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FEEDING BEHAVIOR OF NESTING CHOUGHS IN THE SCOTTISH HEBRIDES

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Abstract.—Three pairs of individually color-banded Choughs (*Pyrrhocorax pyrrhocorax*) were studied on the island of Islay during the 1992 incubation and nestling periods (21 April–16 June), to investigate the effects of land management factors on adult feeding behavior. The behavior of individual birds was recorded at 1-min intervals. The land utilized by the birds was mapped by farm management unit (compartment) and the use of these, and of 10 biotopes, were recorded together with nine behavioral activities. A total of 15,128 1-min observations was collected on these birds. All three pairs showed distinct selection for grass pasture (either old or new grassland). Over 90% of each pair's time was spent in food collection activity, and invertebrate sampling suggested that the birds were feeding mainly on soil-dwelling tipulid fly larvae (Diptera: Tipulidae). Analyses of compartment agricultural management characteristics data indicated that the small number of preferentially used compartments were those in which (1) management during June–September 1991 produced medium-high grass sward heights, and (2) management between January and May 1992 produced short, open swards. It is suggested that this combination of seasonal management encouraged high numbers of tipulid larvae in the soil during winter and spring and provided optimum foraging conditions for the birds both before and during the incubation and nestling periods. The implications of the findings for pasture management are discussed in relation to their potential to provide relatively simple agricultural management prescriptions to favor Choughs on Islay during the incubation and nestling periods.

CONDUCTA ALIMENTARIA DE INDIVIDUOS REPRODUCTIVOS DE *PYRRHOCORAX PYRRHOCORAX* EN LAS HÉBRIDES DE ESCOCIA

Sinopsis.—Tres parejas anilladas de individuos de *Pyrrhocorax pyrrhocorax* fueron estudiadas en el 1992 en la isla de Islay, durante el período de incubación y crianza de los pichones (21 de abril al 16 de junio), para determinar los efectos del manejo de la tierra de cosecho en la conducta alimentaria de los adultos. La conducta de las aves fue tomada a intervalos de un minuto. El área utilizada por las aves fue trazada en unidades de manejo agrícola (compartimientos) y el uso de estas y de 10 biotipos, fue recogida en conjunto con nueve actividades de conducta. Se tomaron un total de 15,128 observaciones de un minuto de las tres parejas de aves. Las parejas mostraron diferencias en la selección de pastizales (nuevos o viejos). Estas utilizaron más del 90% del tiempo para buscar alimentos. El muestreo de invertebrados sugiere que las aves se estaban alimentando principalmente de larvas de moscas (Diptera: Tipulidae). El análisis de las características de los comportamientos agrícolas indica que el pequeño número de comportamientos utilizados con preferencia fueron aquellos en donde: 1) el manejo durante junio–septiembre de 1991 produjo pastizales de mediana a alta altura y 2) el manejo entre enero y mayo de 1992 produjo pastizales cortos y abiertos.

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Se sugiere que este tipo de manejo provee para que se establezcan en los suelos números considerables de larvas de tipúlidos durante el invierno y la primavera, lo que a su vez provee de condiciones óptimas para el forrajeo de los adultos durante el período de incubación y el de crianza de pichones. Se discuten alternativas de manejo en beneficio de estas aves en la isla de Islay.

The Chough (*Pyrrhocorax pyrrhocorax*) has a fragmented distribution in the palearctic, particularly in the west (Blanco et al. 1991), and is declining over much of Europe. Over half of the estimated minimum European population of 16,000 pairs is concentrated in Spain, Greece and Italy, most populations are small, and many are declining (Tucker and Heath 1994). Chough are sedentary, there is little evidence of interchange between breeding populations, and previous contractions and declines have eventually resulted in extinctions (e.g., from England in 1947 and Austria in the early 1950s). This history suggests that the viability of many of the surviving small populations in mainland Scotland, Northern Ireland, Brittany and Sardinia with 1, 2, 35 and 30 pairs respectively (Bignal and Curtis 1989), may be doubtful.

In 1985 the Chough was added to Annex 1 of European Community Directive 79/409 on the Conservation of Wild Birds. Article 4 of this Directive requires Member States to designate Special Protection Areas (SPAs) in which the biotopes used by species on Annex 1 are maintained. Those used by Choughs have been described for a number of European areas but there is little published on biotope use during critical periods or on which factors limit Chough productivity. The importance of pastoral agriculture has been recognized for a wide range of biotopes (Bignal and Curtis 1989), but the functional relationships between pasture management and Chough utilization and breeding success have not been investigated in detail. Understanding these relationships will be essential for the successful management of SPAs. The results presented here report on a preliminary investigation of habitat use and foraging behavior of adult Chough while they are provisioning nestlings.

Chough breeding ecology and the annual cycle.—Choughs nest in caves and rock crevices and in artefacts that mimic these conditions. They feed principally on soil-living, surface-active and dung-associated invertebrates in extensive (i.e., managed at low intensity) natural and semi-natural pastures. In Europe the combination of suitable nesting sites and feeding areas is now confined to remote areas, mostly mountain or coastal (Bignal and Curtis 1989). Optimum feeding conditions can occur in a wide range of arid to temperate vegetation types with bare ground and short or open vegetation cover. Strong seasonal shifts occur in diet, including changes in the species of invertebrates consumed and inclusion of cereals, seeds and/or fruit (Blanco et al. 1994, McCracken et al. 1992). Even within areas which appear to be highly suitable for Choughs, however, Chough productivity is often low, suggesting that recruitment is less than adult mortality (Pienkowski 1991).

In Scotland Choughs occur principally on the Hebridean islands of Islay, Jura and Colonsay. This paper concerns preliminary results on biotope selection and use by nesting Choughs on Islay, where over 90% of the Scottish population is found (Monaghan et al. 1989). Here continuing research has identified two factors limiting Chough productivity: high nestling mortality and low post-fledging survival (Bignal et al. 1987, Bignal et al. 1989, Curtis et al. 1989). To appreciate the significance of these "bottlenecks" to population recruitment and the focus of this paper, a brief description of Chough behavior through the year on Islay is given below based on resightings of individually identifiable Choughs (733 color-banded as nestlings in 13 cohorts between 1981 and 1993 and 19 trapped and banded as adults or sub-adults during the same period).

