Habitat selection and movements of golden plover Pluvialis apricaria broods in the flow country of Sutherland

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Habitat Selection and Movements of Golden Plover *Pluvialis apricaria* Broods in the Flow Country of Sutherland

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SUMMARY

(1) A study was carried out to investigate the habitat selection and movements of Golden Plover broods in the Flow Country of Sutherland.

(2) Two study sites ("Achentoul" and "Badenloch") were surveyed between 3/06/94 and 28/06/94. The positions of all broods were recorded, individual pairs being identified where possible.

(3) Vegetation data was collected after the brood survey period. Within each site, circular plots 50m in diameter were centred on all brood locations and on an equal number of random points stratified over 0.25 km squares. The percentage coverages and patch shapes of 13 vegetation categories were recorded.

(4) A comparison was made of brood location and random plots. Broods used each of the two major habitat types - Bog (raised mire) and Non-bog habitats - according to their avilability within each study site.

(5) Within Bog habitat, pool type D (with the most well defined pools) was significantly selected over both sites taken together. Pool type X ("dry bog") was avoided at each site. The intermediate pool types A and B were used according to their availability at each site.

(6) Within Non-bog habitat, U4 (short grazed grass) and U4 with *Juncus* were strongly selected at each site. M17 (*Eriophorum vaginatum* blanket mire) was siginificantly avoided at Badenloch and highly siginificantly avoided at both sites together, whilst large tracts of H9 (heather moorland) were apparently avoided at both sites together. Dense, monotypic *Juncus* stands were avoided at Achentoul but were not recorded at Badenloch.

(7) U4 with *Juncus* occurred in larger patches in plover plots than random plots, but the largest available patches of U4 (without *Juncus*) were apparently avoided by broods. This may have been due to lack of cover in this vegetation category.

(8) There was no difference in home range area or maximum dimension between the sites or the habitat types. No patterns of biological significance could be discerned in the distances moved by broods between consecutive visits.

(9) There was evidence of assortative mating on the basis of plumage darkness, whilst pairs in Bog habitat were significantly darker than pairs in Non-bog habitat.

(10) It is contended that optimal Non-bog habitat may be better than Bog habitat. The importance of sheep grazing in Non-bog areas and the significance of plumage variation between the habitats are discussed.

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1 INTRODUCTION

This project was carried out under the umbrella of a project entitled *Functional Needs of Peatland Animals within SPA's* (FNPA), a Scottish Natural Heritage (SNH) contract to Dr. C. J. Thomas and Prof. P. R. Evans of the Department of Biological Sciences, University of Durham. As part of FNPA they are investigating the habitat requirements of breeding shorebirds in the Flow Country of Sutherland (Figure 1). Several Special Protection Areas (SPA's) have been proposed by SNH in the peatlands of Caithness and Sutherland in partial fulfillment of their obligations to protect populations and habitats of species listed under Annex 1 of EC Directive 79/409 on the Conservation of Wild Birds. The aim of the FNPA is to provide information to enable SNH to delimit and prescibe management for SPA's in such a way as to maximise their effectiveness in conserving certain flagship species, primarily Golden Plover (*Pluvialis apricaria*) and Greenshank (*Tringa nebularia*).

Golden Plover and Greenshank inhabit the Flow Country only during the breeding season. Just as it is necessary to consider the whole annual cycle of these and other migratory species in planning conservation action, on a smaller spatio-temporal scale it is necessary to conduct studies throughout the breeding season since different habitats may be utilized at different stages. For instance, different habitats may be required for feeding by off-duty adults prior to and during the nesting period; for nest sites; for brood rearing; and for feeding by adults and juveniles once breeding is over, before they depart from the area. Loss of or change to any key habitat may result in a reduction of population size (e.g. Galbraith *et al.* 1992, Thompson, Stroud and Pienkowski 1988). Clearly, delimitation of SPA's must, then, be based on a thorough knowledge of habitat use by the target species throughout their breeding cycle. My study aimed to investigate the habitat use by Golden Plover broods during the period from leaving the nest through to fledging. The need to complete all fieldwork (including vegetation surveys) by mid-July prohibited investigation of habitat use by fledged juveniles.

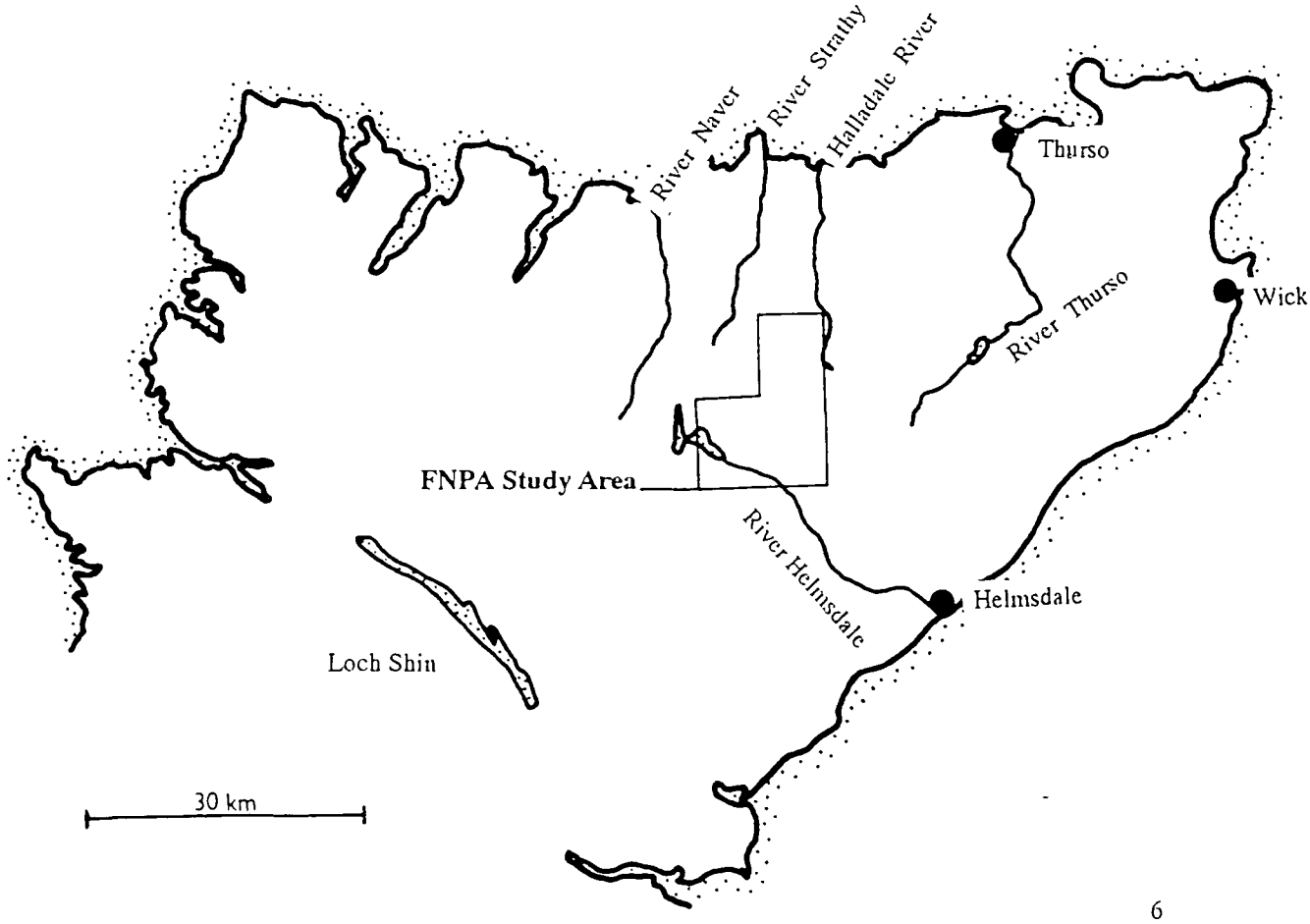
1.1 Biology and habitat selection of the Golden Plover

The Golden Plover breeds across the northern Palaearctic from Iceland to central Siberia, primarily in arctic and subarctic regions but extending south into the northern part of the temperate zone where suitable habitat occurs, as in Britain. It breeds in a range of open, treeless habitats from wet blanket bog to drier moorland, selecting habitats with low growing vegetation but apparently being less partial to bare areas than many other plovers (Cramp & Simmons 1983). During the breeding season

Figure 1: Location of the FNPA study area

(a) Map of Britain with extent of map (b) boxed.

(b) Sutherland and Caithness showing FNPA study area.



they feed on a wide spectrum of invertebrates, especially Coleoptera and Lumbricidae (Ratcliffe 1976, Byrkjedal 1980), which are taken from the surface or by probing 1-2cm. into the substrate in a typically plover-like run-stop feeding technique. Three main feeding actions of adults have been identified (Byrkjedal 1985, pers. obs.): (1) Pecking at vegetation (for berries and adult insects). (2) Pecking at the ground (for adult insects, especially Carabids). (3) Probing in the ground (for larvae and earthworms). Chicks take food primarily from the surface of the ground (pers. obs.). M. Whittingham (pers. comm.) suggests that tipulids are a very important food of chicks in Upper Teesdale, northern England, whilst Yalden (1991) found that tipulids were the main food of Golden Plover chicks in the Pennines, England.

Golden Plovers are thought to have a monogamous mating system, with a life-long pair bond. Pairs are often faithful to territories on which they were succesful for several seasons. Both sexes commonly breed in their first summer (Parr 1980), and both parents care for the precocial brood - although males may be left in sole charge of broods later in the season. Byrkjedal (1985) suggests that this biparental brood care is an adaptation to avoiding nest and chick predation, the strategy for which is based on vigilance and alarm calls. This, in combination with the open habitat, make it impossible to closely approach broods unnoticed and the adults will not return to the chicks while an intruder remains in the area (Yalden and Yalden 1989, pers. obs.). Pair (re)formation occurs in spring flocks or on arrival at the breeding grounds. Courtship and threat displays centre on two plumage features - the underwing/axillaries and the breast (but involve a large vocal element). The underwing and axillaries are displayed during wing-raising actions in a variety of contexts, including courtship. Interestingly, these feathers are pure white and provide a clear distinction from congeners. They are likely to have evolved to prevent deleterious interbreeding with the partially sympatric Grey Plover (*Pluvialis squatorola*), which has black axillaries, and Asiatic Golden Plover (*Pluvialis fulva*), which has grey underwings and axillaries. The breast of Golden Plovers is black during breeding, the extent of black varying between individuals. This feature is displayed in a high-upright posture adopted in various (especially threat) displays. It has thus been suggested (somewhat controversially) that variation in this feature has evolved as an honest signal of individual quality, to reduce conflict for scarce resources (e.g. territories and mates) (Edwards 1982).

In evolutionary terms, there is a reciprocal three-way interaction between a species' morphology, behaviour and habitat selction which exerts an ultimate influence on fitness through affecting individuals ability to find food, shelter from physical conditions and cover from predation (Cody 1985), whilst additional requirements linked to reproduction (securing a mate, nesting and raising young) impose further constraints during the breeding season. As with other shorebirds it is likely, as

lanuginosum heath and montane bog was selected. Apparently it provided both adult and chick feeding opprtunites. Ratcliffe (1976) reviewed the habitats used by breeding Golden Plovers in Great Britain, but not explicitly those chosen during brood rearing. He recognizes that nests are sited in the proximity of suitable brood rearing habitat, however, and reports that a wide variety of habitats are used as "nesting areas": heather moor, wet heath, blanket bog, acid grassland and calcareous grassland in the submontane zone, and dwarf shrub heath, moss and lichen heath, blanket bog and acidic grassland in the montane zone. He suggested that open areas with patches of low vegetation, not blocking the distant view but affording some cover, with some raised areas suitable as lookout-posts, are preferred for nesting. However, no quantification of the relative selection of these habitats was given, nor is any detailed attention paid to the precise foraging sites selected by broods. Stillman and Brown (1994) looked at the habitat associations of upland birds on a coarse scale and found that Golden Plover were associated with upland bogs. The scale at which this study was carried out was not, however, appropriate to provide the kind of detailed information necessary to facilitate the delimitation of protected areas.

1.3 The Flow Country

Habitat associations found for a species in one area may dissolve when comparative studies are undertaken in even quite similar environments in different geographical areas (Cody 1985, Wiens 1989). For this reason this section outlines the general features of the Flow Country environment. Detailed site descriptions are given in the methodology.

1.3 (1) General

The lowland blanket bog of the Flow Country is one of the most important and impressive expanses in the world, covering some 4000 km^2. The exact proportion of the global total which this represents is unknown, largely due to difficulties in surveying and precisely defining blanket bog (Lindsay *et al.* 1988). The appropriate climatic conditions for its formation are found only in regions between 45 and 60^o on the fringes of oceans, since a cool climate with high rainfall and no drought periods are essential. Within these regions, it is found only where topography is suitable - gentle contours providing the appropriate hydrology. Although there are many mountains to the west of the Flows, from central Sutherland eastwards the terrain is generally flat, with the gently sloping land of the west of the area being interspersed with low summits. The optimal topography and geology of the region supercede the fact that rainfall is lower than to the west, where the rugged terrain precludes extensive blanket bog formation. It is thought that climatic change c.4000 years ago was responsible for

the decline of the *Pinus sylvestris* forest which formerly covered the area, although human impact has probably reduced the extent of taiga birchwood in some areas. The present climate is thought to be as favourable to bog formation as any in previous times, with a vigourous growth of peat forming vegetation found all over the area.

