 1980). Data on plumage scores were pooled from males and females due to small sample sizes. Plumage was scored as either dark (six for males and four for females) or light (four or five for males and two or three for females) using the system devised by Parr (1980). Slope was classified as either flat (0°) or sloping (2–8°). Six and four were the highest scores assigned to males and females respectively in our study. We used Chi-square tests, with Yates' correction where appropriate, to compare slope with plumage.

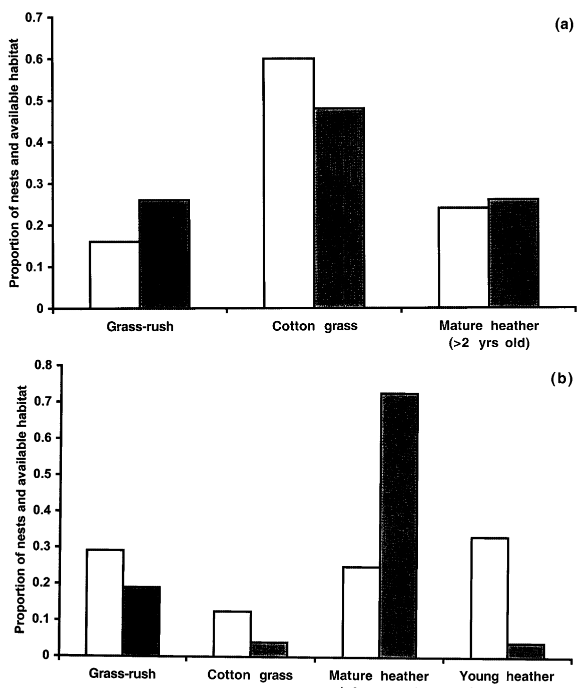

Fig. 1. Golden plover nest sites and habitat availability on (a) Chapel Fell (n = 25 nests) and (b) Widdybank Fell (n = 24 nests). Unshaded bars represent the proportion of nests in each habitat and shaded bars represent the proportion of habitat available. There was no young heather on Chapel Fell.

Results

Nest-site selection

Golden plover clearly showed strong selection for flat and gently sloping area on both of the study areas. The median slope of nest areas on Chapel Fell was 1° (n = 23) compared to a random point slope of 7° (n = 50) (Mann-Whitney test, W = 2585.5, $P < 0.001$) and on Widdybank, the median was 0° (n = 21) and the random point slope 3° (n = 50) (Mann-Whitney test, W = 2216.0, $P < 0.001$). Random point slopes on Chapel Fell were steeper on average than on Widdybank (W = 2092, $P < 0.001$, n = 100) but the slopes of the nest areas on the two sites did not differ significantly (W = 949, P = 0.16, n = 44). In other words, despite the greater area of steeper ground on Chapel Fell, birds still selected flat areas on which to nest.

Figs 1a and b compare the proportion of nests associated with each of the main habitats available on Chapel Fell and Widdybank. Birds at Chapel Fell showed no significant preferences for nesting habitat: the habitats in which nests were located did not differ from that expected if the birds nested at random ($\chi^2 =$ 1.75, d.f. = 2, P = 0.42). At Widdybank there was significant nest-habitat selection; birds avoided mature heather and selected young heather, *Eriophorum vaginatum* mire and grass-rush habitats ($\chi^2 = 13.25$, d.f. = 2, $P < 0.002$ after Yates' correction).

Nest survival models

Of the total of 66 nests; 27 (41%) hatched successfully, 37 (56%) were depredated and two were deserted. Of the nests preyed upon, 14 were taken by stoats *Mustela erminea*, five by corvids, one by a hedgehog or badger and 17 by unknown predators. Twenty-five of the 44 nests used in model 2 (which investigated the effect of slope) were depredated, 10 were taken by stoats, two by corvids and the predators were not identified in 13 cases.

Neither habitat, year, site nor hatch date was found to have a significant effect on nest survival in any of the three models ($P > 0.24$ in all cases). Slope was found to be significantly negatively associated with nest survival in both the models in which it was included: model 2 ($\chi^2 = 5.82$, d.f. = 1, $P < 0.02$) and model 3 ($\chi^2 = 4.03$, d.f. = 1, $P < 0.05$). Neither of the measures of concealment, vegetation height (P = 0.50) and density (P = 0.76), was found to affect nest survival in model 3.

