Density-dependence and winter weather as factors affecting the size of a population of Golden Plovers Pluvialis apricaria

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The results of annual censuses of a Golden Plover population in the Peak District, covering 24 years, are analysed. A strong density-dependent effect of the population in the previous year explained 26.7% of the variation in population growth. An additional 15.3% of the variation was accounted for by the severity of winter weather, as measured by mean monthly air temperature for November to February. There was no significant effect of weather during the breeding season upon Golden Plover population size, implying that any effects which spring and summer temperature or rainfall may have upon fledging success are masked by other factors. The importance of these results is discussed in the light of work on other wader species, and possible declines in Golden Plover numbers.

There have been few long-term population studies of breeding waders (Charadrii) due to the difficulties involved, and none of them has accurately measured birth rates, death rates, immigration and emigration. Nevertheless, two components are responsible for much of the variation in wader populations: reproductive success and winter mortality. Reproductive success can be affected by a range of factors. Heavy predation, bad weather, and low prey availability can all reduce recruitment and therefore limit population size.

In general, winter mortality appears low in the Charadrii but is dependent upon individual competitive ability and, as a consequence, mortality is greatest amongst first-year birds. Winter is often the time of highest adult mortality and this can limit population size, due to the low reproductive rates of many shorebirds. In particular, death rates can be very high in periods of extreme winter weather, leading to significant reductions in the size of breeding populations.

It is very difficult to assess accurately the relative importance of either reproductive success or winter mortality, due to the inherent problems of monitoring a discrete population throughout the year. However, winter mortality should affect reproductive success in a density-dependent fashion, through competition on the breeding grounds, although Evans & Pienkowski suggest that populations of waders breeding at high latitudes may not be regulated in this way. They argue that weather conditions stochastically affect either recruitment or winter mortality, leading to fluctuations in population size, which largely mask density-dependence. This implies that wader populations are prevented from reaching their carrying capacity by random events of high mortality.

Numbers of breeding Golden Plover Pluvialis apricaria declined in the south of their range by 15% from 1970–1990. Much of this reduction has been linked with a loss of breeding habitat, due to large-scale afforestation of blanket bog and an associated increase in

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predators. Additional changes to the upland landscape, such as a decline in the intensity of moorland management and overgrazing may also have led to losses across some of the range.

The only detailed study of Golden Plover population dynamics has been undertaken at Kerloch, Scotland, following a population to extinction. Despite a high predation rate of clutches, due to a cessation of game keeping, and afforestation near the site, the decline was attributed to poor survival during harsh winters although the low level of recruitment may have prevented a recovery. However, a subsequent reanalysis of these data by Harding et al. casts doubt on these conclusions. They suggest that the observed population decline can be accounted for by the reduction in breeding success, although an effect of winter weather is not totally ruled out. Severe winter weather has been demonstrated to affect adult and first-year survival in the Lapwing Vanellus vanellus. Both Golden Plover and Lapwing winter on lowland pasture and arable land and show reduced foraging efficiency in cold weather. If cold weather persists, flocks undertake costly movements to the coast or continental Europe.

In the Peak District, England, the annual monitoring of a population of Golden Plovers along a section of the Pennine Way long-distance footpath showed a strong decline, leading to the suggestion that recreational disturbance was another factor influencing Golden Plover populations. In particular, numbers recovered somewhat in two years, 1980 and 1984, when the moors were closed to public access during May because of fire risk. This was followed by a more intensive study of this area from 1986–1988 which demonstrated the undoubted behavioural effects of recreational disturbance, but found the population to increase (despite continuing and severe recreational disturbance) over the three years from a low of 14 pairs in 1986 to 29 pairs in 1988.

This casts doubt on the hypothesis that recreational disturbance has affected this population, but leaves the fluctuations in population unexplained. Attempts during the 1986–1989 study to relate them to (breeding season) weather failed, but the subsequent interest in the impact of winter weather on both Golden Plover and Lapwing has prompted this re-examination of the situation.

METHODS

Since 1972, a population of Golden Plovers on the moors between Snake Summit (SK 0891) and Mill Hill (SK 0590) has been monitored annually. The site consists of a 4.6 km² area of blanket bog dominated by Hare’s-tail Cotton Grass Eriophorum vaginatum. A standard route, taking about 7 hours, was walked at the end of May, when censusing efficiency is greatest. All possible territories were visited and the position and sex of Golden Plovers seen were recorded on 1:25 000 scale maps. Although this cannot provide a precise figure for population size, weekly censuses undertaken in 1986–1988 confirm that a single census in May gives a good estimate of the number of territories in a given year and accurately reflects annual changes in the population.