1.3 (2) Vegetation

The communities found in the Flows are mostly ombrotrophic, although minerotrophic fens do occur (Lindsay *et al.* 1988). Below is a brief description (taken from Rodwell, 1991) of each of the NVC categories recorded within the FNPA study area by Twiss *et al.*. (1993).

M18 - *Erica tetralix-Sphagnum papillosum* raised and blanket mire. Dominated by *Sphagna* with ericoid shrubs and monocotyledons often playing a subordinate role, increasing in prominence in drier areas. This is the main bog community, the only one in which pool systems occur, developing where peat accumulation gives an elevated mire surface above the immediate controlling influence of the groundwater-table.

M17 - *Scirpus cespitosus* - *Eriophorum vaginatum* blanket mire. Dominated by mixtures of monocotyledons, ericoid subshrubs and *Sphagna*, the monocotyledons giving it its distinctive character when seen from a distance. This characteristic blanket bog vegetation of the more oceanic parts of Britain can result from modification of M18 by draining.

H9 - *Calluna vulgaris* - *Deschampsia flexuosa* heath. *Calluna vulgaris* is always the most abundant plant, often with a low, sometimes quite open, canopy of immature individuals. Occurs on the best drained areas - e.g. in small patches on the short, steep slopes at the edges of raised mires, with more extensive areas on the upper portions of dry hummocks and ridges within the bogs.

M15 - *Scirpus cespitosus* - *Erica tetralix* wet heath. A variable community with few constant species and a wide pattern of dominance. *Molinia caerulea*, *Scirpus cespitosus*, *Erica tetralix* and *Calluna vulgaris* are all of commonly present but one or two may be missing. Within the FNPA study area it occurs as a degraded form of H9 in the most exposed locations.

M25 - *Molinia caerulea* - *Potentilla erecta* mire. Characterised by the overwhelming abundance of *Molinia caerulea*, which sometimes forms dense monotypic stands. Occurs on moist but well aerated ground such as at the fringes of bogs and, particularly, along the flushed margins of streams.

U4 - *Festuca ovina* - *Agrostis capillaris* - *Galium saxatile* grassland. Dominated by grass mixtures occuring in intimate mixed swards that are short, often close-cropped into a tight, fine-textured turf. A plagioclimax, owing its nature to the influence of

grazing, it occurs on better drained base-poor mineral soils such as are found along streams and in improved pasture.

Twiss *et al.* (1993) subdivided M18 into a series of Pool Types, as it was found that the NVC classification was too coarse to allow evaluation of the use of different types of bog. This classification was based on pool structure and vegetation and the nature of the inter-pool matrix. Below is a brief description of each category (from Twiss *et al.* 1993).

Pool Type A - Pools choked with *Sphagnum*, with a 5-15cm. layer of overlying standing water. These pools have no distinct edges, the *Sphagnum* carpet sloping gently into the pool, and are generally elongated (1-2m. x up to 20m). The surrounding *Sphagnum* carpet is wet, with few *Racomitrium lanuginosum* hummocks. This pool type often occurs around the edges of D pools.

Pool Type B - Irregularly shaped pools less than $2m^2$, with a bed devoid of vegetation and covered by 5-10cm. of standing water. There is no distinct edge to these pools and the ground between them is broken and irregular with many *Racomitrium lanuginosum* hummocks. This pool type often occurs on slopes surrounding D pools or at the edges of complexes of A and D pools.

Pool Type D - Proper dubh lochans with distinct, vertical edges. Usually found at the centre of pool complexes, these pools have standing water to a depth of 10-30cm., below which is very deep liquid peat. They are larger than $2m^2$ and often irregularly shaped, as they may have small islands and narrow causeways between adjacent pools. The interpool land is often relatively dry, although it is formed of a thick layer of *Sphagnum*, but may include damp, sparsely vegetated patches of ground.

Pool Type X - Dryer areas with no standing water, generally found along ridges within mires or around the edges of bogs.

Pool Type O - Very wet areas with no pools but a thick *Sphagnum* carpet. Often around the periphery of pool complexes.

1.3 (3) Human impact

The main economic uses of the Flow Country are as grazing land for sheep (*Ovis aries*), Red Deer (*Cervus elaphus*) and Red Grouse (*Lagopus lagopus scoticus*). Whilst the impact of grazing itself on blanket bog is not well known (Lindsay *et al.* 1988), management has largely centred around it. Drainage is particularly prevalent and impacting, the idea being to improve grazing and reduce the danger of boggy ground to livestock. 27.8% of sites surveyed by the NCC had evidence of at least some drainage, which often led to a change in vegetation to dwarf shrub/shrub dominated communities (Lindsay *et al.* 1988). Burning of surface vegetation to improve/maintain grazing quality by removing old vegetation and stimulating fresh

growth can damage blanket bog if the *Sphagnum* layer is damaged. This causes a shift to the dominance of other mosses and vascular plants and is especially likely on moor-gripped land or if fires are poorly managed. Other mangement associated with these activities includes includes the control of Red Grouse predators (particularly Hooded Crows (*Corvus corone corone*) and Red Foxes (*Vulpes vulpes*)) and the provision of feeding stations for Red Deer.

Much blanket bog has been lost to forestry in the last 20 years, this causing complete destruction of the original habitat within a few years as well as modifications to adjacent areas. Stroud *et al.* (1987) report that the land most suitable for forestry apparently coincides with the highest densities of breeding Golden Plovers.

1.3 (4) Ornithological importance

The Flow Country holds breeding populations of 15 species of shorebird which are ecologically separated by habitat and feeding technique. In addition to including 17%, 66% and 35% of the EC populations of Golden Plover, Greenshank and Dunlin respectively, this region includes southern extensions to the distribution of several boreal/arctic breeding species including Temminck's Stint (*Calidris temminickii*), Red-necked Phalarope (*Phalaropus lobatus*) and Wood Sandpiper (*Tringa glareola*). Open-water birds are well represented on the lochs and dubh lochans, with large proportions of the EC breeding populations of Red-throated Diver (*Gavia stellata*), Black-throated Diver (*Gavia arctica*), Wigeon (*Anas penelope*) and Common Scoter (*Melanitta nigra*).

According to Lindsay et al. (1988) there is a high degree of overlap between the conservation needs of birds, blanket bog and openwater habitats in the Flows which are thus mutually reinforcing. However, as outlined earlier, it is essential to carry out detailed studies of the total habitat requirements of breeding shorebirds before it is possible to draw up conservation plans with any degree of confidence and this individual project, and the FNPA as a whole, will contribute to these plans.

1.4 Aims of the study

(1) To evaluate habitat selection by Golden Plover broods,and to follow the movements of known broods, within predefined study areas in the FNPA study area with the aim of assessing habitat requirements for the species during the brood rearing period.

(2) To attempt to evaluate the quality of the different habitats used by assessing variation in territory size, breeding success and in the plumage of individuals between habitat types.

2 METHODS

2.1 Study sites

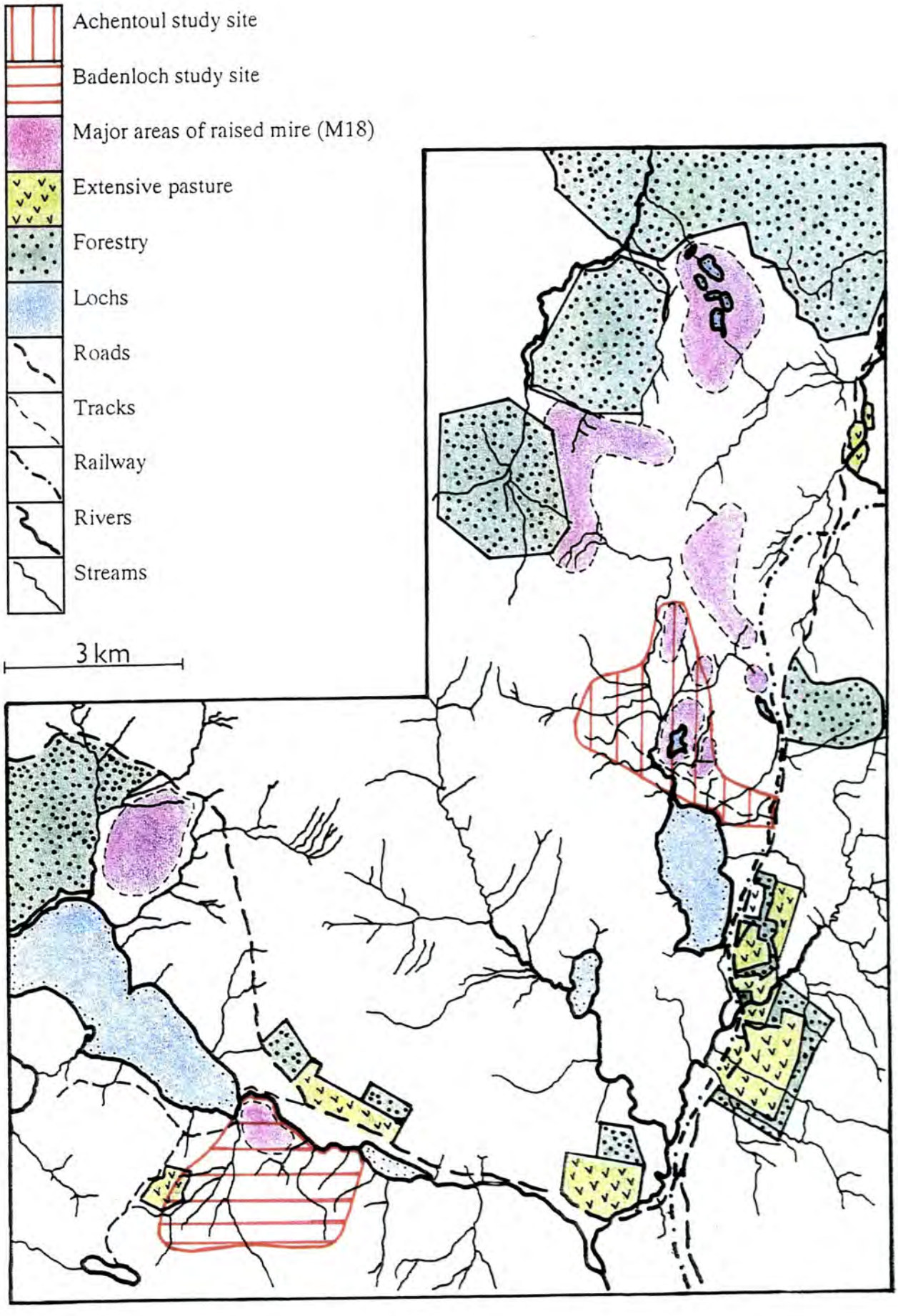
Two study sites were selected within the FNPA study area: an area of 4.5 km^2 immediately north of Loch Rutha on the Achentoul Estate (hereafter referred to as "Achentoul") and an area of 6 km^2 to the east and southeast of Loch Badenloch on the Badenloch Estate ("Badenloch") (Figure 2). The sites were selected (1) to give a good representation of the habitats available in the area, and (2) for the relatively high densities of Golden Plovers they held - densities in surrounding areas being so low that data collection would have been prohibitively slow. Furthermore, both sites were easily accessible by road.

The distribution of habitat within the sites is determined primarily by a combination of relief, drainage and management, as well as by grazing pressure from Red Deer, Mountain Hares (*Lepus timidus*) and Rabbits (*Oryctolagus cuniculus*). Both sites are managed for Red Grouse and sheep grazing, the latter imposing strong grazing pressure in some areas and necessitating drainage improvement. In some very wet and poorly drained areas raised bog with pools (M18) has developed, which is grazed by Red Deer and Mountain Hares. This is replaced by *Eriophorum* mire (M17) in better drained areas, including on gentle slopes and where ditches have been dug. In drier areas, including steeper slopes and dry hummocks, heather moorland (H9) occurs when *Sphagnum* drops out of the plant assemblages. Along water courses tussocky *Molinia* grassland/mire (M25) is dominant, with pockets of short grassland (U4 / U4 with *Juncus*) occurring along the more heavily Rabbit and sheep grazed, and better drained, margins. Dense *Juncus effusus* stands are scattered in slack, waterlogged margins and are quite extensive in places, particularly where stream junctions at low gradient cause water to build up and flood laterally. A brief description of each site is given below.

2.1 (1) Achentoul

This site includes the southern end of a very extensive tract of blanket bog which is dissected by several well-spaced streams draining individually into Loch Ruitha to the south. The western part of the site lies at the foot of a steep east facing basin and includes four streams draining the slope as well as Greamchary cottage and the improved pasture of a ruined croft here. It is complex in terms of vegetation and topography with lines of dry hummocks between the stream channels and small patches of bog forming in the areas between two lines of hummocks, as well as including the lower section of the basin slope. The central section of the site is comprised largely of

Figure 2: Extent of FNPA study area showing Achentoul and Badenloch study sites.



raised bog around and to the north of Loch Culaidh, with a full range of pool systems and streams draining the small individual blocks of bog. The eastern arm of the site lies along the access track for Greamchary cottage and is largely well-drained boggy ground which is well grazed by sheep.

