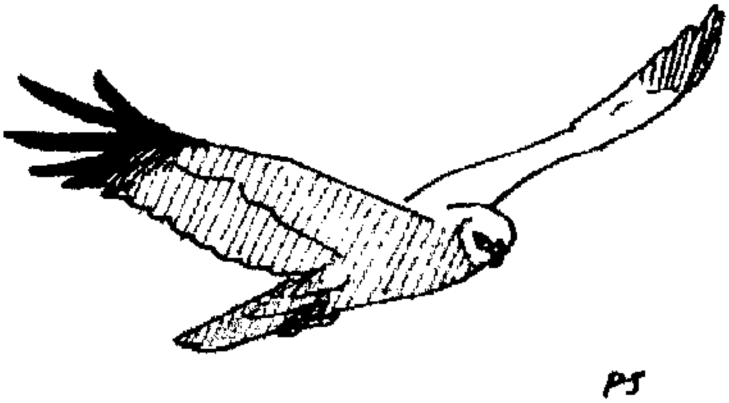
The effects of forestry on hen harriers *Circus cyaneus*

Michael Madders



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CONTENTS

SUMMARY

Changes in the Scottish hen harrier population over the past 50 years appear to be associated with the development of coniferous afforestation. Increases or range extensions have occurred in some areas with recently established first rotation forests, where harriers are believed to have benefited from the increased cover and prey resources that result from fencing. Conversely, population declines have been reported in areas where maturing trees have reduced the availability of open and semi-open ground for nesting and hunting. Clear-felled plantations restocked with trees could potentially provide suitable habitat for a further period, although current evidence suggests that harriers make only sporadic use of second rotation forests for nesting.

The extent to which harriers utilise first and second rotation forests for hunting has not previously been quantified, yet this knowledge is vital if we are to manage harrier populations effectively. This study examines time budget information from watches of breeding harriers which had access to various types of forest and moorland habitat. The relative use made of each habitat was determined, and preferences related to measures of vegetation cover and structure and estimates of prey abundance. Site occupancy and breeding success were related to the availability of the habitats studied. The study was undertaken in Argyll, west Scotland.

Habitat selection by foraging harriers was investigated at 2 scales, the first reflecting the process by which a harrier came to be in a particular habitat, the second identifying specific components within habitats that were selected. A chronosequence was used to investigate the responses of harriers to forest succession. Observations of foraging harriers were made in sample areas, stratified by location and habitat-type. Within each observation area the time harriers spent foraging, vegetation characteristics, and relative abundance of prey were measured. Flight behaviour and the frequency with which foraging harriers made prey strikes and successful prey captures was recorded.

Foraging time was found to be dependent on the proximity of harrier nests. When this was taken into account, harriers showed a strong preference for afforested habitats with limited tree development. Habitat use declined as the volume of foliage 2-5m tall increased. Thus, areas where tree canopy closure had occurred tended to be avoided. Harriers exhibited neither strong preference for, nor avoidance of, the unafforested habitats studied. Foraging preferences tended to reflect the frequency with which harriers struck at, and captured, prey. Differences in foraging behaviour between male and female

harriers were difficult to establish due to the problem of consistently discriminating female and one year old males, and the relatively short period during which females hunted.

When making route decisions foraging harriers tended to avoid trees, and select routes in the higher parts of the areas observed. Flight paths tended to be associated with linear landscape features and boundaries, such as streams, ditches, walls and tracks. Areas with much bracken and grass were generally avoided. Harriers foraging within forests selected areas of least canopy cover and avoided stands of bracken. In forests with limited tree development harriers were able to hunt for prey in the rank vegetation between trees.

Harriers mostly hunted low over the ground and avoided fast flying speeds, suggesting that they were searching mainly for concealed and relatively immobile prey which they expected to capture without the element of surprise. Alternative foraging strategies, involving greater flying elevations and faster speeds, were used least in newly afforested habitats. This may have been related to the availability of large numbers of field voles, which harriers are able to locate using aural cues.