The daily failure rates, the number of nest exposure days and nest failures for each category of slope for the 43 nests in model 2 are presented in Table 1. To test whether the few nests on steeper slopes were unduly influencing the data, we repeated models 2 and 3 with slope included as a two-level factor with category 'a' as

Table 1. Failure rates of nests with respect to the slope on which the nest was located.

Slope on which nest located (in degrees)	Daily failure rate (numbers of failed nests/exposure days)	Sample size
0	0.028 (9/319)	22
1	0.038 (2/52.5)	4
2	0.042 (4/94.5)	6
3	0.082 (4/49)	4
4	0.051 (2/39)	3
5	0.078 (2/25.5)	2
6	0.087 (1/11.5)	1
8	0.18 (1/5.5)	1

Table 2. Plumage characteristics of birds with respect to the slope on which their nest was situated. We scored birds using the system illustrated in Parr (1980). Dark-plumaged birds scored six (males) and four (females); light-plumaged birds scored four or five (males) and two or three (females).

		Slope on which nest located	
		Flat (0°)	Sloping (2–8°)
Plumage	Dark	8 (all male)	9 (7 male)
	Light	14 (7 male)	1 (0 male)

nests on slopes of 0° or 1° and category 'b' as nests on slopes 2° or more. Slope was still significantly ($P < 0.05$) negatively related to nest survival in both cases. To illustrate the different fates of nests over the 30-day incubation period, a nest on a slope of 0° or 1° would have a 41% chance of reaching hatching without being preyed upon. In contrast, a nest on a slope greater than 2° would have only a 15% chance of hatching without some, or all, of the eggs in the nest being depredated.

We investigated how robust the effect of slope was by re-running model 2 with a sub-set of data from 30 nests with at least one parent known to be independent (as shown by colour-ringing). Slope was still found to have a significant negative effect on nest survival ($\chi^2 = 6.08$, d.f. = 1, $P < 0.02$), whilst no other predictors had a significant effect. We also ran the model with all 66 nests and also found slope had a significant effect ($\chi^2 = 5.26$, d.f. = 1, $P < 0.03$), with no other predictors being significant.

Slope (either as a variable or a two-level factor, see above) was not related to the height of vegetation at the nest, hatch date, the density of vegetation at the nest or habitat type (grass vs heather or light vs dark) ($P > 0.15$ in all cases).

Plumage of birds nesting on different slopes

Plumage characteristics of parents were related to the slope on which their nests were found. Plumage scores were significantly lower for males and females nesting on flat areas (0°) than those nesting on slopes (2–8°) ($\chi^2 = 5.94$, d.f. = 1, $P < 0.02$ after Yates' correction). The scores for both males and females are shown in Table 2. There was no tendency for birds with light plumage to breed earlier than those scored as dark ($T = 0.94$, d.f. = 31, $p = 0.37$).

Discussion

Why do nests survive longer on flat ground?

We can think of at least three mechanisms that could result in nests surviving longer on flat ground. First, there may be differences in the habitats between slopes and plateaus that affect nest survival rates directly. Clearly, more subtle habitat differences than were measured by this study do exist between slopes which could affect nest survival, but we do not believe that these differences are sufficient to explain the differences we observed: there were no significant differences in vegetation height around nests on slopes and on plateaus and subtle habitat differences seem unlikely to affect nest survival when quite large scale differences did not (model 1). Second, visibility (specifically field of view) may be greater from a nest on the flat than on a slope (nearly all slopes were convex), allowing incubating birds nesting on flat ground to detect ground-hunting predators (such as stoats, which depredated most of the nests in our study) earlier, thus reducing predation risk. Golden plovers tend to leave their nests at a considerable distance (hundreds of metres) from approaching ground-hunting predators (Byrkjedal and Thompson 1998) and so a good field of view is likely to be vital to the success of their anti-predator behaviour (Koivula and Rönkä 1998). This may explain the birds' propensity to nest in short vegetation and their habit of constructing nests on the tops of tussocks or clumps of vegetation (Ratcliffe 1976, Whittingham 1996, Byrkjedal and Thompson 1998). If the poorer view of the surroundings of birds breeding on slopes were the cause of the difference in nest survival this would provide a mechanism to explain the selection of plateaus. Third, there may be indirect effects of habitat on nest survival. Let us assume that flat areas provide better habitats (for adults and/or chicks) and that they are therefore occupied preferentially to sloping areas (see below). The differences in nest survival rate may then be a consequence of variability in individual fitness (e.g. individual differences in responses to predators) and not a difference in nest visibility. The consistent differences in plumage between birds nesting on slopes and on plateaus suggests that there is a difference between individuals occupying these sites. Hegyi and Sasvári (1998) noted that heavier lapwing *Vanellus vanellus* and black-tailed godwit *Limosa limosa* increased both their incubation bouts and their care for broods, both of which are likely to enhance reproductive success. This study cannot disentangle the influences of the second and third explanations given above and we believe both are worthy of further study.