2.1 (2) Badenloch

The northern section of this site is a large discrete block of raised bog with a full range of pool types which is bordered by the River Helm to the north, Loch Badenloch to the west, streams to the southwest and southeast, and a line of dry heather hummocks to the south. To the west and southwest is a large north facing basin sloping down towards the bog which contains the edge of the improved pasture of Breacough croft's sheep enclosures as well as several streams which converge before bypassing the raised bog and draining into Loch Badenloch. The southern part of the east of the site is a north facing slope drained by one stream at its eastern end, by which is the ruin of Achnamoine croft and its small patches of improved pasture. To the north of this lies a boggy area south of the River Helm which is drained by three streams and several drainage channels and has consequently failed to develop into extensive raised mire.

2.2 Fieldwork methods

Fieldwork was carried out between 02/06 and 14/07. Golden Plover brood surveys were undertaken between 03/06 and 28/06, each site being visited on alternate days, weather permitting, giving a total of 10 visits to each site. This meant that broods had (potentially) been followed for 25 days - long enough for chicks to complete most/all of their development, especially as they may have been a few days old at the beginning of the period. A whole day was required for each survey, starting from c.0900 hrs., which ensured each survey was carried out at roughly the same time of day - eliminating possible biases relating to diurnal activity patterns or movements (Reed *et al.* 1985, Bibby, Burgess and Hill 1992) . Furthermore, visiting every 2-3 days minimsed the frequency of disturbance to the birds. A survey was not carried out if the weather was considered sufficiently inclement to render disturbance to the birds unacceptable or to decrease survey validity. With respect to the latter, high wind made hearing calls and locating their origin difficult, and dishevelled birds' plumage - impeding individual recognition. Rain, on the other hand, prohibited the efficient use of optical equipment. Habitat data was collected between 01/07 and 14/07. This was done after the survey period (a) because time prohibited collecting it during the surveys, and (b) to keep disturbance of the birds to a minimum.

2.2 (1) Brood location surveys

On each visit a complete survey of the entire study area was carried out on foot to locate all the Golden Plover broods present, working on the assumption of an average response distance of 200m. for adults (Yalden and Yalden 1989, pers. obs.), using 10x binoculars and a 30x telescope as required.

The exact position of broods was recorded on a 1:10,000 scale map by taking compass bearings from three landscape features. This was supplemented by notes and sketch maps as required to allow the exact location to be refound at a later date. Attempts were made to locate chicks by sight before they were alerted to the presence of the observer by their parents, this being considered the best indication of their habitat utilisation. However, this was not usually possible due mainly to the high level of vigilance of attendant adults, which gave alarm calls in response to the observer. On several occasions it was observed that the chicks would hide in the nearest cover on hearing these and then became extremely difficult to find. If chicks could not be seen, the position of adult birds was recorded as soon as possible after initial contact, in order to minimise any movement by them in response to the observer. The observer then walked to the point of initial location and was often able to narrow down the position of the chicks by careful observation of the parents' behaviour. The parents' initial response was usually to attempt to lead the observer away from the chicks. However, the level of anxiety the adults displayed increased as the observer approached the chick location. This anxiety presented itself in the form of: (1) Increased rate of alarm calls. (2) Higher pitch of alarm calls. (3) Increased closeness of approach to the observer. (4) Increased rate of displacement activities (stylised preening / feeding). (5) On very close approach to the chick location, distraction displays by a parent. The validity of these methods was confirmed (1) on two occasions when chicks were subsequently found hiding, and (2) by applying this procedure five times when the hiding location of the chicks was known and simultaneously monitoring adult behaviour. It was considered that it was possible to determine the location of the chicks to within 10-15m. using this method (greater accuracy was probably precluded by the spread of chicks in the brood and by adults reaching high levels of anxiety by this distance).

2.2 (2) Individual recognition of Golden Plovers

Where possible pairs of adults were identified individually on each visit to allow the progress and movements of known broods to be followed. This was carried out primarily with reference to idiosyncrasies in the plumage patterns of the birds, as outlined below. One pair at Badenloch, however, was trapped on the nest and

individually colour ringed just prior to the study, whilst the female of another pair at the same site had been colour ringed on North Ronaldsay in January 1992.

The major source of individual plumage variation was the amount of summer plumage which had been attained by the birds in the prenuptial moult of the body feathers. This was especially obvious on the underparts, where black summer plumage contrasted strongly with retained white winter plumage feathers. Each bird was scored on the 10 point scale used by Thomas (1986) for the darkness of their underparts/face, plumage score 10 being the darkest. Where a bird was judged to be intermediate between categories, it was assigned the score which best represented its the overall appearance. In addition, all birds were sketched in detail to record the exact pattern of black and white in the underparts, other obvious moult-related features such as the number of summer plumage tertials, and details of the facial pattern. Facial pattern variation was noted in the following features: (1) extent and whiteness of the pale forehead and foreface; (2) broadness and whiteness of the supercilium; (3) shape and darkness of the loral crescent; (4) width and darkness of eyestripe behind the eye and of the "supercilium cut-off" (backward extension of the eyestripe which often separates the supercilium from the sometimes-confluent pale earcovert surround); (5) shape and darkness of the postoccular spot; (6) exact colour and shading of the earcoverts, chin, throat and upper neck sides. Figure 3 illustrates these facial features.

It is believed that these features allowed recognition of all pairs when both individuals were present and of most individuals seen alone. However, as there was no form of independent verification it must be recognised that it is possible that this is an overestimate of the accuracy of the individual identification.

2.2 (3) Behavioural observations

Observations of the behaviour of adults with broods (and chicks when possible) were collected on an opportunistic basis during the surveys. However, these were very limited in frequency and duration due to: (1) Difficulty in locating the birds before they became aware of the observer. (2) Problems of sustaining the observations as adults often soon became aware of the observer, and broods often moved during feeding. (3) The need to ensure the whole study area was surveyed on each visit, which limited the amount of time it was possible to spend attempting to obtain behavioural observations.

The above problems mean that what data was collected is best treated as anecdotal, rather than be used for any analysis, despite the fact that it was collected in a systematic fashion. Time / activity data was recorded for one of the adults (or both simultaneously if possible) for 30 seconds of each 60 second period. I recorded the number of seconds spent in the following categories of behaviour adapted from Byrkjedal (1985): (1) Lookout (2) Alert Lookout (3) Loafing (4) Running (5) Walking (6) Flying (7) Preening (8) Wing and/or leg stretch (9) Ground probe

(10) Surface peck (11) Alarm call (including number of notes) (12) Time spent out of sight.

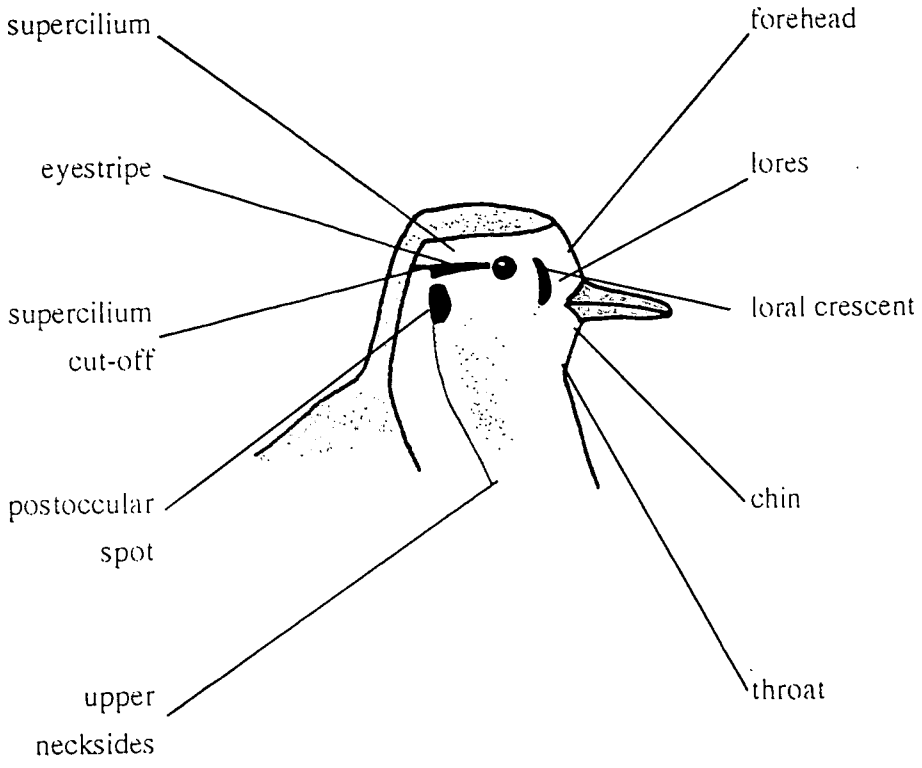


Figure 3: Schematic representation of facial features used to in individual recognition of adult Golden Plovers.

2.2 (4) Habitat data

Vegetation data was collected for each of the sites where broods were recorded. At each location the percentage coverage of each vegetation category was recorded within a 25m. radius. This plot size was chosen to give a high probability of including the actual habitat utilised by the broods bearing in mind (1) a conservative estimate of the accuracy of chick location, (2) the fact that chicks may have moved a short distance into cover from a feeding location, and (3) the fact that chicks in a brood may spread out to a certain extent (Yalden, 1991, found the largest scattering of a brood of four radio-tagged chicks was in a circle 35m. in diameter). Thus the sample plot was considered to be sufficiently large to encompass the functional habitat unit selected by the birds without being so large that it included large adjacent unselected areas. Table 1 shows the vegetation categories discriminated by eye during vegetation data collection.

Table 1: Vegetation categories used during data collection and their definitions

Vegetation Category	Definition
M18 A	NVC community M18 (*Erica tetralix-Spagnum papillosum* raised and blanket mire); Pool type A (after Twiss et al 1993).
M18 B	NVC community M18; Pool type B
M18 D	NVC community M18; Pool type D
M18 X	NVC community M18; Pool type X
M18 O	NVC community M18; Pool type O
M17	NVC community M17 (*Scirpus cespitosus-Eriophorum vaginatum* blanket mire).
H9	NVC community H9 (*Calluna vulgaris-Deschampsia flexuosa* heath).
M15	NVC community M15 (*Scirpus cespitosus-Erica tetralix* wet heath).
M25	NVC community M25 (*Molinia caerulea-Potentilla erecta* mire).
U4	NVC community U4 (*Festuca ovina-Agrostis capilloris-Galium saxatile* grassland).
U4 with Juncus	NVC community U4 with clumps of *Juncus effusus* scattered throughout. Defined as all U4 within 2m. of a clump of *J. effusus*.
Juncus	Stands composed purely or primarily of *Juncus effusus*
Moss flush	Flushes carpeted solely (or nearly so) by a variety of mosses, including Sphagna, Polytrichum and Acrocarpus spp.

(See Introduction for a detailed description of the structure and floristic composition of each of these habitats.)

For each vegetation category recorded in each sample plot, a measure of patch shape and fragmentation was obtained by estimating the maximum distance from that category within the plot to the four nearest other vegetation categories (either in or out of the plot), estimates being made to the nearest metre up to 12m., to the nearest 5m. interval from 15m. and to the nearest 10m. interval from 100m. This was thought to provide the best representation of fragmentation from the point of view of the birds by

recognition of the fact that ecotones differ in their properties and thus possibly also in their functional significance to chicks.

2.2 (5) Random plots

A number of randomly generated plots equal to the number of brood location plots within each study site was surveyed in an identical manner in order to obtain a measure of habitat availability. An equal number of random plots was surveyed to ensure that the random sample was directly comparable with the organism-centred sample, in particular that equal total areas were surveyed in order to circumvent the need for ranking statistics during analysis.

In order to ensure that as accurate an assessment of availability within the study sites as possible was obtained, the random plots were stratified in 0.25 km squares derived from the 1km grid of 1:10,000 scale O/S maps. Within each square, points were obtained by using randomly-generated numbers between 1 and 1000 as eastings and northings. This scale of stratification was used as it allowed the random location of 3 or 4 plots within each unit of stratification and because it was sufficient to ensure a much broader coverage of the sites than the aggregations of brood locations had done. Furthermore, it is the habitat unit used in the Moorland Bird Survey methodology adopted by SNH and other conservation organizations (Brown and Shepherd, 1993).

Vegetation category data alone was collected since this was quick, easy and simple to obtain. Detailed vegetation structure data could not be collected due to the constraints of time. However, Rotenberry (1985) found that for some grassland species, floristics explained species' distributions better than structural data. Whilst the NVC categories and Pool Type classifications on which the habitat data is based are essentially arbitrary classifications with respect to the cues that the birds are likely to use to select habitat, they have the following advantages: (1) Each plant community has a characteristic range of structures and thus some information about vegetation structure is conveyed. (2) As each category is found in a characteristic range of landscape situations, additional information about the physical environment is conveyed without the need to measure extra variables. (3) Certain invertebrate prey species may show strong relationships with certain plant species / communities. (4) These vegetation classifications are standards used by conservation bodies (e.g. SNH) and using them allows findings to be made in parameters likely to be used when conservation action is planned. Wiens (1989) argues convincingly that simple habitat analyses combined with thorough knowledge of species' biology are a far sounder

approach to studying habitat selection (certainly initially) than highly complex multivariate studies which may yield results that are difficult to interpret.