Harrier diet was assessed from pellets of undigested matter regurgitated at nests. A wide range of prey was recorded, including 35 bird and 7 mammal species, ranging in size from 9 to 400g. Four prey-types predominated: passerines, waders and gamebirds, lagomorphs, and small mammals. Passerines were the most important prey-type, accounting for 65% of items taken, and 43% of food by weight. Of the remaining prey, small mammals were most important numerically, but their contribution by weight was similar to that of other prey-types. Variation in the contribution of prey-types could be explained by spatial differences in the abundance of lagomorphs, and temporal fluctuations in small mammal abundance. Meadow pipits and field voles were the most frequently taken species.

Harriers spent most time foraging in areas where meadow pipit and (especially) field vole were relatively abundant. The strength of this effect increased with the density of vegetation less than 0.5m tall. Large prey, such as gamebirds and lagomorphs, were scarce and their distribution did not appear to influence harrier foraging effort.

Land cover and terrain data for different annuli of distance from harrier nest sites were extracted from a Geographic Information System. Nest occupancy was found to be associated with the amounts of heathland and forestry below 250m altitude. Nest sites whose core foraging range contained much heathland, and that had a relatively elevated hinterland, produced the largest broods. Unexpectedly, productivity did not appear to decline as a result of tree development in young first rotation forests. This may have been because harriers were able to increase their use of alternative habitats, or extend their foraging range, or both.

CHAPTER 1

INTRODUCTION

Contents:

The hen (northern) harrier *Circus cyaneus* is one of the world's most elegant and spectacular birds, and a unique asset to our natural heritage. It is also rare, and currently under threat from a range of human activities, mainly as a result of the way in which we use land. The wise management of hen harrier populations is therefore an essential part of land-use planning. This study investigates the foraging ecology of hen harriers in order that we may better understand the bird's requirements and the way in which it is affected by land-use change, in particular the afforestation of upland heaths and grasslands.

I studied the foraging behaviour, resource use and breeding performance of hen harriers in Argyll, west Scotland during 1992-94. The habitats in this region are predominantly upland, and are used mainly for extensive sheep *Oves aries* rearing and commercial forestry. This has led to a polarisation in vegetation-type between, on the one hand, grazed grassland and heath mosaics and, on the other, densely foliated forests. Furthermore, whereas moorland habitats change relatively little from year to year, forests are dynamic ecosystems that host a rapid succession of flora and fauna. West Scottish harriers must therefore operate in a challenging environment that varies both spatially and temporally.

This chapter summarises the principal ecological and conservation issues relating to harriers, and outlines the main objectives of study.

ECOLOGY OF HEN HARRIERS

Description

Hen harriers are medium-sized diurnal birds of prey with long, narrow wings and tails. In common with many species of raptor they show marked reversed sexual size dimorphism: females are ca. 10% larger than males (mean wing lengths[1] ±*S.D.*: adult males 338mm ±*7.8* [n = 18]; adult females 376mm ±*8.2* [n = 25]; Nieboer 1973), and ca. 50% heavier (adult males 346g ±*38.5* [n = 5]; adult females 527g ±*89.7* [n = 8]; Cramp and Simmons 1980). Juveniles of each sex have shorter wings, but not tails, than adults (Bildstein and Hamerstrom 1980).

The plumage of adult birds differs strikingly between the sexes. Males have a grey head and breast, white underparts, black primaries and a narrow dark band along the trailing edge of the underwing (absent in older birds; Watson 1977). Females are dark brown above except for paler median wing coverts, conspicuous white rump, and brown-grey banded tail. The underparts are buff-brown, streaked on the body, and with darker

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[1] distance from carpal joint to tip of longest primary

barring on the underwing and tail. Juveniles of either sex closely resemble adult females but are darker brown above (and, in Nearctic forms, russet below). Males do not start to moult into grey plumage until their 2nd year; by the time they are 18 months old they are predominantly grey, but have a distinctive brown "saddle", caused by the retention of darker feathers on the mantle and scapulars.