Most Choughs first attempt to breed in their third year, spending their first 2 yr in a sub-adult flock. Established breeders maintain contact with their nest site and their home-range feeding area throughout the year often roosting at or close to their nest. Sub-adults and non-breeding birds form flocks that feed in particular areas and roost communally. During January and February adjacent breeders flock with few territorial disputes. Nest building begins in March and egg-laying in late March or early April. With the onset of egg-laying, pairs become strongly territorial and will not tolerate adjacent pairs in their territories. Incubation begins before the clutch is complete, the most frequent clutch size being five eggs. While the female incubates, the male defends the territory, forages within it and feeds the female at or close to the nest. The young hatch asynchronously and both parents make regular foraging trips to collect food and feed the nestlings by regurgitation.

When the young fledge they stay at or close to the nest for several days (e.g., in a cave) and are fed there by their parents. Thereafter they follow the parents to the foraging areas and beg for food. After a variable period (around 2 wk) the parents move with the fledglings to a sub-adult feeding area and roost with the sub-adults. During this period the fledglings begin to forage for themselves. After 2–3 wk the parents return alone to their home-range. In autumn and winter the pairs forage in the home-ranges, sometimes in flocks with other breeders. The sub-adults, now including fledglings, continue to feed in flocks in particular areas. If the breeders survive the winter, the cycle starts again in the spring.

METHODS

Field methods and analyses.—To compile detailed information on foraging behavior in large, open territories, observations were restricted to three pairs selected for study in March 1992. All six individuals were already color-banded and were nesting in farm buildings that were easily accessible. The sites were close to each other (Fig. 1) and existing knowledge of the approximate territories of the pairs meant that each was known to contain a number of farmland and semi-natural biotopes. Teams of 4–6 observers (volunteers from Earthwatch) spent four 8-d periods following the birds during the nesting period (21–28 April, 5–12 May, 20–26 May, 9–16 June). Each volunteer was provided with a compartment map of the area around each study pair's nest site. This map also con-

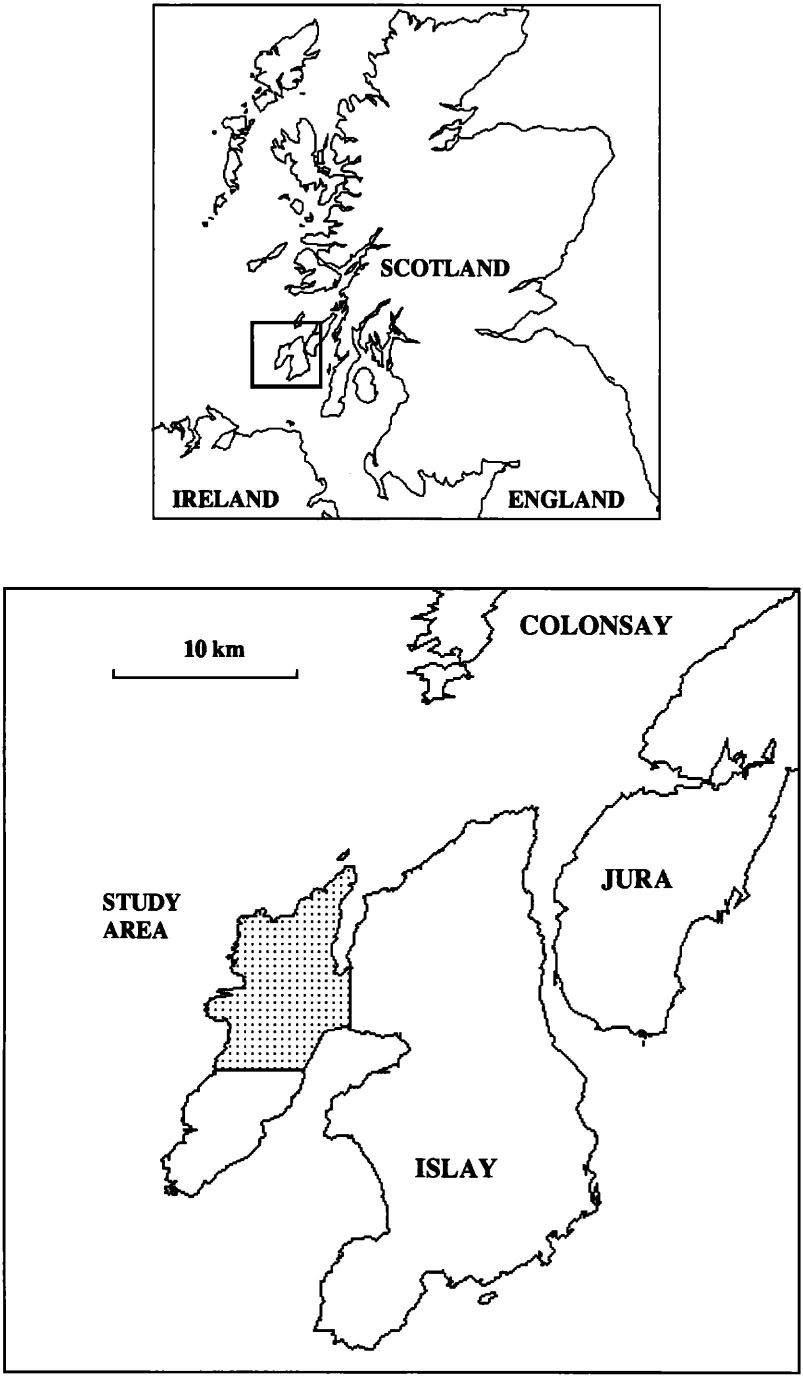

FIGURE 1. The study area on Islay. For security the locations of the nest sites are not shown.

TABLE 1. Definitions of the categories used to describe a focal bird's behavior and the biotope in which it occurred.