The potential role of weather in affecting Golden Plover population size was investigated using multiple regression analysis in which population growth, calculated using Equation 1, was taken as the dependent variable.

\[
\begin{equation}
\log \text{Population growth rate} = \ln \left( \frac{\text{Population size}}{\text{Population in previous year}} \right)
\end{equation}
\]

Winter (November to February inclusive) weather data for Elmdon, Birmingham, weather station were readily available from Weather Log, and were used as a measure of conditions on the non-breeding grounds. Although the wintering grounds of birds from the Golden Plover population at Snake Summit are not known, they are likely to lie close to the breeding grounds in the lowlands of central or northwest England. Information from Buxton weather station, 19 km south of Snake Summit, at 307 m, provided a measure of conditions on the breeding grounds (April to June inclusive). Data for July to October, and March, were not used because it is unclear whether the birds are located in the uplands or...
lowlands during these times. Measures of temperature and rainfall, which Peach et al.\textsuperscript{14} found significantly to affect over-winter survival in Lapwings, were used as independent variables (Table 1). In addition, previous population size was entered into the model to examine the possibility of density-dependent growth.

Stepwise multiple regression was used to determine the primary factors affecting the

Table 1. Variables investigated for their effect on the growth rate of the Golden Plover population. Note the census occurred at the end of May, so weather data for June are not included in the breeding season variables.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Previous population size</td>
<td>Census result from the previous year</td>
</tr>
<tr>
<td>Previous breeding season rainfall</td>
<td>Total rainfall (mm) at Buxton, from April–June inclusive in the previous year</td>
</tr>
<tr>
<td>Previous breeding season mean monthly mean daily air temperature</td>
<td>Mean monthly mean daily air temperature (°C) at Buxton, from April–June inclusive in the previous year</td>
</tr>
<tr>
<td>Breeding season rainfall</td>
<td>Total rainfall (mm) at Buxton, from April–May inclusive in the census year</td>
</tr>
<tr>
<td>Breeding season mean monthly mean daily air temperature</td>
<td>Mean monthly mean daily air temperature (°C) at Buxton, from April–May inclusive in the census year</td>
</tr>
<tr>
<td>Winter rainfall</td>
<td>Total rainfall (mm) at Elmdon, from November–February inclusive prior to the census</td>
</tr>
<tr>
<td>Winter mean monthly mean daily air temperature</td>
<td>Mean monthly mean daily air temperature (°C) at Elmdon, from November–February inclusive prior to the census</td>
</tr>
</tbody>
</table>

Figure 1. Annual changes in the number of Golden Plover territories at Snake Summit in relation to the mean monthly air temperature of the previous winter.
growth of the study population. All statistics were investigated using SPSS for Windows (SPSS Inc., 1993).

RESULTS

The size of the Snake Summit Golden Plover population averaged 18.5 territories, but fluctuated over the years of the census between a minimum of five territories in 1981 and a peak of 30 territories in 1994 (Fig. 1). Significant declines can be clearly seen in 1977, 1978, 1981 and 1985, which led to a population level below the average from 1977 to 1987, with the exception of 1980. Since 1987, the size of the population has remained consistently above 18.5 territories.

The results from stepwise multiple regression analysis are given in Table 2. The most important factor affecting the degree of population growth was the size of the population in the year prior to the census, which explained 26.6% of the variation (Fig. 2). This suggests that population growth is density-dependent, with the greatest increases in population size occurring after years with a small population. Such density-dependence could be regulated in a number of ways, either through reduced reproductive success in large populations, mediated by some intrinsic factor, or by

Table 2. Results of the stepwise multiple regression analyses to examine the relationship between Golden Plover population size and weather. The T values for variables not in the equation give the significance of each term after both previous population size and winter temperature have been incorporated into the model.

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>Slope</th>
<th>Slope se</th>
<th>T</th>
<th>P</th>
<th>R² (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Variables in the equation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Previous population size</td>
<td>−0.051</td>
<td>0.014</td>
<td>−3.753</td>
<td>0.001</td>
<td>26.6</td>
</tr>
<tr>
<td>Winter temperature</td>
<td>0.252</td>
<td>0.110</td>
<td>2.289</td>
<td>0.033</td>
<td>15.3</td>
</tr>
<tr>
<td>Constant</td>
<td>−0.227</td>
<td>0.466</td>
<td>−0.487</td>
<td>0.631</td>
<td></td>
</tr>
<tr>
<td>Variables not in the equation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Breeding season temperature</td>
<td>1.465</td>
<td>0.159</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Previous breeding season temperature</td>
<td>1.459</td>
<td>0.161</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Previous breeding season rainfall</td>
<td>1.216</td>
<td>0.239</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Breeding season rainfall</td>
<td>−0.918</td>
<td>0.370</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Winter rainfall</td>
<td>0.020</td>
<td>0.984</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 2. Natural log of population growth between two years in relation to the population size in the first year of the pair, as described by the linear regression equation.

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emigration from the study area once the carrying capacity has been reached.

In addition to the strong density-dependent effect outlined above, winter temperature was positively correlated with population growth (Fig. 3). This additional effect accounted for a further 15.3% of the variation in population growth (Table 2) and suggests that cold winter weather increases the level of mortality, resulting in fewer Golden Plovers returning to Snake Summit the following season. The two most deviant points, 1978 and 1981, were years in which sharp population declines coincided with mild winters and cannot be readily explained.