Compared with sympatric harrier species (marsh harrier *C. aeruginosus*, Montagu's harrier *C. pygargus*, and pallid harrier *C. macrourus*), hen harriers have broad wings, short wing tips and a relatively high tail/wing area ratio (Nieboer 1973; Watson 1977). These features are likely to result in enhanced agility and manoeuvrability (Lorenz 1933) and may reduce competition with other *Circus spp.* (Schipper 1977; Schipper *et al.* 1975). Hen harriers have owl-like facial discs with large ear apertures, enabling acoustic location of prey (Rice 1982), and long legs relative to their body size, permitting prey to be the seized within rank vegetation. These abilities appear to be adaptive for the detection and capture of concealed prey.

Distribution and abundance

The species has a circumpolar distribution. Hen harriers *C. c. cyaneus* breed in a broad band across the Palearctic region, between 40°N and 70°N, and winter in southern Asia and western and southern Europe (Batten *et al.* 1990). Northern harriers *C. c. hudsonius* breed in the Nearctic between 30°N and 70°N, and winter mainly below latitude 40°N as far south as Panama (MacWhirter and Bildstein 1996). Current European population estimates range from 22,000 to 32,000 breeding pairs (Tucker and Heath 1994), of which the UK population comprises approximately 630 pairs (2-3%) (Bibby and Etheridge 1993; Bellamy 1992).

Habitat

A wide range of (mostly) open terrain is used for both breeding and foraging, including steppe and other grasslands, open taiga, upland moors, heaths, low scrub, forest bogs and clearings, young tree plantations, croplands, river valley meadows, freshwater and brackish marshes, wetland borders, and coastal sand dunes (Cramp and Simmons 1980; Boedeltje and Zulstra 1981; Tucker and Heath 1994; MacWhirter and Bildstein 1996). In Britain, hen harriers mainly occupy undulating moorlands below 500m, and young (<10 year old) conifer plantations (Watson 1977; Batten *et al.* 1990).

Diet

Birds and mammals are principally eaten, although other prey can be important locally, e.g. insects, reptiles, amphibians, and fish (Uttendörfer 1939; Witherby *et al.* 1939; Dementiev and Gladkov 1951). Prey are occasionally taken as carrion (Dementiev and Gladkov 1951; Schipper 1973; Picozzi 1978). Avian prey are mainly passerines and young nidifugous birds, and mammalian prey mainly small rodents (especially *Microtine* voles) and young lagomorphs (Cramp and Simmons 1980). In North America, vertebrate prey masses range from ca. 7-1000g (MacWhirter and Bildstein 1996).

Comparison of dietary studies (e.g. Errington and Breckenridge 1936; Randall 1940; Craighead and Craighead 1956; Hagen 1969; Balfour and Macdonald 1970; Dickson 1970; Schipper 1973; Picozzi 1978, 1980; MacWhirter 1985; Simmons *et al.* 1986b; Barnard *et al.* 1987; Redpath 1991; Watson 1977) shows that harrier diet varies seasonally, annually and regionally. Many studies (e.g. Schipper 1973; Bildstein 1978; Hamerstrom 1979; Hamerstrom *et al.* 1985; Bildstein 1987) have stressed the importance of voles, particularly in the northern parts of the harrier's range, and during the non-breeding season. It has been suggested that voles are taken preferentially where they are numerous (Schipper 1973; MacWhirter 1985). However, birds appear to be readily taken if voles are scarce or absent (Schipper *et al.* 1975; Marquis 1980; Picozzi and Cuthbert 1982). Redpath (1992) found that harriers in north-east Scotland hunted principally for large prey (e.g. young gamebirds and lagomorphs), and where these prey were scarce hunted for passerine species.