Behavior	
Stationary feeding	Intensive pecking, digging or probing in one location.
Mobile feeding	Walking, running and sometimes making short flights within a compartment; pecking at the soil and probing for short periods.
Dung feeding	Feeding in animal dung.
Resting	Preening, sheltering in bad weather, roosting, bill cleaning.
Vigilant	Not feeding and either in an upright posture, wing-flicking, rapid bill wiping or calling.
Interaction	Recorded as being between a pair, with conspecifics or with another species.
Biotope	
New grassland	Pasture ploughed and sown within the last 5 yr. Dominated by agricultural grasses, with few other species, and forming an open sward with patches of bare ground.
Old grassland	Pasture which has never been ploughed or which has been ploughed and sown more than 5 yr ago. Dominated by agricultural grasses and containing a variety of mosses and broad-leaved plants. Sward appears smooth and even with very few tussocks or patches of bare ground.
Rough pasture	Land usually adjoining moorland. Dominated by coarse grasses, sedges, rushes, dead vegetation and sometimes containing small amounts of *Calluna vulgaris*. Mixture of species and vegetation heights gives sward an uneven, rough appearance and there are often many closely spaced tussocks.
Moorland	Mostly unenclosed land with a mixture of vegetation but dominated by *Calluna vulgaris* and containing *Carex* spp. and *Eriophorum* spp.

tained details of the biotopes within each compartment. Bird movements around their territories were relayed between observers by radio and as far as possible the Choughs were always kept in view. Observations were recorded at 1-min intervals to describe behavior and biotope use of focal birds during 33 d of the 57-d nesting period. Definitions of the behavior and biotope categories used are given in Table 1. The selection of biotopes was investigated using the density of 1-min records within each biotope in each territory: occurrence density = (number of one minute records in biotope)/(area of biotope in home range). The territory of each pair during this period was defined by the farthermost boundary from the nest site of all compartments in which they were recorded foraging.

Compartment agricultural management characteristics.—Farmers were interviewed to obtain management details for all of the compartments during the 14 mo prior to July 1992. These details were summarized to provide information on each of six agricultural management characteristics (Figs. 5 and 6). Grazing pressure and herbage length for each compartment were estimated (as none, low, medium or high) using the absolute numbers of livestock and grazing wild geese present in association with the size of compartment, the time of year and the history of grazing/cutting over the previous months. Vegetation heights of 0 cm, <3 cm, 3–7 cm and >7 cm were taken to represent herbage length levels of none, low, medium or high to a Chough. Adjacent compartments with the same management were treated as one in the analyses, reducing the number of compartments under consideration from 44 to 40.

Compartments were initially grouped on the basis of their management characteristics using Detrended Correspondence Analysis (DECORANA: Hill 1979a). Compartments and management characteristics data were ordinated on two axes using DECORANA, with all the management characteristics data being considered after downweighting to minimize the influence of rare variables on the ordination (Hill 1979a). Preliminary DECORANA analysis indicated that while there were two major axes of variation in the data set, the variation appeared to be continuous (i.e., discrete groups of compartments with similar management characteristic associations were not immediately clear). Data sets with continuous rather than disjunct variation are not suitable for classification using conventional classification algorithms such as Two-Way Indicator Species Analysis (Hill 1979b) because they effectively force hard partitions on what is effectively non-discrete data (Equihua 1990). Where variation is continuous, classifications that allow memberships of more than one class are more appropriate. Classification algorithms of this type have been developed from fuzzy set theory.

The fuzzy c-means algorithm used by Bedzek (1981) was used to divide the 40 compartments into groups with similar histories of management characteristics. The first and second axes of the DECORANA ordination were used as descriptor variables for each compartment (Equihua 1990, McCracken 1994). Fuzzy clustering allocates compartments to groups on the basis of membership values, but to provide a visual impression of compartment allocation to groups it was necessary to convert the fuzzy partition into a "hard" partition. This was achieved by assigning each compartment to the group for which it had the highest membership value. These multivariate techniques enabled objective analyses of the data independent of any prior knowledge about the compartments other than the management characteristics data.

Invertebrate sampling.—Invertebrates were sampled during each 8-d observation period in the compartments most frequently used by each pair during that period. Five soil cores (11 cm in diameter and 10-cm deep) were taken at random from within a 2 × 2 m quadrat positioned in the most frequently used feeding area within each of these compartments. Concurrently a control set of five soil cores was collected in each compartment from an area where the birds had never been observed feeding, but which nevertheless was similar to the relevant feeding area with regard to distance and direction from boundary features, vegetation composition and structure, soil conditions and topography. The soil samples were hand-sorted and the larger invertebrate taxa extracted, counted and their size (biomass) estimated in terms of units, where one unit was equivalent

TABLE 2. Details of the three pairs of Choughs studied and their breeding success on the island of Islay during 1992.

		Pair 1	Pair 2	Pair 3
Age (yr)	Male	8	5	3
	Female	9 or 10	7	5
Years at current site	Male	2	3	1
	Female	2	5	3
Laying date (first egg)		12 April	8 April	8 April
Hatching date		6 May	2 May	30 April
Fledging date		18 June	14 June	18 June
Number of eggs		5	6	5
Number of eggs hatched		5	6	5
Number of young fledged		4	4	2

to the biomass of a 1-cm long tipulid fly larva (Diptera: Tipulidae). Thirteen compartments were sampled during the study period (one was sampled five times, three thrice, three twice and six once) providing a total of 26 paired samples. The number of samples associated with each breeding pair (six with pair 1; 12 with pair 2; and eight with pair 3) were too small to allow statistical analysis on a pair basis. The 26 samples were therefore pooled and analysed together, with analyses of invertebrate densities and estimated biomass data being based on $\log(x + 1)$ transformed counts.

RESULTS

Chough breeding details and observation frequency.—Details of the three pairs of Choughs studied and their breeding success are given in Table 2. Over the whole of Islay in 1992 the mean number of young fledged per pair that laid eggs was 2.1 ± 0.3 ($n = 30$ pairs). The frequency of observations of males relative to those of females showed similar trends throughout the season in each of the study pairs. During 21–28 April, approximately 100% of records were of males, since the females were incubating. The frequency of observations of males decreased to 60% during 5–12 May following egg hatching. In the third and fourth observation periods (20–26 May, 9–16 June), equal numbers of male and female observations were recorded for pairs 2 and 3. No sightings were made for the male of pair 1 during the last observation period and this individual was therefore presumed to have died. He was not replaced and the widowed female reared her young unaided.