How likely is it that plateau areas provide better habitats for golden plover? Extensive stands of heather are avoided by both chicks (Whittingham et al. 2001) and adults (Whittingham et al. 2000a). In contrast, both chicks and adults select grassland. We tested for an association between ratios of grass to heather on flat versus sloping ground but found no significant relationship ($\chi^2 = 2.67$, d.f. = 1, $p = 0.10$, $n = 44$ random points). However, the peat on the tops of hills is often thicker and consequently wetter than on slopes, allowing marshy patches to form. This may facilitate deeper probing by birds for soil invertebrates as well as supporting different surface-dwelling invertebrate communities (Coulson 1988). We tested for differences in re-sighting/survival of broods (using logistic regression, see Whittingham et al. 1999) between nests on slopes and nests placed on flat ground, but found no difference ($\chi^2 = 0.27$, d.f. = 1, $P = 0.60$, $n = 16$ broods), though this was based on a small sample size.

We found darker birds tended to nest on slopes, on which nests were less likely to survive. The findings from our study suggest that birds with more black on their plumage are likely to be less dominant (presuming that intra-specific competition excluded dark-plumaged birds from plateaus with flat nest sites). This is in contrast to the predictions of Edwards (1982) who found darker males were dominant to lighter ones.

Could there have been more predators on slopes than on flat areas?

Overall, in 70% of the cases (from the total dataset of 66 nests) when the nest predator was identified, the predator was a stoat (83% in the subset of nests used in the model 2, which investigated the effect of slope). Therefore it seems likely that stoats took most of the nests. Stoats often move over distances greater than one kilometre in a day and often much further (Sandell 1986) and some individuals were watched crossing large tracts of both study sites (MJW, pers. obs). It therefore seems unlikely that the density of the relevant predators differed between slopes and plateaus within our study areas.

Management of heather moors for golden plover

Other factors also affected the birds' choice of nest sites but were less significant than slope. Birds avoided mature heather and selected recently burnt patches of heather (present only on Widdybank) but otherwise showed no clear habitat selection. Heather moor managers may therefore wish to consider enhancing conditions for nesting golden plover by burning heather on a short rotation. This should be done in conjunction with a series of other measures to maintain or encourage habitat suitable for both chicks (e.g. providing heather/grass mosaics and marshes, Whittingham et al. 2001), and adults (e.g. encouraging retention of calcareous grassland and earthworm-rich enclosed fields near the moorland edge, Whittingham et al. 2000a).

It is traditionally considered that concealment is beneficial to nesting birds (see Martin 1992) but recent work has shown that this is not always the case. Koivula and Rönkä (1998) found that nest success in Temminck's stints *Calidris lemminckii* was higher in more open habitats with greater visibility (wide as opposed to narrow shorelines) but that it was unrelated to microhabitat differences. Filliater et al. (1994) and Götmark et al. (1995) have both shown that the nest success of passerines using cup-shaped nests was not correlated with their degree of concealment. It has thus been suggested that there is some kind of trade-off between nest concealment and the adult's view of the surrounding area (Götmark et al. 1995). Our study suggests that the field of view may be an important component of golden plover nest-site selection. If golden plovers relied solely on their cryptic plumage and tendency to build nests in tussocks of vegetation for concealment as a guard against predation (see Ratcliffe 1976, Whittingham 1996), then a restricted view would not be an important consideration when choosing a nest. Further work on other upland species that have been shown to avoid slopes may reveal similar relationships with slope.