Foraging behaviour

Hen harriers typically hunt low and buoyantly over the ground, using variation in the terrain and vegetation relief to surprise prey (Watson 1977; MacWhirter and Bildstein 1996). Prey are usually sought by methodical quartering, although fast and low 'ambush' techniques are sometimes adopted, reminiscent of sparrowhawk, *Accipter nisus* (Schipper *et al.* 1975; Bildstein 1978; Temeles 1986; Collopy and Bildstein 1987). Male harriers generally fly faster and forage in less structured habitats than females, and tend to take smaller and more agile prey (Balfour and Macdonald 1970; Schipper 1973, 1977; Schipper *et al.* 1975; Picozzi 1978, 1980; Marquiss 1980; Bildstein 1987; Temeles 1987). Bird prey are occasionally pursued and captured in the air, but the majority of prey is taken on the ground (Geyr 1959; Wassenich 1968; Schipper *et al.* 1975; Schipper 1977; Collopy and Bildstein 1987).

During the breeding season, male harriers tend to have larger foraging ranges than females (Schipper 1973; Watson 1977), and have been observed at distances of ≥10km from their nests (Barnard 1983; Thompson-Hanson 1984). Foraging ranges are frequently shared with neighbouring harriers. Range size appears to vary considerably between regions, and has been variously estimated at 2.5km^2 (Breckenridge 1935), 0.6-6.3km^2 (Craighead and Craighead 1956), 8.8km^2 (Hamerstrom and De La Ronde Wilde 1973), 1.8-12.3km^2 (Schipper 1977), 14km^2 (Picozzi 1978), 66km^2 (Balfour 1962), and 72-366km^2 (Thompson-Hanson 1984). In a radio-telemetry study in Idaho, Martin (1987) estimated the mean minimum foraging range of 4 males to be 15.7km^2. Regional differences in range size are probably the result of variation in habitat quality and prey availability.

Breeding biology

Hen harriers are single brooded. Age at first breeding appears to vary regionally (see Hamerstrom *et al.* 1985; Simmons *et al.* 1986b); in Scotland most female harriers commence breeding as one year old birds, and most males as 2 year olds (Etheridge *et al. in prep.*). Harriers are generally monogamous or simultaneously bigamous, although harems of up to 5 females have been recorded in North America (MacWhirter and Bildstein 1996). It has been suggested that polygyny is attributable to an imbalance in the population sex-ratio (Hecht 1951; Balfour and Cadbury 1975, 1979; Picozzi 1984a), and differences in male quality and resource abundance (especially voles; Picozzi 1978; Hamerstrom 1979; Simmons *et al.* 1986a, b). Pair fidelity from year to year is rare (Hamerstrom 1969).

Various reproductive parameters have been found to be strongly influenced by vole abundance, including size of breeding population, age at first breeding, polygyny, nest defence and clutch size (Hagen 1956; Hamerstrom 1979; Simmons *et al.* 1986b). However, Simmons *et al.* (1986b) found that fledging success was only weakly correlated with vole numbers, probably because of the large numbers of highly vulnerable juvenile birds available to harriers later in the breeding season (Barnard *et al.* 1987).

Nest sites. Hen harrier nests are normally located on the ground in dense vegetation 0.5-1m high (Watson 1977), although a range of sites from almost barren ground (Schipper 1978) to tree nests (Scott *et al.* 1991) have been recorded. Populations in parts of North America appear to prefer damper and more open nest sites than those in Europe (Apfelbaum and Seelbach 1983; Simmons and Smith 1985). Unlike those in many parts of Britain, harriers in North America have not adapted to forest nesting (Hamerstrom 1969; Hamerstrom and Kopeny 1981). In Scotland, nests are mainly situated in moorland and open forest habitats, especially where there is deep [35-60cm] heather *Calluna vulgaris* (Bibby and Etheridge 1993; Redpath *et al.*, *in press.*). Of 922 nests reported by

Etheridge and Summers (1993), 76% were in heather moorland, of which 49% were located on moorland managed for red grouse *Lagopus lagopus scotticus*.