Compartment utilization.—Figure 2 shows the proportion of visits made by each breeding pair to compartments in their territories. These values are based on the number of visits made by a breeding pair to a compartment, and corresponded closely with the total amount of time spent in the compartment summed for all visits ($r = 0.97$, $n = 48$, $P < 0.001$). Although as many as 25 different compartments were visited by a single pair, most visits were to a small number of compartments. More than half

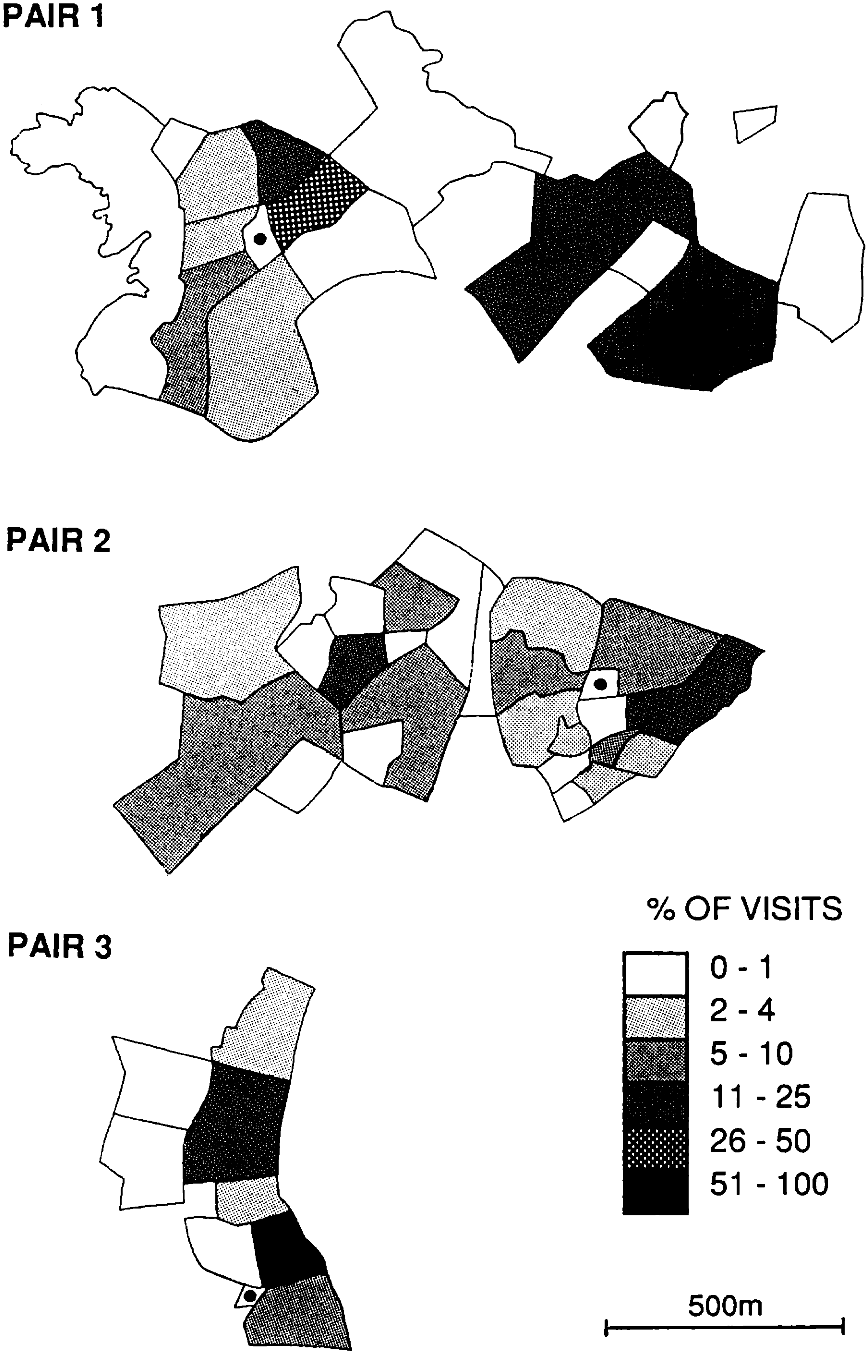
PAIR 1
PAIR 2
PAIR 3
% OF VISITS
0 - 1
2 - 4
5 - 10
11 - 25
26 - 50
51 - 100
500m

TABLE 3. Summary statistics for the compartments used by each of the study pairs within their home-ranges.

		Pair 1	Pair 2	Pair 3
Number		17	25	8
Size (ha)	Mean	12.7	6.4	8.8
	Range	2–38	1–31	4–15
	Total	215	160	70
Distance to nest (m)	Mean	432	315	270
	Range	30–1200	30–830	120–610
Biotope cover (%)	Old grassland	42.1	47.3	41.4
	New grassland	3.3	14.7	30.9
	Rough pasture	42.9	24.6	27.7
	Moorland	11.8	13.3	0.0

of all visits were made to only two, four and one compartments by pairs 1, 2 and 3 respectively. Pair 3 visited a total of only eight compartments and 73% of all visits were made to a single compartment. The compartments most frequently used by all three pairs included locations close to the nest site and others up to one km away. The relationship between the number of visits to a compartment and its distance from the nest site was examined to determine whether travel distance affected compartment choice. No correlation was apparent even after excluding all compartments to which only one visit was made (pair 1: $r_s = -0.071$, $n = 10$, $P > 0.5$; pair 2: $r_s = -0.075$, $n = 23$, $P > 0.5$; pair 3: $r_s = -0.162$, $n = 7$, $P > 0.5$).

A total of 44 compartments was visited by the three pairs (with pairs 1 and 2 using different parts of four compartments) but the size of territories of each pair differed substantially (Table 3). The size of individual compartments (to which more than one visit was made) was not related to the number of visits made by a pair ($r_s = 0.094$, $n = 40$, $P > 0.5$). It was known from the field observations, however, that certain parts of a compartment were preferentially used by the birds, so compartment size is unlikely to be a good indicator of resource patch size. The distribution of compartments visited around the nest site was highly asymmetrical in all cases (Fig. 2). Pairs 1 and 2 visited all compartments encircling the nest site and made joint use of a cluster of compartments approximately 1 km from each nest. Pair 3 visited only eight compartments to the west and north of the nest site. Compartment distribution was constrained to some extent by topography, but at each nest site compartments were present that were not visited despite being visually similar to those used.