Conclusions

Golden plovers strongly select nest sites on flat ground and such nests are less prone to predation than those on slopes. This finding is consistent with those from wider-scale studies of the distribution of upland breeding birds which indicate strong associations, not only of golden plover, but also of other shorebird species, with flat ground (Haworth and Thompson 1990, Brown and Stillman 1993, Stillman and Brown 1994). We found that golden plovers on slopes tended to be darker on the underparts, suggesting possible differences in individual quality between birds nesting on sloping as opposed to flat ground. Differences in nest survival may be due to differences in individual effectiveness in responding to predators and/or impairment of view, but our study cannot distinguish between them. Future work could attempt to test for differences in the responses to predators of birds nesting on slopes and on flat ground. In addition, future work should concentrate on following individuals over longer time periods to examine individual nest-site preferences between years.

Acknowledgements – We would like to thank Lord Barnard, Raby Estate and the tenant farmers for permission to carry out this study on their land. We are particularly grateful for all the assistance from Lindsay Waddell. Thanks also to Chris Smith, Ian Findlay, Paul Eady, Simon Hodge, Tracey Percival, Laura Livingston, Glen Robson and Chris Spray. Thanks to Sue Holt, Will Cresswell, Adam Watson and Jim Reynolds for constructive criticisms of earlier drafts of the manuscript. The work was funded jointly by English Nature and Northumbrian Water.

References

Aebischer, N. J. 1999. Multi-way comparisons and generalised linear models of nest success: extensions of the Mayfield method. – Bird Study 46 (supplement): S22–31.

Brown, A. F. 1993. The status of the golden plover in the southern Pennines. – Bird Study 40: 196–202.

Brown, A. F. and Stillman, R. A. 1993. Bird-habitat associations in the eastern highlands of Scotland. – J. Appl. Ecol. 30: 31–42.

Byrkjedal, I. 1980. Summer food of the golden plover *Pluvialis apricaria* at Hardangervidda, Southern Norway. – Holarct. Ecol. 3: 40–49.

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

Byrkjedal, I. and Thompson, D. B. A. 1998. Tundra plovers: the Eurasian, Pacific and American golden plovers and grey plover. T and AD Poyser, London.

Collias, N. E. and Collias, E. C. 1984. Nest building and bird behaviour. Princeton University Press, Princeton, New Jersey.

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

Crawley, M. J. 1993. Methods in ecology: GLIM for ecologists. Blackwell Scientific Publications, Oxford.

Drent, R. H. 1970. Functional aspects of incubation in the herring gull *Larus argentatus*. – Behaviour Supplement 17: 1–132.

Edwards, P. J. 1982. Plumage variation, territoriality and breeding displays of the golden plover *Pluvialis apricaria* in southwest Scotland. – Ibis 124: 88–95.

Filliater, T. S., Breitwisch, R. and Nealen, P. M. 1994. Predation on northern cardinal nests: does choice of nest site matter? – Condor 96: 761–768.

Galbraith, H., Murray, S., Duncan, K., Smith, R., Whitfield, D. P. and Thompson, D. B. A. 1993. Diet and habitat use of the dotterel *Charadrius morinellus* in Scotland. – Ibis 135: 148–155.

Gibbons, D. W., Reid, J. B. and Chapman, R. A. 1993. The new atlas of breeding birds in Britain and Ireland: 1988–1991. T and AD Poyser, London.

Götmark, F., Blomqvist, D., Johansson, O. C. and Bergkvist, J. 1995. Nest site selection: a trade-off between concealment and view of the surroundings? – J. Avian Biol. 26: 305–312.

Green, R. E., Hawell, J. and Johnson, T. H. 1987. Identification of predators of wader eggs from egg remnants. – Bird Study 34: 87–91.

Haworth, P. F. and Thompson, D. B. A. 1990. Factors associated with the breeding distribution of upland birds in the South Pennines, England. – J. Appl. Ecol. 27: 562–577.