Nesting areas are normally used for many years in succession (Watson 1977), although not necessarily by the same birds (Hamerstrom 1969; Picozzi 1978, 1984; Korpimaki 1984). Within these areas, the precise location of nests may vary by several hundred metres between years. The area defined by outlying nest site locations (defined in this thesis as the 'nest range') has been estimated at ca. 2.6 km^2 (North America) and 2.6-3.9 km^2 (Orkney) (Brown and Amadon 1968). Harriers are not strongly territorial, and usually defend only the area near the nest against conspecifics. The size of this area has been variously estimated at ca. 28ha (Brown and Amadon 1968), 110ha (MacWhirter 1985), and 0.78ha (Martin 1987). Inter-nest distances are highly variable, depending on the degree of polygyny, and distribution of nesting habitat and prey. However, nests are rarely closer than 100m, even when harriers breed in loose assemblages (MacWhirter and Bildstein 1996).

Courtship and display. In Britain, nesting areas are generally occupied from February/March (Watson 1977), although some west Scottish nest ranges appear to remain vacant until early April (*pers. obs.*). Males generally arrive on the breeding grounds 5-10 days before females (Hamerstrom 1969). Territorial displays may be seen from late March onwards, and initially involve high circling flights over the nest area. By mid-April more complex aerial 'sky-dance' displays are performed, involving conspicuous and uninhibited steep undulations covering a distance of up to 1km at a height of ca. 10-300m (Balfour 1959; Doran 1976; Watson 1977; MacWhirter and Bildstein 1996). Either sex may be involved, although most displays are by males (Simmons *et al.* 1987). The frequency and intensity of male displays are greater in food-rich than food-poor years (Simmons 1988). During this period males begin to provide females with food. This is initially transferred on the ground, but by the time egg-laying commences food is delivered by aerial food pass (Watson 1977).

Egg-laying and incubation. In Scotland, laying generally occurs between late April and mid-May (median first egg date May 5; Etheridge *et al. in prep.*), although early failures sometimes result in replacement clutches well into June (*pers. obs.*). Older females (≥3 years) precede younger ones by several days (MacWhirter and Bildstein 1996). Clutches of 4-6 eggs are normally laid. Clutch size is negatively related to date of laying, partly because replacement clutches are smaller (Etheridge and Summers *in prep.*). Eggs are usually laid at intervals of ca. 48 hours (Watson 1977) and take 29-30 days to hatch. Incubation is exclusively by the female, during which time all food is provided by the male. Partial incubation usually begins on the day following the laying of the first egg, with full incubation commencing before the clutch is complete (*pers. obs*). Eggs hatch asynchronously in the order in which they were laid, resulting in size-rank hierarchy between the nestlings.

Fledging and dispersal. Young harriers are semi-altricial and nidiculous. They are normally brooded continuously by the female for 10-15 days after hatching, and are provisioned by the male. Both sexes hunt during the remainder of the fledging period. Saunders (1986) found that males provided ca. 67% of the food items delivered to monogamous broods and those of alpha females in harems. Polygynous females begin provisioning nests earlier in the nestling period than do monogamous or alpha females (Simmons 1983). Chicks are fed bill-to-bill by the female until they are able to tear-up prey for themselves at 3-4 weeks old (*pers. obs.*). The latest-hatched chick is usually the first to succumb to stress caused by cold, rain, or lack of food (Breckenridge 1935; Hamerstrom 1969; Scharf and Balfour 1971; Picozzi 1980). There is no evidence of sibling fratricide, although dead chicks are often eaten by the surviving chicks (Balfour and MacDonald 1970). In North America, a high incidence of late-stage nestling starvation due to male desertion has been reported (Simmons *et al.* 1987).

Unless prematurely disturbed, male harriers usually fledge at 31-34 days and females at 35-38 days (Scharf and Balfour 1971). Recently-fledged harriers remain in the nest area for 2-4 weeks after fledging, after which time they appear to be fully independent (Beske 1982) and disperse widely.