2.2 (6) Definitions of some terms used

For clarity of understanding, the precise definitions of some terms used in this dissertation are given below:

Vegetation category: One of the plant communities discriminated during the collection of habitat data (listed in Table 1).

Habitat type: A broader division of the vegetation category array, encompassing several vegetation categories (see Section 3.1).

Plots: The 50m. diameter sample circles, centred on brood location and random points, which were described during the collection of vegetation data.

Patch: Either a single patch of a single vegetation category contained completely within a brood location or random plot, or that part of a larger tract of a vegetation category that is contained within a plot.

3 RESULTS

3.1 Habitat selection

In the field and from Appendices A and B it is clear that there are two distinct and mutually exclusive habitat types available to and used by Golden Plover broods: (1) Raised mire ("Bog") - comprised of all M18 pool types, and (2) Habitats away from or at the edge of raised mire ("Non-bog") - comprised by all other vegetation categories. Because of this dichotomy, a hierarchical approach was taken to assessing the habitat selection of the Golden Plover broods within the study sites. Three main stages were involved: (1) Assessment of the relative use of Bog and Non-bog habitats. (2) Identification of which vegetation categories were selected or avoided within these habitats. (3) Identification of other characteristics of brood location plots which distinguished them from random plots.

3.1 (1) Use of the major Habitat Types

All plots were classified as either Bog (B)or Non-bog (N) plots, Bog plots being defined as those made up of at least 50% M18 and including some M18 A, B or D pool types, or those that were at least 90% M18 X. The high value for M18 X was used to avoid classifying as Bog marginal patches of M18 X which occurred in a mosaic with M17 in Non-bog areas. The number of brood location plots ("plover plots") and random plots in each habitat class was used in 2x2 Chi squared contingency tables for Achentoul and Badenloch separately and for both sites together to test the following null hypothesis:

H^{O}= There was no difference between the use and availability of Bog and Non-bog habitats by Golden Plover broods within the study sites.

The null hypothesis could not be rejected for Achentoul (χ^2= 0.066; 1 d.f.; P>0.05), for Badenloch (χ^2= 0.827; 1 d.f.; P>0.05) or both sites together (χ^2= 0.655; 1 d.f.; P>0.05). Therefore it can be concluded that Bog and Non-bog habitats were not used significantly differently from their availability within the study sites. Figures 4 illustrates the availability and use of Bog and Non-bog habitat at each site.

3.1 (2) Selection of vegetation categories within the habitat types

The number of records of each vegetation category in plover plots and random plots was counted for B and N plots within each site. All plover plots were entered into the analysis. It is believed there were very few erroneous plots (brought about by brood locations being incorrectly assessed or broods being recorded in transit between

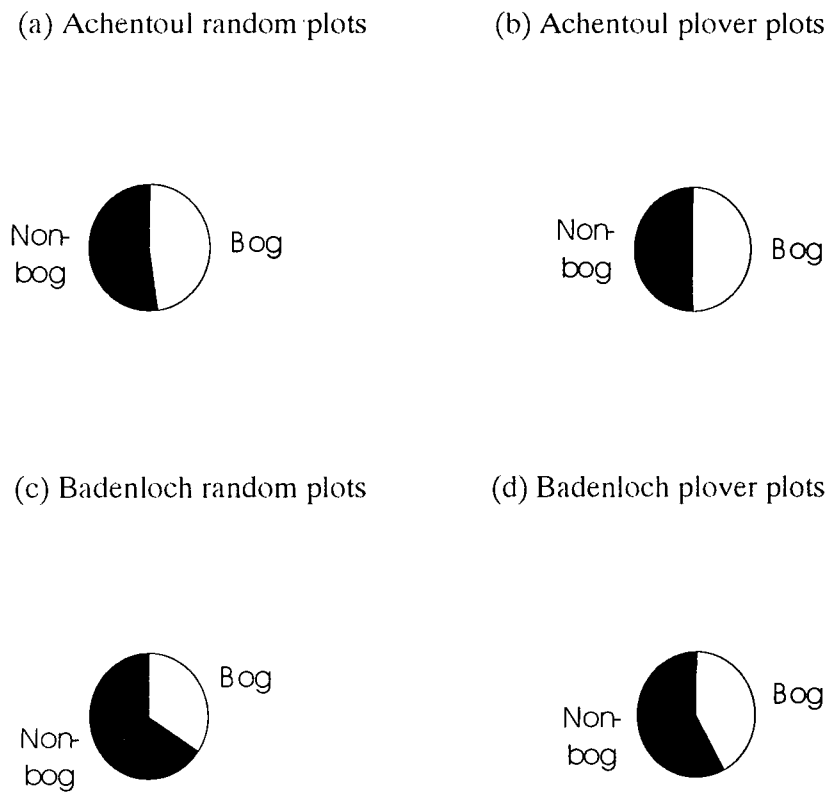


Figure 4: Use and availability of Bog and Non-bog habitats at Achentoul (a and b) and Badenloch (c and d).

feeding areas). This is based on: (1) The validation of brood location methods described in Section 2.2 (1). (2) The fact that few movements of broods across habitat not used for feeding were observed during the behavioural observations. When these were undertaken , they were accomplished quickly. The probability of many broods being recorded in transit during the surveys is therefore low. However, if erroneous plots were included these would tend to obscure habitat selection patterns rather than create spurious ones.

For each habitat type, Chi squared contingency tables comparing the frequency of occurrence of the vegetation categories in plover plots and random plots were constructed. This tested the following null hypothesis:

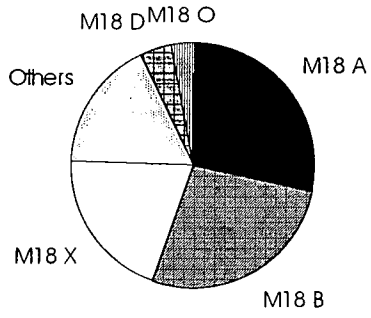
H^O= There is no difference between plover plots and random plots in the distribution of vegetation category records between the categories.

For Bog plots the null hypothesis was rejected for Achentoul (χ^2= 12.275; 5 d.f.; $p<0.05$), for Badenloch (χ^2= 10.086; 4 d.f.; $P<0.05$) and for both sites together (χ

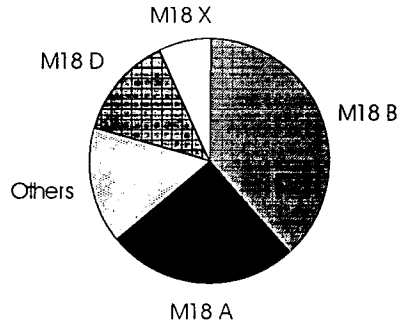
^{2}= 21.494; 6 d.f.; P<0.01). For Non-bog plots the null hypothesis was again rejected for Achentoul (χ^2= 33.329; 7 d.f.; P<0.001), for Badenloch (χ^2= 33.572; 6 d.f; P<0.001) and for both sites together (χ^2= 63.807; 8 d.f.; P<0.001). Therefore it can be concluded that there was significant selection of certain vegetation categories within both habitats at both sites. This was more significant when both sites were considered together (indicating that patterns of selection were similar between the sites) and more highly significant within Non-bog habitat than Bog habitat (indicating that Bog vegetation categories may be used more according to their availability than Non-bog categories). These suggestions are only tentative, however, due to the different number of degrees of freedom for the two habitat types, which renders the results not completely comparable. Figures 5 and 6 illustrate the relative frequencies of occurrence vegetation categories in plover plots and random plots for the two habitat types at each site.

The χ^2 contributions for each vegetation category were examined to determine which were significant at at least P<0.05 for 1 degree of freedom. Whether these categories were selected or avoided by the broods was determined from whether the expected or observed value was higher for the plover plots. In Bog habitat, M18 X was avoided at Achentoul (χ^2= 4.93; 1 d.f.; P<0.05), Badenloch (χ^2= 6.44; 1 d.f.; P<0.05) and both sites together (χ^2= 11.05; 1 d.f.; P<0.001). M18 D was significantly selected at both sites taken together (χ^2= 6.23; 1 d.f.; P<0.05) but the selection was not significant at the P=0.05 level at either site separately. In Non-bog habitat, M17 was significantly avoided at Badenloch (χ^2= 9.43; 1 d.f.; P<0.005) and at both sites together (χ^2= 12.45; 1 d.f.; P<0.001) but not at Achentoul. U4 was significantly selected at Achentoul (χ^2=9.24; 1 d.f.; P<0.005), at Badenloch (χ^2= 14.31; 1 d.f.; P< 0.001) and both sites together (χ^2= 23.110; 1 d.f.; P<0.001), as was U4 with *Juncus* (Achentoul : χ^2= 8.39; 1 d.f.; P<0.005; Badenloch: χ^2= 6.52; 1 d.f.; P<0.01; both sites together: χ^2= 14.78; 1 d.f.; P<0.001). Details of non-significant χ^2 contributions are given in Appendix C. Table 2 summarises these results.

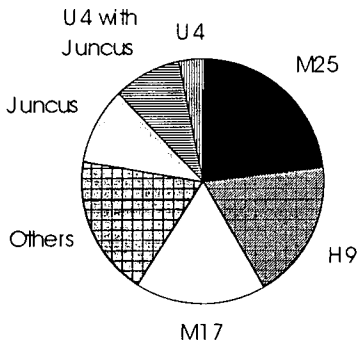
(a) Achentoul Bog random plots (n= 70)



(b) Achentoul Bog plover plots (n= 73)



(c) Achentoul Non-bog random plots (n= 91)



(d) Achentoul Non-bog plover plots (n= 117)

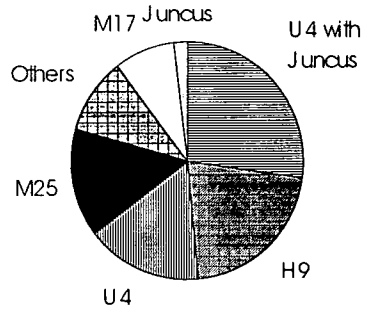
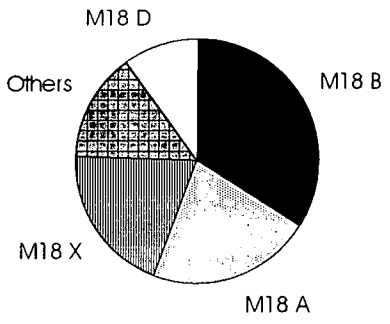
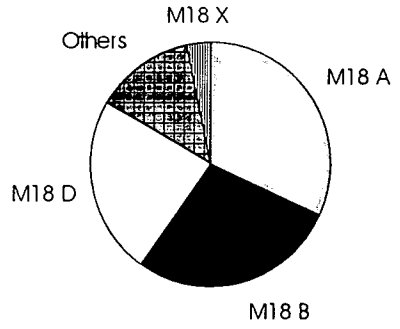


Figure 5: Frequency of occurrence for vegetation categories at Achentoul. Others = Vegetation categories associated with the other habitat type. M15 (one occurrence) grouped with others in (d).

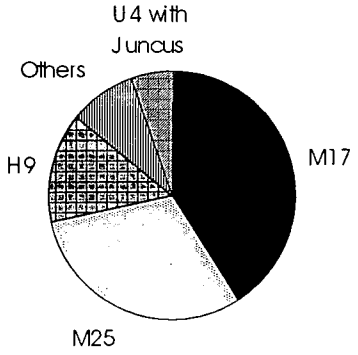
(a) Badenloch Bog random plots (n= 41)



(b) Badenloch Bog plover plots (n= 60)



(c) Badenloch Non-bog random plots(n= 92)



(d) Badenloch Non-bog plover plots (n= 134)

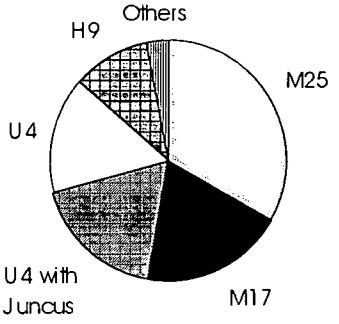


Figure 6: Frequency of occurrence of vegetation categories for Badenloch. Others = vegetation categories associated with other habitat type. M15 (one occurrence) grouped with others in (c). Moss (one occurrence) grouped with others in (d).

Table 2: Results of Chi-square tests on frequency of occurrence of vegetation categories.
(a) Bog plots. (b) Non-bog plots.* = P<0.05; ** = P<0.01; *** = P<0.005; **** = P<0.001.