Biotope selection.—The percentage covers of major biotopes available in

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FIGURE 2. The proportion of visits made by each pair to compartments in their home-range during the breeding season. Shading indicates the percentage of the total recorded visits made by each pair to individual compartments. Nest sites are indicated by a ●.

the territories of the study birds are shown in Table 3. For an individual bird the relative occurrence densities indicate which biotopes were preferentially used as feeding areas (Fig. 3). Although the different pairs show contrasting occurrence densities in different biotopes, the male and female birds within a pair show similar patterns. The highest occurrence densities for pair 1 were in old grassland. In contrast, occurrence densities were highest for pairs 2 and 3 in new grassland, but also relatively high in old grassland. All three pairs were recorded at low densities in rough pasture and moorland. Old or new grassland were preferred as feeding areas to rough pasture and moorland, but there were no obvious patterns in the relative selection in relation to the age of grassland.

Chough behavior.—The proportions of time spent in different behaviors were similar between all three pairs, and also within pairs. A minimum of 87% of any individual bird's time in a compartment was spent in feeding activities and less than 6% was spent on any other single activity, either resting, being vigilant or in conspecific interactions. All birds except one spent only 3–4% of their total feeding time feeding in dung. The exception was the male bird of pair 3, a young bird breeding for the first time, which fed in dung 12% of the time. The birds in pairs 1 and 2 spent more time mobile feeding than stationary feeding (on average 30% stationary feeding and 58% mobile feeding). This pattern was in contrast with pair 3 where the relative proportions of these feeding activities was reversed (on average 51% stationary feeding and 34% mobile feeding). Stationary feeding implies a clumped food patch, but more detailed observations are required to determine whether prey capture rate is actually higher or whether prey quality is better than when mobile feeding.

Compartment agricultural management characteristics.—The eigenvalues for the DECORANA ordination (which give some indication of the amount of variation associated with each axis) were 0.136, 0.069, 0.040 and 0.026 for axes 1 to 4 respectively. In other words, 50% of the between-compartment variation in management characteristics history accounted for by these four axes was explained by axis 1, 25% by axis 2, 15% by axis 3 and 10% by axis 4. Because axes 1 and 2 accounted for most of the between-compartment variation in history of management characteristics, axes 3 and 4 were not considered any further. Figure 4 shows the compartment scores for the first two axes of the ordination. The largest fuzzy-clustering partition coefficient (0.531) was obtained for the classification of the DECORANA compartment scores based on 5 clusters. These clusters are shown, after hard partitioning, in Figure 4 and details of the "typical" management characteristics of the compartments within each are given in Figures 5 and 6. The compartment groups representing each cluster were described as follows.

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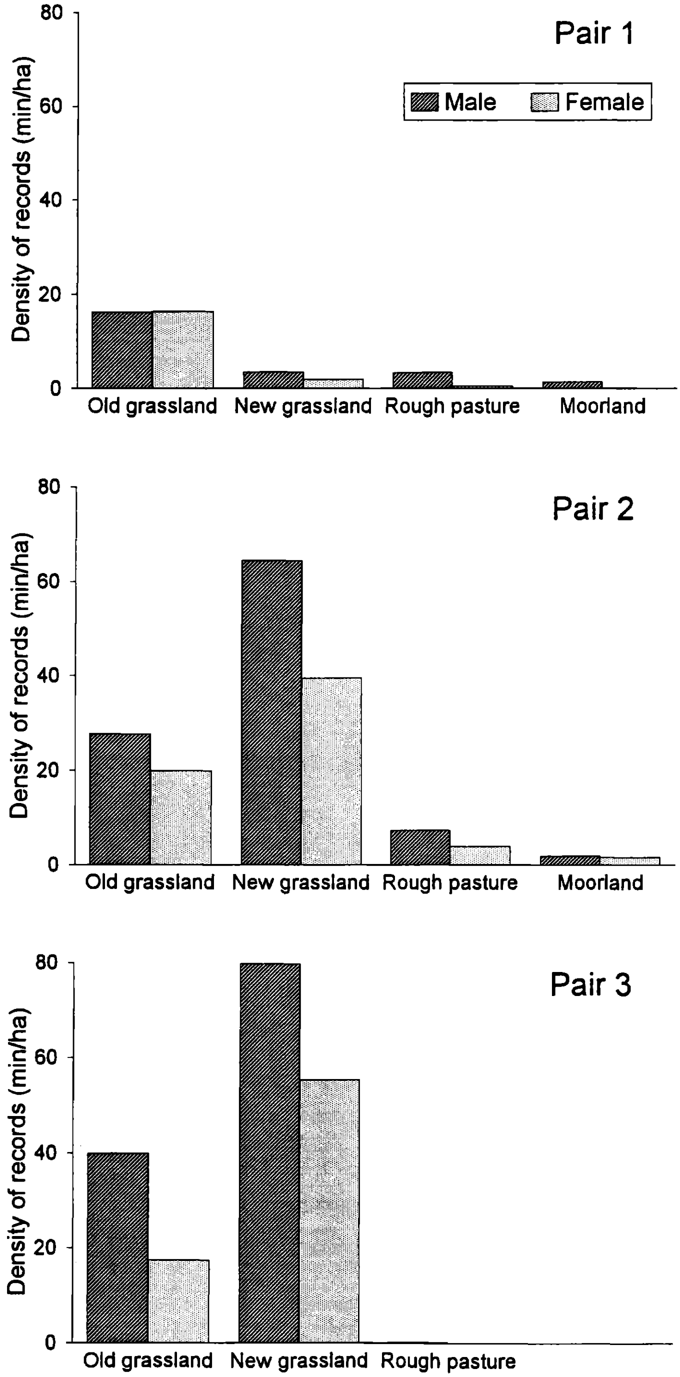
FIGURE 3. The density of 1-min records obtained for each study pair in each of the four main biotopes.