Hegyi, Z. and Sasvári, L. 1998. Parental condition and breeding effort in waders. – J. Anim. Ecol. 67: 41–53.

Jones, A. V. 1973. A phytosociological study of Widdybank Fell in Upper Teesdale. – Unpubl. Ph.D. thesis, University of Durham, Durham.

Koivula, K. and Rönkä, A. 1998. Habitat deterioration and efficiency of antipredator strategy in a meadow-breeding wader, Temminck's stint *Calidris temminckii*. – Oecologia 116: 348–355.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

Martin, T. E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? – In: Hagan, J. M. III and Johnston, D. W. (eds). Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, DC, pp. 455–472.

Martin, T. E. 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. – Am. Nat. 141: 897–913.

Mayfield, H. F. 1961. Nesting success calculated from exposure. – Wilson Bull. 73: 255–261.

Mayfield, H. F. 1975. Suggestions for calculating nest success. – Wilson Bull. 87: 456–466.

NAG 1993. General linear interactive modelling. The Numerical Algorithms Group Ltd., Oxford, UK.

Parr, R. 1980. Population study of golden plovers, *Pluvialis apricaria*, using marked birds. – Ornis Scand. 11: 179–189.

Parr, R. 1992. The decline to extinction of a population of golden plover in Northeast Scotland. – Ornis Scand. 23: 152–158.

Percival, S. M. and Smith, C. 1992. Habitat requirements of golden plover: a pilot study. – English Nature research report no. 1. English Nature, Peterborough.

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

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. – Smithsonian Contrib. Zool. 9: 1–48.

Rodwell, J. (ed.). 1991a. British plant communities. Vol. 2: Mires and Heaths. – Cambridge University Press, Cambridge.

Rodwell, J. (ed.). 1991b. British plant communities. Vol. 3: Grasslands and Montane Communities. – Cambridge University Press, Cambridge.

Sandell, M. 1986. Movement patterns of male stoats *Mustela erminea* during the mating season: differences in relation to social status. – Oikos 47: 63–70.

Siegel, S. and Castellan, N. J. 1988. Nonparametric statistics for the behavioral sciences. McGraw-Hill, Singapore.

Stillman, R. A. and Brown, A. F. 1994. Population sizes and habitat associations of upland breeding birds in the South Pennines, England. – Biol. Cons. 69: 307–314.

Whittingham, M. J. 1996. Habitat requirements of breeding golden plover, *Pluvialis apricaria*. – Ph.D. thesis, University of Sunderland.

Whittingham, M. J., Percival, S. M. and Brown, A. F. 1999. Evaluation of radiotelemetry methods in measuring habitat choice by young Golden Plover *Pluvialis apricaria* chicks. – Bird Study 46: 363–368.

Whittingham, M. J., Percival, S. M. and Brown, A. F. 2000a. Time budgets and foraging of breeding golden plover *Pluvialis apricaria*. – J. Appl. Ecol. 37: 632–646.

Whittingham, M. J., Percival, S. M. and Brown, A. F. 2000b. Time budgets and foraging of breeding golden plover *Pluvialis apricaria*. – J. Appl. Ecol. 37: 895–895.

Whittingham, M. J., Percival, S. M. and Brown, A. F. 2001. Habitat selection by golden plover *Pluvialis apricaria* chicks. – Basic Appl. Ecol. 2: 177–191.

Williams, G. C. 1966. Natural selection, the cost of reproduction and a refinement of Lack's principle. – Am. Nat. 100: 687–690.

Yalden, D. W. and Yalden, P. E. 1989a. The sensitivity of breeding Golden Plovers *Pluvialis apricaria* to human intruders. – Bird Study 36: 49–55.

Yalden, D. W. and Yalden, P. E. 1989b. Estimating the date of hatching of eggs of Golden Plover *Pluvialis apricaria*. – Wader Study Group Bull. 55: 19–20.

Yalden, D. W. and Yalden, P. E. 1990. Recreational disturbance of breeding golden plover, *Pluvialis apricaria*. – Biol. Cons. 51: 243–262.

(*Received 5 April 2001, revised 12 June 2001, accepted 14 August 2001.*)