(a)

BOG	Site		
Vegetation Category	Both	Achentoul	Badenloch
M18 A			
M18 B			
M18 D	Selected *		
M18 X	Avoided ****	Avoided *	Avoided *
M18 0			Not Recorded

(b)

NON-BOG	Site		
Vegetation Category	Both	Achentoul	Badenloch
M17	Avoided ****		Avoided ***
H9			
M15			
M25			
U4	Selected ****	Selected ***	Selected ****
U4 with *Juncus*	Selected ****	Selected ***	Selected **
Juncus		Avoided *	Not recorded
Moss		Not recorded	

It is evident that patterns of selection are very similar between the sites, the only differences being that M17 was not avoided at Achentoul and *Juncus* was not avoided at Badenloch (where it was not recorded). The slight selection for M18 D within the Bog habitat was not significant at either site, but cumulatively it was significant for both considered together.

3.1 (3) Number of vegetation categories per plot

Mann-Whitney U tests were used to test for a difference in the number of vegetation categories recorded per plot in plover plots and random plots. T-tests were not used, in spite of the large sample size and apparent normal distribution of the data when graphed (Figure 7), as the data were not continuous. There was no significant difference for Bog plots, but in Non-bog habitat plover plots (median 3) had significantly more categories than random plots (median 2) ($z=6.8915$; $n= 62,72$; $P<0.001$).

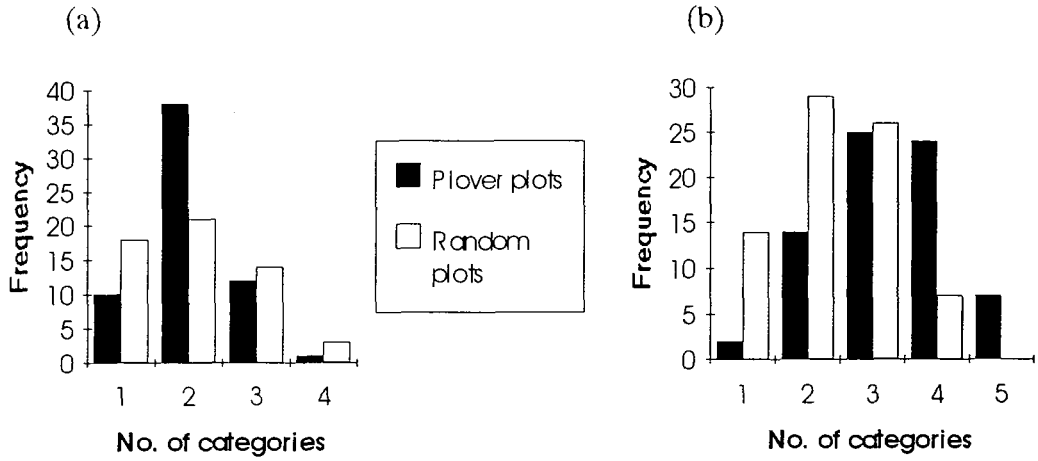


Figure 7: Number of vegetation categories recorded per plot, (a) Bog; (b) Non-bog.

3.1 (4) Availability between the sites

In order to investigate whether the differences between the two sites recorded in Table xxxx could be attributed to differences in availability of the vegetation categories, χ^2 contingency tables were constructed for the two habitat types to compare the random plots at the two sites. There was no significant difference between the sites for Bog plots ($\chi^2= 2.429$; 4 d.f.; $P>0.05$) but there was a significant difference for Non-bog plots ($\chi^2= 26.672$; 6 d.f.; $P<0.001$). The vegetation categories for which the difference was significant were M17, which occurred more at Badenloch ($\chi^2= 8.715$: 1 d.f.; $P<0.005$), and *Juncus*, which occurred significantly more at Achentoul ($\chi^2= 9.098$; 1 d.f.; $P<0.005$). These results are consistent with the supposition that significant avoidance of M17 at Achentoul and *Juncus* at Badenloch was not proven because these categories were in low availability at those sites. If present, the interior of extensive tracts of these avoided categories would be recorded in random plots but not plover plots. However, if small patches of them (i.e. the edges of tracts) were recorded in plover plots as their "extra" categories in Non-bog habitat

(Section 3.1 (3)), in the absence of extensive tracts any actual avoidance of these categories would be masked.

3.1 (5) Characteristics of selected patches

Mann-Whitney U tests were carried out to test whether the percentage coverages of vegetation categories were significantly different in plover plots from random plots. This is salient in that a category that was selected by the broods may make up a larger percentage of those plover plots in which it was recorded than in those random plots in which it was recorded, whilst an avoided category may occur in plover plots in smaller patches. Thus it may be possible to identify avoidance or selection of a category that was not apparent from the frequency data. Alternatively, there may be selection for certain patch sizes of selected categories. Plots with zero coverage of a particular category were excluded from the analysis to avoid including the confounding influence of frequency of occurrence, which has been considered separately (Section 3.1 (2)). Parametric statistics were not used as: (1) The data were recorded in terms of percentage coverage and thus can not be normally distributed. (2) In some cases, sample sizes were very small. In order to conserve sample sizes (and thus statistical power) both sites were considered together, but not separately. This was valid given the similarities in habitat selection between the sites already outlined.

In Bog habitat, there was no significant difference between the percentage coverage of M18 A, B, D or X in plover plots and random plots. M18 O could not be tested since it did not occur in any plover plots. In Non-bog habitats, there was no significant difference between plover plots and random plots in the coverage of M25 or *Juncus*. The coverage of M17 was significantly greater in random (median = 60%) than plover plots (median = 37.5%) ($z= 2.5899$; n=36,54; $P= 0.0096$), supporting the frequency data evidence of avoidance of this category. H9 occurred in significantly smaller patches in plover plots (median = 22.5%) than in random plots (median = 35%) ($z= 3.4946$; n+30,40; $P= 0.01$), suggesting possible avoidance of large tracts of this category. U4 with *Juncus* occurred in significantly larger patches in plover plots (median = 30%) than random plots (median = 15%) ($z= 2.7304$; n= 13,56; $P= 0.006$), as would be expected for a selected category (provided it fulfils the broods' functional needs) since (a) random plots are stochastically positioned with respect to vegetation categories and may therefore include just a small amount of a scarce category, and (b) very small patches of the category may be ignored by the broods. Conversely, U4 occurred in significantly smaller amounts in plover plots (median = 20%) than random plots (median = 45%) ($z= 2.0529$; n= 3,40; $P=0.04$). Although this result should be treated with caution due to the very small number of random plots in which U4 was recorded, this is a surprising result for a selected category. Figure 8 illustrates this

result. It is possible that this indicates that the broods' avoided the largest patches of U4 available to them.

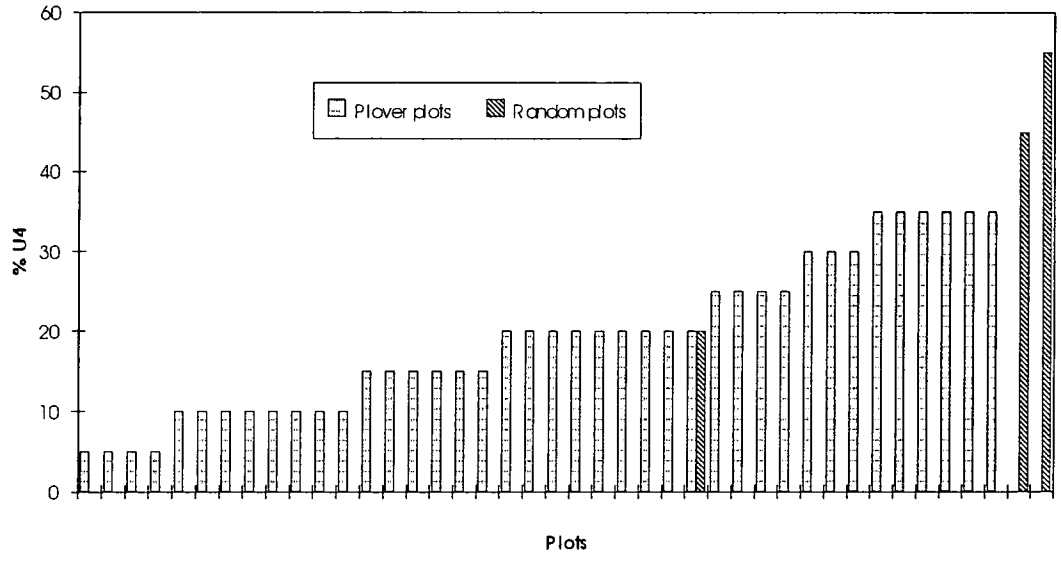


Figure 8: Percentage coverage of U4 in Plover and Random Plots.

3.1 (6) Distance to other vegetation categories

The large coverages of U4 recorded in some random plots could be made up of many small patches or of one large patch; alternatively, the coverage could be made up of a large elongate patch in random plots. To determine which of these scenarios was the case, the maximum distance to the nearest other vegetation category within the patches of U4 was examined for all plover plots and random plots in which U4 occurred. There was a significant difference between plover plots (median = 2.5m.) and random plots (median = 20m) ($z= 2.0689$; $n= 3,40$; $P=0.0386$; Mann-Whitney U test), although again this should be treated with caution due to the low random plot sample size. Thus, not only did U4 contribute a significantly larger % coverage in random plots than plover plots, but it occurred in patches with a significantly larger maximum distance to another vegetation category.

3.1 (7) Effects of sheep grazing

The study site at Achentoul is divided into three sections by two fences. Sections one and three are grazed by sheep, whilst the central section (two) is not. To provide anecdotal evidence about the effects of sheep, a comparison was made of the three sections. For each section indices of (1) plover density (number of plover plots / number of random plots), (2) bog selection (proportion of plover plots which were in Bog habitat / proportion of random plots which were in Bog habitat) and (3) U4 / U4

with *Juncus* availabilty (proportion of Non-bog random plots which contained either of these categories) were calculated. The results are summarised in table 3.

Table 3: Indices of plover density, bog selection and U4 / U4 with *Juncus* availability for grazed and ungrazed sections of Achentoul.

Section	Density index	Bog selection index	U4/U4 with *J.* index
1 and 3 (Grazed)	1.6	1	0.4
2 (Ungrazed)	0.55	1.5	0.25

These results show a higher overall density of brood locations within the grazed sections. Within grazed areas the bog was used according to its availability, but more intensely in the ungrazed section. The grazed sections also had a higher prevalence of U4 and U4 with *Juncus*.

3.1 (8) Temporal variation in habitat selection

In order to test whether the habitat use of broods changed through time, χ^2 contingency tables were constructed to compare the number of Bog and Non-bog plover plots during three sections of the brood survey period. The survey period was split into three, by date, as this was the finest division that could be made without sample sizes becoming prohibitively low. It was not possible to group brood locations according to the stage of chick development since the date of hatching of each brood was not known.

For both sites, visits 1-3= period 1, visits 4-7= period 2; visits 8-10= period 3. There was a significant difference between the periods in the relative use of Bog and Non-bog habitats at Achentoul (χ^2= 13.2; 2 d.f.; P<0.005) and for both sites together (χ^2= 16.01; 2 d.f.; P<0.001). In both cases period one was the only period with a significant χ^2 contribution - in both cases there being significantly fewer records than expected in Bog habitat in this period (Achentoul χ^2= 8.91; 1 d.f.; P<0.005: Both sitesχ^2= 11.11; 1 d.f.; P<0.001). Thus a significantly higher proportion of brood locations were on Bog habitat after the first period. The pattern was similar at Badenloch but it was not significant.

There are three main possible interpretations of these results: (1) broods were more likely to use the Bog as they grew older (implying a developmental causation, such as increased ease of locomotion with increased leg length); (2) broods, irrespective of age, were more likely to use the Bog after a certain date (implying a temporal change in the suitability of the habitat, possibly linked to the phenology of

invertebrate prey species); or (3) broods that used Bog habitat were, overall, later hatchers than broods which used Non-bog habitat (e.g. early breeders exhibited a bias towards Non-bog habitat). Since (a) the date of hatching of each brood was not known and (b) birds not recorded on the first visit may have either hatched after that visit or moved into the study area from adjacent areas, it was not possible to differentiate between the three possible causes. However, the tests were repeated excluding records of pairs that were not seen on the first visit to each site, in order to control for the effects of possible late hatchers. Again, there was a significant (but not so marked) difference between the periods at Achentoul (χ^2= 6.168; 2 d.f.; P<0.05) and for both sites together (χ^2= 9.214; 2 d.f.; P<0.01), the χ^2 contribution for period one being significant for both sites together (χ^2= 5.603; 1 d.f.; P<0.05) but not at Achentoul. Again, there was no significant difference at Badenloch. Thus the effect cannot be attributed solely to any bias of late hatchers towards Bog habitat, although this seems to strengthen the effect. There is no evidence to distinguish between developmental causation and the effects of habitat change.

3.2 Movements and home range sizes

3.2 (1) Movements of pairs

The distance between the positions of pairs recorded on two consecutive visits was measured directly from a 1:10,000 O/S map. This data was used to produce descriptive statistics and to test for associations between the distance moved and the following variables:

(1) Site - Achentoul or Badenloch.

(2) Individual pair. Pairs with less than four distances recorded were omitted to conserve statistical power.

(3) Habitat. Pairs were designated as either Bog or Non-bog, depending on which habitat held the majority of chick locations.