Pair 1
Male
Female
Density of records (min/ha)
80
60
40
20
0
Old grassland
New grassland
Rough pasture
Moorland
Pair 2
Density of records (min/ha)
80
60
40
20
0
Old grassland
New grassland
Rough pasture
Moorland
Pair 3
Density of records (min/ha)
80
60
40
20
0
Old grassland
New grassland
Rough pasture

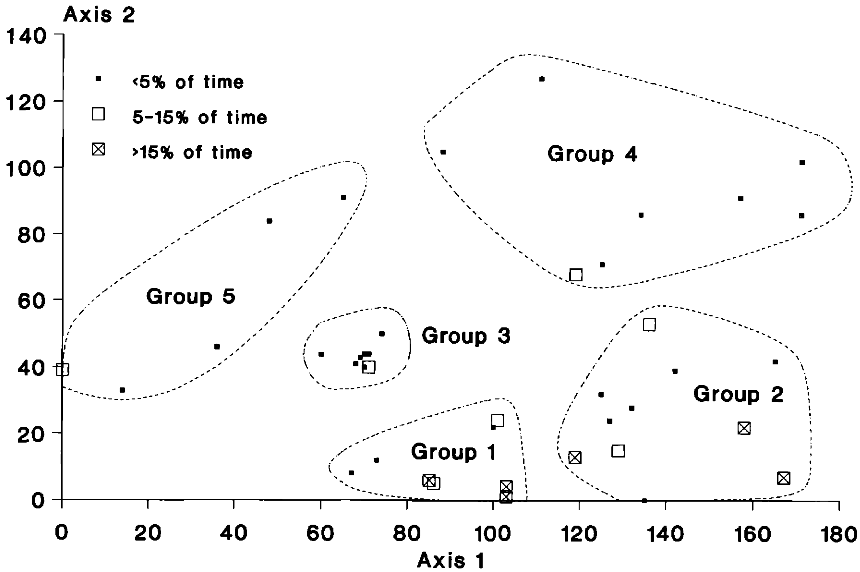


FIGURE 4. Axis 1 by axis 2 plot of the DECORANA ordination of the compartment management characteristics data, with downweighting of rare management variables. Polygons enclose space containing the compartments within each of the groups derived from a hard partition of a fuzzy-c means clustering of the ordination scores. The proportion of time spent by the three pairs of Choughs in each compartment is also shown.

Group 1: Eight old or new grassland compartments used as pastures, grazed mainly by cattle throughout the 14-mo period, with an increase in grazing pressure during the winter months when sheep and geese were also present.

Group 2: Eleven old or new grassland compartments, mainly used for late-cut silage production (and therefore not grazed between May and August) and then grazed heavily by a combination of sheep, cattle and/or geese during the winter months.

Group 3: Eight old grassland compartments, lightly grazed by both sheep and cattle throughout the 14-mo period.

Group 4: A group containing eight mainly old grassland compartments, either not grazed at all or only very lightly grazed (mainly by sheep) between May to October 1991 and February to June 1992. These compartments were only heavily grazed by sheep between November 1991 and January 1992.

Group 5: A small group of five old grassland compartments, lightly grazed by sheep and/or cattle between May to October 1991 and May to June 1992, and not grazed at all between November 1991 and April 1992.

Use of each compartment by the three pairs of Choughs has also been superimposed on Figure 4. Significantly more compartments in groups 1 and 2 and significantly fewer in groups 3, 4 and 5 were used by the study

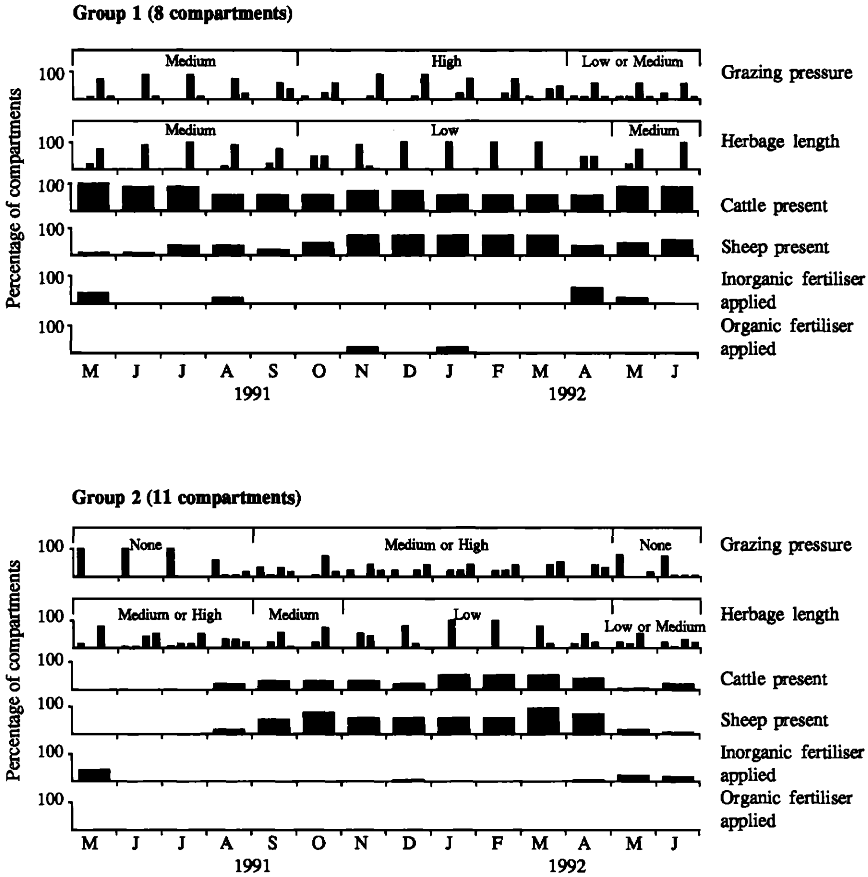
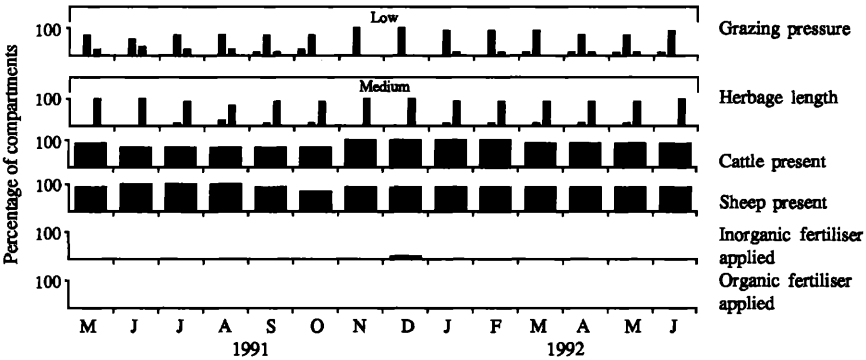