A total of 41.9% of the variation in population growth at Snake Summit is therefore explained by a density-dependent effect of population size and the impact of severe winter weather. The regression equation which describes this relationship is:

\[
\log \text{Population growth rate} = -0.051 \text{Previous population size} + 0.252 \text{winter temperature} - 0.227
\]  

DISCUSSION

Fluctuations in Golden Plover numbers at Snake Summit appear to be under strong density-dependent control, with a ceiling of about 30 territories. Such a ceiling could be produced through a variety of intraspecific competition mechanisms. It is possible that the study site is only large enough to support about 30 territories, for which the birds compete. Excess pairs unable to occupy a territory at Snake Summit would therefore either breed outside the study area, or remain on areas of nearby pasture in non-breeding flocks. Although the maximum density of Golden Plover pairs at Snake Summit is 6.5 pairs km\(^{-2}\) (30 pairs per 4.8 km\(^2\) area) which would be rated as high by Ratcliffe\(^{26}\) and is greater than any density found by Brown,\(^{42}\) even at this level there appear to be unoccupied areas which could support additional territories. An alternative hypothesis is that at such high densities, intraspecific competition between adjacent pairs reduces breeding success to, or below, the level required to maintain the population. As a consequence, true density-dependent population regulation would be achieved. However, without information concerning interactions with other nearby areas of suitable Golden Plover habitat, or data on the size of any non-breeding flock, it is not possible to be sure of the exact mechanism underlying the observed density-dependence. What is clear is that this population of Golden Plovers is not stochastically regulated by weather, largely masking any density-dependent effects, as Evans & Pienkowski\(^{2}\)
suggested may occur in high-latitude waders. However, the severity of winter weather does have a significant impact upon the size of this Golden Plover population. This reiterates the case made by Parr\textsuperscript{20} that winter weather can be an important cause of mortality amongst Golden Plover populations. Harding et al.\textsuperscript{21} cast doubt on the importance of winter weather in this case, due to confounding variables in Parr’s study. Although not entirely ruling out changes in winter survival as a factor affecting the population, they argued that a reduction in breeding success caused by an increase in predators more fully accounted for the population decline documented by Parr. Similar research on the Lapwing has indicated a strong effect of the severity of winter weather, as measured by mean winter soil temperature, upon survival.\textsuperscript{14} Interestingly, there was also a significant correlation between total winter rainfall and Lapwing mortality, but no such relationship was apparent from this study for Golden Plovers. This effect of winter temperature upon Golden Plovers conforms to other studies of wintering waders suggesting that although adult mortality is often low,\textsuperscript{11} episodes of severe weather can depress the breeding population.\textsuperscript{16}

It is perhaps surprising that weather conditions on the breeding grounds did not play a significant role in regulating population size. Wader chicks have been shown to be susceptible to rain and low temperatures,\textsuperscript{7,8} although the effects of weather upon invertebrate prey availability make such relationships complex.\textsuperscript{43} Effects of variation in breeding success on subsequent population size could be masked by the dominant effects of density-dependence and winter weather. Measures of fledging success, which are very difficult to obtain for Golden Plovers, would be needed to assess the precise effect of weather during the breeding season.

Unlike the study population at Kerloch\textsuperscript{20} where nest predation prevented a recovery,\textsuperscript{23,31} the Golden Plover population at Snake Summit has not declined during the study period. It is likely that predation of Golden Plover nests at Snake Summit is low, being a heavily keepered area, which may account for the difference between the two sites. In addition, Parr\textsuperscript{20} suggested that the widespread decline of Golden Plovers may be related to modern farming practices, resulting in less permanent pasture and leading to increased susceptibility of Plovers to sustained frost. This does not appear to have affected the Snake Summit population, although without research on the wintering grounds, one cannot be sure. If changes in agricultural techniques have reduced the survival of overwintering Golden Plovers, this could have implications for the large Fenno-Scandinavian populations which winter in Great Britain.\textsuperscript{31,32,44}

This re-examination of the Snake Summit censuses suggests that recreational disturbance is not the major problem that Yalden\textsuperscript{26} and others have thought it to be. However, the contrast between the heavily disturbed Snake Summit area and the less-disturbed Saddleworth Moors site 15 km further north remains to be explained; there the population from single-visit censuses was 17 pairs in 1971–1973, and 14, 17 and 14 pairs in 1986–1988,\textsuperscript{37,45} demonstrating greater stability than at Snake Summit. In particular, there was no evidence of a low population in 1986 and subsequent recovery, as there was at Snake Summit. It is therefore a tenable hypothesis that recreational disturbance makes Snake Summit a lower quality breeding site than Saddleworth Moors, so that it is avoided by territorial pairs when the population is low. The pattern of settlement at Snake Summit and the evident avoidance behaviour of pairs with chicks\textsuperscript{48} also suggest that it would be premature to discount recreational disturbance entirely as a factor in planning recreational activities on these moors.

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studies of breeding waders. 


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