(4) Period - Movements between different visit numbers. As this was designed to test any difference in distance moved with the developmental stage of the chicks, only those pairs originally seen on the first visit to each site were included to avoid the confounding influence of possible late hatchers.

(5) Length of interim between visits - two or three days.

For variables two to five, analyses were undertaken for both sites together and for each site separately. Nonparametric statistics were used for the following reasons: (1) The sample sizes were too small for parametric statistics to be used with

confidence. (2) The distances were not normally distributed when graphed. (3) The distances were estimated to the nearest 10m.

The distances moved and summary statistics are shown in Table 4. Table 5 summarises the results of the statistical tests. The only significant difference was between the habitat types at Achentoul (z=2.278; n=5.5; P=0.022). Bog pairs moved significantly further than Non-bog pairs (Non-bog pairs: median distance moved = 160m., minimum = 30, maximum = 320, semiquartile range = 92.5. Bog pairs: median distance = 260m. (minimum = 40, maximum = 680, semiquartile range = 211.25). The differences between pairs were significant at P=0.1 for Badenloch (χ^2= 9.2538; 5 d.f.; P=0.099) and both sites together (χ^2= 15.25; 9 d.f.; P=0.084) but not for Achentoul.

3.2 (2) Home range sizes

The home range size of each pair was obtained to give an estimate of the areas spanned, which is a function of the movements made and their direction relative to each other. The term home range is used because although a dynamic territory around the broods is defended by each pair, the whole area spanned by a brood is not defended at any one time (pers. obs.). Home ranges were delimited on a 1:10,000 O/S map using the minimum convex polygon of the brood location plots. These were then digitised into Arc/Info coverages and the area of each obtained from the Polygon Attribute Tables in the database. The maximum dimension of the home range was also measured to take account of home range shape. This was used rather than the perimeter to area ratio as it was considered more applicable to real world problems and more easily interpreted.

The territory area and maximum dimension for each pair is given in Table 6. For both variables, tests were made for difference between sites and habitat types, and between habitat types by site, using Mann-Whitney U tests. There was no significant difference between sites in the sizes of home ranges (z= 0.6736; n= 8,9; P= 0.5006) or the maximum dimension of home ranges (z= 0.6262; n= 8,9; P= 0.5312). There was no significant difference in home range size between Bog and Non-bog pairs at Achentoul (z= 0.8660; n= 5,5; P= 0.3865), at Badenloch (z= 0.0000; P= 1.0000; P=1.0000) or for both sites together (z= 0.7807; n= 8,11; P=0.4350). There was no significant difference between the habitat types in the maximum dimension of home ranges at Achentoul (z= 0.1307; n= 5,5; P= 0.1913), at Badenloch (z= 0.5164; n= 3,6; P= 0.6056) or for both sites together (z= 0.5374; n= 8,11; P= 0.5910). Thus there was no evidence of any association between home range area or maximum dimension and site or habitat type.

Table 4: Distances moved by pairs between consecutive visits (metres). A= Achentoul, B= Badenloch.

Pair	Habitat Type	Visits 1 - 2	Visits 2 - 3	Visits 3 - 4	Visits 4 - 5	Visits 5 - 6	Visits 6 - 7	Visits 7 - 8	Visits 8 - 9	Visits 9 - 10	Pair median	Pair maximum	Pair minimum
A1	Non-bog	30	210	210	230	160	100	300	310	30	210	310	30
A2	Non-bog	50	60	60	90	180	240	320	290	160	160	320	50
A3	Bog	260	680			330					330	680	260
A4	Bog	40	160	260	500	490	490	570	60	660	490	660	40
A5	Non-bog	20	30	30							30	30	20
A6	Non-bog	40	230	40	200						120	230	40
A7	Bog		30	110							70	110	30
A8	Bog					70			480		275	480	70
A9	Bog							40	110	240	110	240	40
B1	Bog			50	70	190	110	70	70	100	70	190	50
B2	Bog	70	210	220	380	75	140	50	470	540	210	540	50
B3	Non-bog	240	620	160	640	250	170	180	100	120	180	640	100
B4	Non-bog	300	80	480	330	370	220	150	230		265	480	80
B5	Non-bog	70	30	280	180	200					180	280	30
B6	Non-bog	290	320	360							320	360	290
B7	Non-bog			30	90	30	460	80			80	460	30
B8	Bog				330	260				410	330	410	260
B9	Non-bog						50	40			45	50	40
Period median		70	185	160	230	195	170	115	230	200			
Period maximum		300	680	480	640	490	490	570	480	660			
Period minimum		20	30	30	70	30	50	40	60	30			

Table 5: Results of tests for association of movement distances with site, individual pairs, habitat type, period and interval length.
* = Significant at P=0.05.

VARIABLE	TEST	SITE								
		Both			Achentoul			Badenloch		
		z / χ^2	n / d.f.	P=	z / χ^2	n / d.f.	P=	z / χ^2	n / d.f.	P=
Site	Mann-Whitney U	0.889	54,41	0.374	-	-	-	-	-	-
Pairs	Kruskall-Wallis H	15.25	9	0.084	4.891	3	0.179	9.2538	5	0.099
Habitat	Mann-Whitney U	1.175	6,10	0.242	2.278	5,5	0.022*	0.525	3,7	0.599
Period	Kruskall-Wallis H	8.168	8	0.417	12.45	8	0.132	8.386	9	0.395
Interval	Mann-Whitney U	0.134	44,51	0.417	0.941	21,23	0.346	1.427	23,28	0.153

Table 6: Home range areas and maximum dimensions of all pairs with at least four brood locations.

SITE	PAIR NUMBER	HABITAT TYPE	MAXIMUM DIMENSION (m)	HOME RANGE AREA (m^2)
Achentoul	1	Non-bog	590	95,600
	2	Non-bog	520	62,600
	3	Bog	1300	313,900
	4	Bog	820	287,500
	5	Non-bog	470	42,500
	6	Non-bog	280	31,900
	8	Bog	590	65,000
	9	Bog	320	24,700
Badenloch	1	Bog	400	58,000
	2	Bog	710	194,600
	3	Non-bog	1490	486,200
	4	Non-bog	890	160,400
	5	Non-bog	480	94,300
	6	Non-bog	860	136,700
	7	Non-bog	520	60,800
	8	Bog	630	112,400
	9	Non-bog	180	13,100

3.3 Analysis of plumage variation

3.3 (1) Plumage score and sex

During analysis of plumage scores I assumed that the darker bird was the male (after Byrkjedal 1978 and Parr 1980). In total, plumage scores were recorded for both the male and female of 17 pairs (eight at Achentoul and nine at Badenloch) (Table 7). Male plumage scores ranged between five and eight, females between two and five. Nonparametric statistics were used in analysis of plumage scores due to (1) the fact

that the data was recorded in nominal categories and (2) the small sample sizes meant that parametric statistics could not be used with confidence.

Table 7: Plumage scores of pairs for which the scores of both the male and female were recorded.

SITE	PAIR NUMBER	HABITAT TYPE	PLUMAGE SCORE		
			MALE	FEMALE	MEDIAN
Achentoul	1	Non-bog	7	2	4.5
	2	Non-bog	7	2	4.5
	3	Bog	8	6	7
	4	Bog	6	2	4
	5	Non-bog	6	2	4
	6	Non-bog	5	3	4
	8	Bog	7	3	5
	9	Bog	7	3	5
Badenloch	1	Bog	8	5	6.5
	2	Bog	7	2	4.5
	3	Non-bog	7	3	5
	4	Non-bog	6	2	4
	5	Non-bog	7	3	5
	6	Non-bog	6	2	4
	7	Non-bog	8	4	6
	8	Bog	8	3	5.5
	9	Non-bog	6	2	4

3.3 (2) Plumage score and site

There was no significant difference between Achentoul and Badenloch in the plumage scores of males ($z= 0.763$; $n=17,17$; $P=0.4455$), females ($z=0.2603$; $n=17,17$; $P=0.7946$) or the mean plumage scores of pairs ($z=0.5459$; $n=17,17$; $P=0.5851$).

3.3 (3) Assortative mating

Spearman's rank correlation coefficients (r_S) were calculated for the plumage scores of males versus females, to test whether darker males paired with darker females and lighter males with lighter females. For Achentoul pairs alone there was no

significant correlation between the plumage scores of males and females in pairs (r_S=0.3917; n=8; P=0.337), but for Badenloch pairs there was a highly significant correlation (r_S=0.8692; n=9; P=0.002). One pair at Achentoul had a particularly large effect on the correlation coefficient (without which r_S=0.733; n=7; P=0.061). It was thus considered more appropriate to pool the pairs of both sites for this analysis, to overcome any effect of the stochastic distribution of pairs between the sites. This was valid as there was no significant difference in plumage scores between the sites. For both sites together, there was a highly significant correlation between the scores of males and females in pairs (r_S=0.6778; n=17; P=0.003). Thus it can be concluded that there is evidence of assortative mating on the basis of plumage darkness within the sites.

3.3 (4) Plumage score and habitat

All pairs were categorised as "Bog" or "Non-bog", depending on which habitat type held the majority brood locations. Mann-Whitney U-tests were then applied to see if there was any significant difference in the plumage scores of the pairs in the two groups. This methodology was used because the distinction based on utilisation of the two habitat types is observable and biologically significant. Testing for any difference in habitat selection between groups assigned on the basis of plumage scores would involve arbitrary cut off points made without biological justification, as plumage scores vary along a continuum (albeit a stepped continuum). Six pairs were classed as Bog and 10 as Non-bog..

With both sites taken together, there was no significant difference in the plumage scores of males (z=1.8056; n=6,10; P=0.071) or females (z=1.4255; n=6,10; P=0.154) between the habitat categories. However, the median plumage scores of the pairs (which are a more accurate indication of the darkness of each pair) were significantly different between the categories (z=2.073; n=6,10; P=0.0382), Bog pairs (median of median plumage scores = 5) being darker than Non-bog pairs (median of median plumage scores = 4).

Plumage scores were not compared between the habitats by site because of the very small sample sizes available (n=4,4 for Achentoul and n=3,6 for Badenloch) which would greatly reduce the power of the Mann-Whitney U-test.

4 DISCUSSION

4.1 Habitat selection and the functional needs of broods.

4.1 (1) Foraging sites

The quality of a foraging site for chicks is a function of the abundance of surface-active invertebrates and their accessibility to the chicks, which combine to determine the density of available prey. Since chick movement may easily be constrained by dense vegetation, especially early in chick development when their legs are short, the presence of clear or sparsely vegetated areas is important to them. This both allows free locomotion around a foraging site and enhances the ease of prey detection and acquisition. This may partly explain the preference for M18 pool types A, B and D in Bog habitat, since all these vegetation categories have areas which are bare or only have a low *Sphagnum* carpet in the interpool matrix. In contrast, M18 pool types X and, especially, O lack these areas and the taller and denser vegetation would thus constrain chicks' foraging efficiency.

In Non-bog habitat, M17 is similar in structure to M18 X and may be avoided for similar reasons, whilst the strong selection for U4 and U4 with *Juncus* is due to the short grazed grass areas within these habitats. These provide near-ideal foraging conditions. The vegetation gives little or no resistance to chick movement whilst prey items are likely to be conspicuous and readily captured on the grass surface. H9 and M25 were apparently not avoided or selected by broods. For M25 this is likely to be an artefact of its association with U4 and U4 with *Juncus* since its usual extremely dense, tussocky structure is probably nearly impenetrable to chicks.

Prey abundance between these vegetation categories may follow the same patterns as, and therefore reinforce the influence of, structural suitability. M18 pool types A, B and D all have more or less well-defined pools which may harbour emergent insects. Also, Coulson (1959) found that *Tipula subnodicornis* (a very common peatland species that occurs in Sutherland) reached highest density in damp peat. Since the peat in M18 A, B and D is damper and less prone to drying out than in M18 X, densities of Tipulid larvae (and thus emerging adults) may be higher. The increased use of Bog habitat by broods after the first third of the survey period may have been related to emergence of this and other Tipulids. However, Coulson (1990) found there was not such a pronounced synchronous emergence in the Flows as at Moor House in northern England, which may explain why the shift was not more marked.

Ratcliffe (1976) states that the invertebrate communities on grassland at Moor House NNR are more diverse and therefore produce a more reliable and sustained high

level of prey abundance than on blanket bog. Within the study sites, U4 and U4 with *Juncus* both occur on mineral soils and may therefore have higher prey abundance than M17 and all M18 pool types. This difference is likely to be greater in Sutherland if Tipulid emergence is less synchronised. Furthermore, sheep, which intensely graze U4 and U4 with *Juncus,* produce droppings which greatly increase the abundance of various surface-dwelling invertebrates that are potential Golden Plover prey items. The data from the FNPA invertebrate sampling programme may yield more information on the influence of prey abundance on brood habitat selection but these data are not available yet.