FIGURE 5. The "typical" management characteristics of the compartments within end-groups 1 and 2 recognized after fuzzy clustering of the DECORANA axes scores. Column height indicates the percentage of compartments with the relevant characteristic in each month. For the grazing pressure and herbage length characteristics, the four columns from left to right within each month represent none, low, medium and high levels respectively. Many of the compartments within these groups were utilized by the study pairs for >5% of their foraging time.

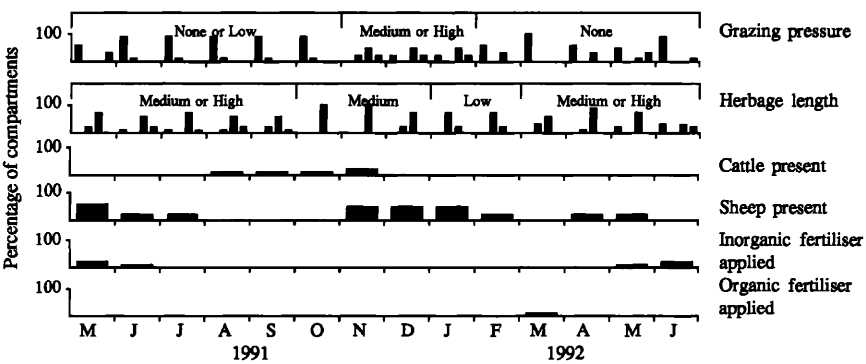
pairs for >5% of their foraging time (contingency table χ^2 after Yates' correction = 6.69, $P < 0.01$).

Invertebrate sampling.—Two main taxa were found in the 26 paired soil samples: earthworms and tipulid larvae. Wilcoxon paired-sample tests indicated that there was no consistent difference in earthworm numbers between feeding and non-feeding areas ($P > 0.5$), but that there were consistently significantly higher numbers of tipulid larvae found at feeding as compared to non-feeding areas ($P < 0.001$). Analyses of the size/biomass data produced the same results and are not presented here.

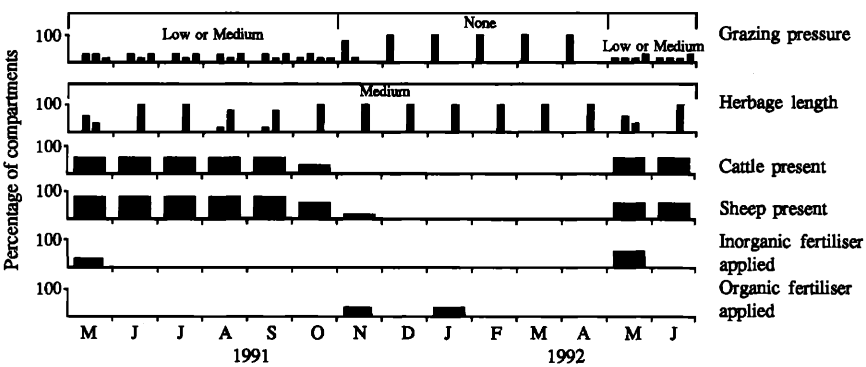
Group 3 (8 compartments)



Group 4 (8 compartments)



Group 5 (5 compartments)



DISCUSSION

Choughs in Europe are associated with farmed land and there is clearly a need to investigate the effects of agricultural management on Chough feeding ecology (Bignal and Curtis 1989). Recent and continuing work in Britain (Bignal et al. 1989, Pienkowski 1991, E. M. Bignal and S. Bignal unpubl. data) and in Spain (Blanco et al. 1991, 1994) has identified that there are (1) different foraging strategies between breeders and subadults, (2) seasonal shifts in diet through the year, and (3) critical periods that may limit recruitment to below the level at which it can meet mortality. Understanding why certain areas are used by breeding birds during one of these critical periods, while others that superficially appear similar are not, is the crux of this paper.

The relationship between compartment agricultural management characteristics and subsequent use by Choughs.—Our results show that pairs selected grasslands preferentially to other biotopes, but that age of pasture was not significant. Behavioral observations indicated that the birds were primarily collecting food from the soil, and invertebrate sampling showed that tipulid larvae were the principal prey items available. On Islay there have been no records of Chough feeding on earthworms (from this or any previous study), and no earthworm remains have been found during examinations of Chough feces (McCracken et al. 1992). Only a small number of compartments were used to any great extent, and the birds foraged in patches where tipulid larvae were more abundant than elsewhere within these compartments.

The field observations suggest that birds knew exactly where to go to find food and that they already had information about patch quality before exploitation. At the very least, the birds would have needed to visit each compartment between January and March (before nest building and egg-laying) to obtain such information. Before January the majority of tipulid larvae in pasture soils are small and therefore probably more difficult to find (McCracken et al. 1992). Observations, made over a number of years, of adjacent breeders feeding together across home-range boundaries during the pre-breeding period have been interpreted as a possible mechanism for locating these "good" compartments (E. M. Bignal and S. Bignal, unpubl. data).