4.1 (2) Cover from predators

Chicks in the study area hid in the nearest available cover in response to disturbance and the alarm calls of adults. The presence of suitable hiding places may constrain choice of foraging location over and above the influence of prey availability. All the vegetation categories in Bog habitat provide at least some cover and thus this need is not likely to have much impact on selection of vegetation categories. In Non-bog areas, U4 with *Juncus* provides what may be an optimal combination of high prey availability on the short grazed grass with clumps of *Juncus* for cover. Chicks foraging on this habitat were observed to run into the *Juncus* in response to disturbance on several occasions during the brood location surveys. Larger patches of U4 (without *Juncus*) may have been avoided by broods because this habitat does not provide cover. Whilst small patches provide good foraging locations close to other vegetation categories, the interior of large patches may become unsuitable as distance from cover increases. Alternative hypotheses are: (1) That chicks did use the large patches of U4 but ran off them into cover when disturbed, giving a brood location well away from the actual foraging site. However, chicks were seen to ignore large patches of U4 near to them during behavioural observations and were not seen running off them during brood location surveys. (2) U4 is not used at all and its apparent selection is an artefact of its close association with U4 with *Juncus*. This is countered by the fact that two observations were made of chicks feeding in small patches of U4, and by the fact that nine of 40 plover plots containing U4 did not also contain U4 with *Juncus*. Evidence from experiments involving the manipulation of the structure of these vegetation categories would, however, be required to confirm the functional significance of *Juncus* and its importance as a cue to habitat selection by Golden Plover broods within the study sites.

4.1 (3) Adults' vigilance posts

As the breeding strategy of Golden Plovers relies on adults warning chicks of predation risk with alarm calls, the presence of suitable posts from which adults can watch for predators is an important functional need. In Bog habitat, vigilance posts observed in

use during behavioural observations and brood surveys were invariably *Racomitrium lanuginosum* hummocks. These occur in M18 A, B and D pool types but not M18 X and O and may reinforce the habitat selection patterns already outlined. In Non-bog habitat a wide variety of vigilance posts were used, seemingly determined by what was available near to chick feeding habitat. These sites included the tops of H9 ridges bordering streams, rocks, any slight hummock affording a good view of the surrounding area and even stone walls. It is therefore unlikely that the need for vigilance posts imposed strong constraints on habitat choice within the study sites, but avoidance of M17 may have been reinforced by the general lack of suitable posts in this category. Along streams, sites adjacent to H9 hummocks and ridges may have been selected but the avoidance of large areas of this category (due to its dense *Calluna vulgaris* canopy which makes it unsuitable for chick foraging) meant that this was not evident from the data. Adults often used sites at the side of, rather than in, patches of U4 with *Juncus*, presumably to prevent the *Juncus* obscuring their view and / or due to a paucity of suitable posts within that vegetation category. This may be one reason why extensive U4 with *Juncus* pasture elsewhere in the FNPA study area was not used by Golden Plover broods, although competitive exclusion by Lapwings is also likely to have been important, as Cramp and Simmons (1983) state that Lapwings are the only shorebird species with which Golden Plovers commonly fight and that the Golden Plovers are always the losers.

It appears that a mosaic of vegetation characteristics is required to meet the functional needs of broods, these being fulfilled both within and between vegetation categories in Non-bog habitat and in within-category mosaics in M18 pool types A, B and D. These results conflict with the habitat associations given for Golden Plovers in the Flow Country by Lindsay *et al.* (1988), who state that they show a preference for all bog habitats (their divisions encompassing all M18 pool types and M17) and show no obvious trend with *Juncus* flushes, grass patches or mosaics of vegetation types. They were not, however, referring specifically to brood rearing habitat.

4.2 Movements and home ranges

The distances moved by pairs in this study were much larger than those recorded by Parr (1980), who found that 32 of 38 pairs remained within 100m of the nest. This equates with a home range diameter of 200m. One interpretation of this is that in my study, broods moved in response to disturbance caused during brood location surveys. However, table 3 shows that there was much variation in the distances moved, both within pairs (in the distances moved between different visits) and in the minimum, maximum and

median movements of different pairs. As the level of disturbance was constant, these facts indicate that other factors were important in determining movements. Although it is possible that pairs differed in their response to disturbance, the fact that at least some movements by most pairs were short indicates that this is unlikely to have been solely responsible for the variation. Furthermore, no sightings of "escape" movements were made when behavioural observations were obtained directly after locating broods. The distances moved were comparable with those reported by Yalden (1991), although more disturbance was caused to the brood radio-tracked in that study than was caused to the broods in my study.

Other than the differences between pairs that were significant at the P=0.1 level, the only significant association for movements was with habitat type at Achentoul, where Bog pairs moved further than Non-bog pairs. It might be expected that Non-bog pairs would move further than Bog pairs since they utilise patches of U4 and U4 with *Juncus* that occur chiefly dispersed along streams in a linear fashion. However, one Bog pair at Achentoul (pair four) had an atypically high median movement distance. This arose because it did not inhabit the main areas of Bog at this site, but commuted between two small tracts in the western part of the site. This brood contributed nine of 19 movements for Bog pairs at this site. As they were atypically long movements they may have produced a spurious relationship between habitat type and distance moved, especially coupled with the fact that the largest single movement recorded in the study (680m, in a movement from Non-bog to Bog habitat) was contributed by another Bog pair at this site. The idea that the relationship is spurious is supported by the fact that there was no difference in home range area or maximum dimension between Bog and Non-bog pairs at Achentoul. Thus, w hilst the Bog at Achentoul is more fragmented than that at Badenloch, it appears that the major variations in distance moved are in fact between and within individual pairs and are determined by the precise situation of each. A complex array of factors may influence brood movements, such as the configuration and quality of available foraging areas within broods' home ranges, changes in predation pressure and the responses of broods (or their parents) to stochastic events such as periods of extreme weather. It is perhaps therefore not surprising that no universal patterns can be discerned in the movement distances and that only a short essay on the history of movements of each brood would provide an insight into the causation of the data collected.

The maximum spans of the home ranges have, however, implications for the validity of census methods used in the Moorland Bird Survey (MBS). The methodology adopted in the MBS, outlined in Brown and Shepherd (1993), involves making two visits to 500m x 500m survey units: one between early April and mid-May (when Golden

Plovers are nesting) and one between mid-May and late June (during most of which period Golden Plovers will be rearing chicks). Records of pairs of Golden Plover are considered to be separate if they are at least 1000m apart on the two visits. Table 5 shows that during the 25 days in June in which the broods in my study were followed, two of 17 pairs spanned well over this distance. The pair which moved the maximum distance had been colour-ringed, eliminating doubts over repeated identification. All the brood locations in my study were after the broods had moved away from the nest, whilst the first MBS visit is made during the nesting period. If the nest site is added to the home range, the maximum span of the one brood for which the nest site is known increases by 200m. If conservative totals of 200m or 300m are added to each maximum span to take account of (a) the position of the nest and (b) possible movements of adults from the extreme locations of the home ranges in response to the surveyors, five and seven pairs, respectively, of the 17 pairs could have been counted twice using MBS methodology. Theoretically this could have given an over-estimate in population size of between 29.4 and 41.2 %.

4.3 Relative quality of the habitat types

As it was not possible to assess chick survival and fledging success (due to the low frequency of chick sightings and fact that only four fledged juveniles were seen on the study sites up to mid-July) it is difficult to assess the relative quality of each habitat type. The areas of broods' home ranges provided no evidence of smaller home ranges (possibly indicating better habitat) in either habitat type but these were subject to the classic faults of the minimum convex polygon method of delimitation. Many contained aggregations of brood locations in activity centres with large empty spaces in between, and were vulnerable to the disproportionate effects of extreme locations. Thus they did not accurately represent the area utilised by each brood. Other methods of home range assessment involving the delimitation of core areas were considered but the number of brood locations for each pair was prohibitively low.

Although Bog habitat and Non-bog habitat were both used according to their availability over each study site taken as a whole, the following suggests that Non-bog habitat may be better quality:

(1) Table 2 showed that grazed sections of Achentoul had a higher density of brood locations than the ungrazed area and that a higher proportion of these were in Non-bog habitat. This mirrors the findings of Parr (1980) and may be related to the increased availability of U4 and U4 with *Juncus* in grazed Non-bog areas, but the influence of covariables (such as a negative correlation between the suitability of Bog for grazing

sheep and its suitability for Golden Plover broods) must be borne in mind. Together with the fact that most brood locations occurred on a very small proportion of the available Non-bog habitat at both sites, this intimates that optimal Non-bog habitat (grazed areas with many streams and small patches of mineral soils) may be capable of supporting higher densities of breeding Golden Plover. It is recognised, however, that it is not possible to determine habitat quality from single year studies of distribution and that the habitat supporting the highest density is not necessarily the best quality habitat (Cody, 1985, Rosenzweig, 1985, Wiens, 1989).

(2) The same reasons given by Ratcliffe (1976) for the supply of Golden Plovers' invertebrate prey on limestone grassland being better than that of blanket bog in northern England may hold for the Bog and Non-bog habitats of this project's study sites, as discussed earlier. Furthermore, the Bog habitat in Sutherland may lack the period of Tipulid superabundance described for northern England and instead have a more sustained (but at a lower level) prey supply.

(3) Analysis of plumage scores revealed that pairs in Bog habitat were significantly darker than Non-bog pairs which may indicate a difference in individual quality between the habitat types. This is discussed below.

4.4 Plumage variation

The evidence for assortative mating by plumage darkness concurs with the findings of various previous studies (Byrkjedal 1978, Parr 1980, Thomas 1986). This suggests that individuals select mates at least partly on the basis of plumage darkness or covariant qualities. Edwards (1982) suggested that plumage darkness is an honest signal of individual quality that has evolved to reduce conflict for resources such as mates and territories. He proposed that darker individuals are dominant and occupy the best territories. My study found that pairs on the Bog were darker than Non-bog pairs, which parallels the findings of Thomas (1986), who also found a higher density of Golden Plovers on limestone grassland than acid moorland. If Edwards' assertion is correct, these findings are counter to the suggestion that Non-bog habitat is better than Bog habitat. Whilst despotic exclusion of birds from other habitats could explain the high densities of Golden Plovers in grassland areas, Byrkjedal (1978) suggested that darker birds occupied suboptimal areas in southern Norway. It is known that plumage darkness of Golden Plover populations increases along a gradual cline from south to north in Britain (Ratcliffe 1976, Parr 1980), whilst Byrkjedal (1978) states that plumage darkness increases with latitude and altitude in southern Norway. In both cases, breeding grounds are available earlier where birds are lighter, while P. Whitfield (pers. comm.) reports that within

populations in the Highlands of Scotland, lighter birds arrive first. These findings all support the idea that birds which breed earlier are lighter due to abbreviated prenuptial moult (both between and within populations). Since early arrival on breeding grounds is positively correlated with individual quality in at least one species of migratory bird (e.g. Moller 1994), there being a trade-off between arriving early to compete for optimal resources and risking the effects of environmental inclemency, it seems very unlikely that plumage darkness is an honest signal of individual quality. Rather, earlier (better and less dark) birds should obtain the best territories (and mates) and retain them through site-related dominance. This is supported by the finding that possible late hatching broods strengthened the increased use of Bog habitat that was observed after the first third of the survey period.

The evidence of clinal variation and arrival times indicates that there is little variation in the timing of the onset of moult. Thus, for individuals arriving on the breeding grounds at the same time, plumage darkness may be an honest signal of quality. This could operate through individuals having had the same time since the onset of moult to acquire units of bioenergetic currency to fund the moult of body feathers. Better individuals, able to command optimal foraging sites in spring flocks and to forage more efficiently, would fund more moult (Piersma and Jukema 1993). Competition for resources linked to breeding is likely to be most intense between individuals arriving at the same time, with later (darker) birds not being in direct conflict with earlier birds. This is supported by observations of sequential use of brood rearing areas by different pairs (Parr 1980, pers. obs.). On those occasions when conflict between individuals does escalate, vocalisations often play a prominent role (Cramp and Simmons 1982). It is possible that evolution has emphasised the role of vocalisations in the later stages of conflict to overcome the fact that spread of arrival on the breeding grounds confounds the honesty of plumage signals. For high arctic breeding waders (which have less spread in arrival on the breeding grounds due to the tight schedule of the breeding season) plumage characteristics may be more honest indicators of individual quality, as suggested for the Bar-tailed Godwit by Piersma and Jukema (1993). A comparative study between Golden Plovers and Grey Plovers (which would overcome confounding phylogenetic variables) may provide an insight into the possible effects of migratory strategy on signalling systems in breeding waders.

4.5 Population size and landscape structure

Although Bog and Non-bog habitats were used according to their availability within the study sites, it has been shown that there were marked preferences for certain

vegetation categories within the habitats. In Bog habitat, M18 X was avoided at both sites, M18 D was significantly selected at both sites together and other pool types were used according to their availability. In Non-bog habitat, U4 and U4 with *Juncus* were both strongly selected at each site, whilst *Juncus* and M17 were avoided at Achentoul and Badenloch respectively. It is therefore likely that the use of the habitat types at the two sites is a reflection of their specific composition of vegetation categories and may not be directly translated to other areas of these habitats. If density of breeding Golden Plovers is limited by the availability of brood rearing habitat, the populations of areas of Bog may be related to the area made up of A, B and, especially, D pools rather than to their total area which may include large expanses of pool type X ("dry bog"). Similarly, non-bog areas may hold a population related to the availability of small U4 and U4 with *Juncus* patches (rather than extensive pasture), which in turn is related to stream length density and grazing intensity. As stated previously, the study sites were selected for the good densities of Golden Plovers they held. Both sites contained a combination of well-developed pool systems and Non-bog areas with many streams and well-grazed areas, a combination which may be important given the temporal variation in habitat use already outlined. This may explain why densities were higher than in surrounding areas (see Figure 2). Furthermore, neither area was in close juxtaposition with tracts of forestry, which may limit populations through (a) harbouring nest / chick predators which reduce breeding success of birds breeding in adjacent areas (Thompson, Stroud and Pienkowski, 1988, Parr, 1992), and (b) hydrological edge effects which may change the structure of adjoining areas of Bog (Lindsay *et al.* 1988). At the landscape scale, it may be possible to model populations of Golden Plover both on the level of landscape structure (incorporating availability of potential breeding areas and composition of adjacent land) and at the more fundamental level of causation by considering hydrology (influencing stream abundance and marginal vegetation and raised mire formation) and management (especially the effects of grazing on one hand and drainage on the other). However, as Parr (1992) shows, for these migratory birds consideration of the breeding grounds alone is not necessarily sufficient to explain population sizes and trends, while habitat associations and patterns of occupancy may change with variations in population density (Cody, 1985, Wiens, 1989). Thus the patterns found in this study may not hold for other years, especially given that densities of breeding Golden Plover in the FNPA study area were said to be considerably lower than usual (e.g. G. Stenning, pers. comm.).

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Appendix A: Vegetation category coverages and habitat type classification of plover plots.

ACHENTOUL

Pair	Visit	M18 A	M18 B	M188 D	M18 X	M18 O	M17	H9	U4 w/ J	U4	M25	Junc	M15	Moss	Habitat Type
1	0	10						75		15					Non-bog
1	1								90	10					Non-bog
1	2				10			25	65						Non-bog
1	3						30		65		5				Non-bog
1	4								100						Non-bog
1	5		100												Bog
1	6	45			35			20							Bog
1	7							80		20					Non-bog
1	8				20			35	30		15				Non-bog
1	9				10			25	65						Non-bog
1	10				20			30	50						Non-bog
2	1							35	40	15	10				Non-bog
2	2							35	25	15	25				Non-bog
2	3				35			10	40	10	5				Non-bog
2	4	30	70												Bog
2	5	50	50												Bog
2	6	40	60												Bog
2	7							50	25	20	5				Non-bog
2	8	20						20	30		30				Non-bog
2	9							20	45	20	15				Non-bog
2	10							55	35		10				Non-bog
3	1							35	15	35	15				Non-bog
3	2							35	10	10	20	25			Non-bog
3	3		100												Bog
3	5									20	80				Non-bog
3	6	45	55												Bog
3	8	20	45	35											Bog
3	10	15		85											Bog
4	0	30			60		10								Bog
4	1						5	40	5	35	15				Non-bog
4	2						25		40	35					Non-bog
4	3								30	30					Non-bog
4	4							10	70	20					Non-bog
4	5		75					25							Bog
4	6		90					10							Bog
4	7				30		25	20	10		15				Non-bog
4	8	50					50								Bog
4	9	35	65												Bog
4	10		45		55										Bog
5	1		25				50		25						Non-bog
5	2		45				45		10						Non-bog
5	3		10				75		15						Non-bog

Pair	Visit	M18 A	M18 B	M188 D	M18 X	M18 O	M17	H9	U4 w/ J	U4	M25	Junc	M15	Moss	Habitat Type
5	4						70		30						Non-bog
5	8		20				30	50							Bog
5	10						80	20							Bog
6	1						25	45	20	10					Non-bog
6	2							35	15	20		30			Non-bog
6	3						15	45	40						Non-bog
6	4							15	45	20	20				Non-bog
6	5							75	25						Non-bog
7	2		65	35											Bog
7	3		75	25											Bog
7	4	15	40	45											Bog
8	5		50					15					20	15	Bog
8	6		35		50			15							Bog
8	8		100												Bog
8	9							65	10	15	10				Non-bog
9	7	25	75												Bog
9	8	15	85												Bog
9	9	40	60												Bog
9	10	40	60												Bog
A	4				60			15	15		10				Non-bog
B	4	55			45										Bog
C	4	100													Bog
D	5		65	35											Bog
E	6	5	40	55											Bog
F	7		100												Bog
G	7		20	80											Bog
H	9	20	70	10											Bog
I	9		15	85											Bog

BADENLOCH

Pair	Visit	M18 A	M18 B	M188 D	M18 X	M18 O	M17	H9	U4 w/ J	U4	M25	Junc	M15	Moss	Habitat Type
1	1				50						50				Non-bog
1	3	25		75											Bog
1	4	10		90											Bog
1	5			100											Bog
1	6	75	15		10										Bog
1	7			100											Bog
1	8	35	35	30											Bog
1	9		80		20										Bog
1	10	30	70												Bog
2	1		100												Bog
2	2	55	45												Bog
2	3	15		85											Bog
2	4	25		75											Bog

Pair	Visit	M18 A	M18 B	M188 D	M18 X	M18 O	M17	H9	U4 w/ J	U4	M25	Junc	M15	Moss	Habitat Type
2	5	30	55	15											Bog
2	6		100												Bog
2	7	60	40												Bog
2	8			100											Bog
2	9						30	20		15	35				Non-bog
2	10	60	40												Bog
3	1						15		55		30				Non-bog
3	2						65	10		25					Non-bog
3	3							30	10	35	25				Non-bog
3	4						25		20		55				Non-bog
3	5	85	15												Bog
3	6								100						Non-bog
3	7				60				40						Non-bog
3	8								65	35					Non-bog
3	9	40					35		25						Non-bog
3	10				55				45						Non-bog
4	1						20	15	20	30	15				Non-bog
4	2						35	15		10	40				Non-bog
4	3						5	15	55		25				Non-bog
4	4						65			10	25				Non-bog
4	5							25	10	20	45				Non-bog
4	6							10		35	50			5	Non-bog
4	7						45			5	50				Non-bog
4	8						60		15		25				Non-bog
4	9						40		40		20				Non-bog
5	1						50		25		25				Non-bog
5	2						55		5	20	20				Non-bog
5	3						45	10		25	20				Non-bog
5	4								75	25					Non-bog
5	5								70	30					Non-bog
5	6						40		35	25					Non-bog
6	1							5	50	15	30				Non-bog
6	2						50		10	5	35				Non-bog
6	3						20				80				Non-bog
6	4		75				25								Bog
7	3						35	10		10	45				Non-bog
7	4						45			5	50				Non-bog
7	5						80				20				Non-bog
7	6						90				10				Non-bog
7	7	30		70											Bog
7	8	60	40												Bog
7	10		45	55											Bog
8	4	60		40											Bog
8	5	80		20											Bog
8	6	35	65												Bog
8	9	25	75												Bog
8	10	30	20	50											Bog

Pair	Visit	M18 A	M18 B	M188 D	M18 X	M18 O	M17	H9	U4 w/ J	U4	M25	Junc .	M15	Moss	Habitat Type
A	5						25	5	15	10	45				Non-bog
B	6						20	65	5		10				Non-bog
C	7						30	5	10	5	50				Non-bog
D	10						85		5		10				Non-bog

Appendix B: Vegetation category coverages and habitat type classification for random plots.

ACHENTOUL

Plot	M18 A	M18 B	M18 D	M18 X	M18 O	M17	H9	U4 w/ J.	U4	M25	Junc	M15	Moss	Habitat Type
1		55	45											Bog
2		30				25	30					15		Non-bog
3						50				35	15			Non-bog
4		80	20											Bog
5						45		15		40				Non-bog
6						30	70							Non-bog
7							100							Non-bog
8		50		15		15	20							Bog
9							100							Non-bog
10				35			65							Non-bog
11		90		10										Bog
12		100												Bog
13						65		20		15				Non-bog
14											100			Non-bog
15						100								Non-bog
16						100								Non-bog
17						10				65	25			Non-bog
18		20		10			70							Non-bog
19				10						15	75			Non-bog
20							5	25		70				Non-bog
21										55	45			Non-bog
22		25		75										Bog
23	25		75											Bog
24				55						45				Non-bog
25	10	65								25				Non-bog
26		80	20											Bog
27						45				55				Non-bog
28				65						35				Non-bog
29	20	80												Bog
30	35	55		10										Bog
31	80			10			10							Bog
32	40	60												Bog
33						30	35				35			Non-bog
34						10			45	45				Non-bog
35		70				15	15							Bog
36						25		20	55					Non-bog
37	25	55		20										Bog
38	20			50		20				10				Bog
39				5			95							Non-bog
40	25	25				20	30							Bog
41	100													Bog
42										65	35			Non-bog

Plot	M18 A	M18 B	M18 D	M18 X	M18 O	M17	H9	U4 w/ J.	U4	M25	Junc	M15	Moss	Habitat Type
43		50		50										Bog
44	20			80										Bog
45	100													Bog
46		100												Bog
47		30		25			30	15						Non-bog
48						45	20			35				Non-bog
49								30	20	35	15			Non-bog
50					100									Bog
51	60	40												Bog
52	75				25									Bog
53	50	25		25										Bog
54	0	100												Bog
55	100													Bog
56	100													Bog
57	45	20					35							Bog
58				40			15	10		35				Non-bog
59				100										Bog
60	35			30			35							Bog
61							55	15		30				Non-bog
62	50			30			20							Bog
63				90		10								Bog
64							80			20				Non-bog
65				80						10	10			Non-bog
66						25	75							Non-bog
67	30			40						30				Non-bog
68						60	40							Non-bog
69						30	50			20				Non-bog
70	15	85												Bog

BADENLOCH

Plot	M18 A	M18 B	M18 D	M18 X	M18 O	M17	H9	U4 w/ J	U4	M25	Junc	M15	Moss	Habitat Type
1						100								Non-bog
2						100								Non-bog
3						100								Non-bog
4						80						20		Non-bog
5						100								Non-bog
6				100										Bog
7		25		50			25							Bog
8						35	20	15		30				Non-bog
9	30	20				50								Bog
10				100										Bog
11						85	15							Non-bog
12						5	95							Non-bog
13				30		40				30				Non-bog
14	5			90			5							Bog

Plot	M18 A	M18 B	M18 D	M18 X	M18 O	M17	H9	U4 w/ J.	U4	M25	Junc	M15	Moss	Habitat Type
15						100								Non-bog
16				50		25				25				Non-bog
17	55	45												Bog
18				20		30				50				Non-bog
19						60	40							Non-bog
20						45	35			20				Non-bog
21						70				30				Non-bog
22						30	20	10		40				Non-bog
23				100										Bog
24				100										Bog
25		40		60										Bog
26		100												Bog
27			100											Bog
28	20	30	50											Bog
29		15		65						20				Non-bog
30	40	35	25											Bog
31	25		75											Bog
32	85	15												Bog
33	30	70												Bog
34						20	45	5		30				Non-bog
35						35		5		60				Non-bog
36	50					50								Bog
37						60				40				Non-bog
38		50				20	30							Bog
39						85	10			5				Non-bog
40						100								Non-bog
41						90	10							Non-bog
42						100								Non-bog
43						100								Non-bog
44							100							Non-bog
45						20				80				Non-bog
46						100								Non-bog
47						85				15				Non-bog
48						60				40				Non-bog
49						45				55				Non-bog
50		100												Bog
51				50		15				35				Non-bog
52		100												Bog
53		100												Bog
54						85				15				Non-bog
55						75				25				Non-bog
56				80			10			10				Non-bog
57						85				15				Non-bog
58		60		40										Bog
59							95			5				Non-bog
60							40	15		45				Non-bog
61						55				45				Non-bog

Plot	M18 A	M18 B	M18 D	M18 X	M18 O	M17	H9	U4 w/ J.	U4	M25	Junc	M15	Moss	Habitat Type
62						60				40				Non-bog
63						85	10			5				Non-bog
64						85				15				Non-bog
65				55		15				30				Non-bog

Appendix C: Chi-squared contributions for vegetation category frequency of occurrence tests, plover plots versus random plots

(a) Bog Habitat

BOG	Site		
Vegetation Category	Both	Achentoul	Badenloch
M18 A	0.069	0.145	0.825
M18 B	0.300	1.145	0.267
M18 D	6.240	3.293	2.518
M18 X	11.050	4.930	6.438
M18 O	2.200	2.549	Not recorded
Others	3.716	0.210	0.029

N.B. M18 X and M18 O grouped during analysis; individual contributions shown.
Others = Sum of Chi squared contributions for all Non-bog categories recorded in Bog plots.

(b) Non-bog Habitat

NON-BOG	Site		
Vegetation Category	Both	Achentoul	Badenloch
M17	12.445	3.801	9.430
H9	0.092	0.082	0.649
M15	Grouped with H9	Grouped with H9	Grouped with Moss
M25	0.279	2.475	0.142
U4	23.110	9.240	14.311
U4 with *Juncus*	14.791	8.391	6.524
Juncus	7.296	6.901	Not recorded
Moss	Grouped with H9	Not recorded	0.074
Others	5.016	1.053	2.436

Others = Sum of Chi square contributions for all Bog categories recorded in Non-bog plots.