The compartments used preferentially by the birds were those in which (1) management during June to September 1991 produced medium to

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FIGURE 6. The "typical" management characteristics of the compartments within end-groups 3, 4 and 5 recognized after fuzzy clustering of the DECORANA axes scores. Column height indicates the percentage of compartments with the relevant characteristic in each month. For the grazing pressure and herbage length characteristics, the four columns from left to right within each month represent none, low, medium and high levels respectively. Very few of the compartments within these groups were utilized by the study pairs for >5% of their foraging time.

high grass swards (either through a low stocking density of cattle or the growth of late-cut silage), and (2) management between January and May 1992 reduced the sward heights markedly (through intensive grazing by sheep, cattle and/or geese). Compartments from which livestock had been removed by Jan./Feb. 1992 were used very little by the birds. One possible explanation for this is that the medium to high swards in the autumn tend to encourage high numbers of tipulid larvae during the following winter and spring, whereas the low swards in the late winter and early spring allow the birds access to the tipulid larvae in the soil both before (when they would be prospecting for good feeding sites) and during (when rapid and easy access to food was essential) the incubation and nestling periods. The presence of long grass during the adult flight period (July–September) is known to result in high tipulid larval densities in the soil, through preventing females being blown long distances by the wind and thereby encouraging them to deposit all their eggs in a small area near their emergence site (McCracken et al. 1995).

Some compartments with apparently suitable management characteristics (end-groups 1 and 2) were used very little by our three study pairs. This can be explained by territorial interactions: other Choughs were observed to feed regularly in these compartments, and therefore the study pairs would have been largely excluded from the territories of these other birds. In addition, tipulid larvae populations in the soil are known to cycle from year to year. As a result, the effect of compartment management will also depend on the size of tipulid larvae populations in previous years (McCracken et al. 1995). The three study pairs were also recorded feeding frequently in one compartment in each of end-groups 3, 4 and 5 (i.e., in those end-groups where the compartment management characteristics throughout the previous 14 mo were not interpreted as being suitable for Chough feeding on tipulid larvae during April–June). These apparent contradictions can, however, be readily explained. For example, the compartment used in end-group 3 was large and soil conditions varied greatly across it. This patchiness resulted in preferential use by livestock and geese (especially in spring), producing small areas where short, open swards allowed the birds access to the tipulid larvae in the soil.

The management of compartments within Chough home ranges during January–March appears to be especially important in influencing the feeding strategies (i.e., where and how) employed in later months. Therefore, if after this period there is a substantial change in management (e.g., if grass is encouraged to grow for early crop silage by fertilizer application and cessation of grazing), then the feeding areas pre-selected by the birds will undergo sudden changes and the abundant numbers of prey items will become unavailable. As a result of such "ecological traps" (Beintema et al. 1991), the birds would then have to spend time prospecting for alternative sources of food before they could provision their young. If the extra time involved was excessive, or the alternative food sources were of poorer quality, then there is the possibility that this could lead to nestling losses. However, from the data available through this study, the timing of nestling losses do not appear to form a pattern attributable to common external factors.

Implications for Choughs on Islay.—In some years on Islay, dung-living invertebrates form an important food resource for breeding Choughs (McCracken et al. 1992). Examination of dung pats during this study, however, revealed little or no invertebrate activity (due to a cold and wet spring) and indicated that the range of invertebrate prey items available to the birds was much reduced for most of the study period. The results suggest that even under such conditions the more mature birds were able to achieve above average fledging success. The young (and hence inexperienced) male of pair 3 persisted in searching for food in dung pats (a commonly observed feeding strategy of sub-adults) and his stay times at foraging areas were longer than the other two males. Prey capture-rate data provided no insight into relative feeding success and is not reported here (E. M. Bignal and S. Bignal, unpubl. data), but clearly there was some aspect of the feeding behavior of pair 3 that made them unable to provision their young adequately. There was no suggestion from invertebrate sampling that pair 3's feeding compartments were less rich in tipulid larvae.

Sub-adult male birds must perfect foraging skills to obtain food for themselves, their mate (during egg-laying and incubation) and their nestlings (Gochfeld and Burger 1984). Field observations on Islay suggest that newly fledged birds and sub-adults depend more heavily than more experienced adults on easily obtained prey associated with livestock dung. Such reliance on easily recognizable and obtainable food sources has been recorded in other species. Juvenile European Starlings (*Sturnus vulgaris*) were observed to peck less than adults at the soil and more at cow dung and at cherries lying on the ground (Stevens 1985), and first-year Grey Herons (*Ardea cinerea*) were found to spend more time than adults on a fish farm and on a site where dead fish where dumped than adults (Draulans and van Vessem 1985). These differences can be largely explained in terms of the differences in foraging efficiency between inexperienced and adult birds. It is well documented that older birds expend less effort in capturing a given number of prey items than do younger birds (for review see Gauthreaux 1988). Older birds may also have advantages of dominance, making food resources more available to them. Such low foraging efficiency may limit the reproductive capabilities of young animals (Brandt 1984). Thus the survival of the nestlings of young, inexperienced breeders may be dependent on access to easily obtainable food.

The results enable hypotheses to be formed about the factors affecting Chough nestling survival on Islay. (1) Adult foraging success is influenced by a combination of foraging ability (of the pair) and also the selection of foraging patches (by the male). As a result, populations with a high proportion of young male breeders might be expected to suffer high nestling losses; (2) The combination of autumn and spring pasture management described above can fundamentally affect choice of compartments for foraging during the nesting period. We suggest that this management influences both invertebrate prey abundance and availability; and (3) Under cold and wet spring conditions, when overall invertebrate activity is low, tipulid larvae can provide an important food resource to birds that are experienced enough to exploit them. Clearly a combination of a cold and wet spring and a poor tipulid larvae year could produce the worst possible conditions for breeding Choughs.

Although factors 1 and 3 are largely beyond control, in many years manipulation of pasture management (through suitable management prescriptions based on the above results) could have a beneficial effect on nestling survival. It is important though that the results from this research are not taken out of context nor extrapolated to suggest Chough requirements for the whole year. As indicated above, different feeding strategies were adopted by the study pairs before the period reported here and after the young were fledged. In addition, previous work has clearly demonstrated that Choughs utilize different biotopes and feeding strategies at other times of the year (Bignal et al. 1989, Curtis et al. 1989, McCracken et al. 1992). As Islay is now part of the Argyll Islands Environmentally Sensitive Area, and a significant proportion of the island is a proposed Special Protection Area, the findings from this research could provide important information for the development of relatively simple agricultural management prescriptions to help favor Choughs on Islay during the nestling period.

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