Productivity and survival. In Scotland, the annual reproductive success (mean number of young fledged per pair), averaged across 3 habitat-types, is 1.7 for all nests and 3.2 for successful nests (Etheridge *et al. in prep.*). Comparable data for North America, averaged across various studies, are 1.8 (n = 13 studies) and 3.1 (n = 11 studies), respectively (MacWhirter and Bildstein 1996). Clutch and fledged brood sizes in Scotland are greater in moorland managed for grouse than in other moorland and afforested habitats (Etheridge *et al. in prep.*). However, clutch and brood survival are lowest on grouse moors and annual productivity is therefore poor (0.9 young per breeding pair) compared with other moorland (2.3) and forests (1.9). Annual survival rates for birds 0-6 years old have been estimated at 72% for males and 90% for females (Picozzi 1984), and for breeding females 38% on grouse moors and 78% on other moorland (Etheridge *et al. in prep.*).

Status of hen harriers in Britain

Hen harriers were once widespread in Britain, but dramatic declines occurred during the 19th century, as a result of habitat loss and human persecution (Watson 1977). By 1900 they were confined to a few isolated breeding localities (e.g. Orkney, North and South Uist, Kintyre and Arran), where intensive management for red grouse was absent. Re-colonisation of the Scottish mainland and parts of Wales and northern England began in the 1930s, coincident with the spread of plantation forestry in the uplands which provided harriers with suitable habitat where they were largely free from persecution (Newton 1972; Blake 1976; Sharrock 1976; Watson 1977; Cramp and Simmons 1980). By 1968-72 there were estimated to be 500-600 pairs in Britain and 200-300 pairs in Ireland (Sharrock 1976). Population and range expansions have subsequently occurred in many areas (e.g. parts of the eastern Scottish Highlands, Isle of Skye, and Isle of Man), particularly where there has been further afforestation. However, these gains have been largely offset by losses in other areas (e.g. eastern Grampian and Tayside, and in central and northern England) (Gibbons *et al.* 1993). The most recent population estimates are 570 ±150 pairs in Scotland (Bibby and Etheridge 1993), 40-45 pairs in the Isle of Man (Campbell *et al.* 1994), 20-30 pairs in Wales (Lovegrove *et al.* 1994), 30 pairs in Northern Ireland and 16 pairs in England (Crockford *in prep.*).

Habitat availability and human persecution continue to be important factors limiting harrier populations (Crockford *in prep.*). The largest current cause of change in habitat availability is that resulting from the maturation of upland forests, and their subsequent replacement by 2nd rotations (re-stocks). At present, it appears that harriers are less attracted to re-stock forests than to newly afforested ones (Bibby and Etheridge 1993), although sporadic breeding attempts have been recorded (Petty and Anderson 1986, Madders unpubl. data). There has been a substantial decline in the amount of new forestry in the uplands since 1990, due to the cessation of tax advantages for private investors (Avery and Leslie 1990), and this is likely to lead to an increasing proportion of the harrier population nesting on heather moorland (Redpath *et al.*, *in press.*).

On mainland Scotland, Etheridge *et al.* (*in press.*) estimate that at least 56 breeding female and 215 young harriers are illegally killed on grouse moors each year. Despite their potential for high productivity, many moorland harrier populations may therefore be dependent on recruitment from other areas. Pulliam (1988) proposed a 'source-sink' model to describe local populations connected by dispersal in this way. 'Source' populations generate more young than are needed to fill breeding vacancies arising from adult mortality, while 'sink' populations remain inhabited only because of immigration from sources. However, Etheridge *et al.* calculate that losses on grouse moors (sinks) are too great to be offset by excess production in forests and other moorlands (sources), and that the overall population of harriers on mainland Scotland is therefore currently in decline.

Intensive grazing by sheep and deer, and the burning of large areas of hill ground to promote grass development at the expense of heather, may also be excluding hen harriers from many parts of their former range (Crockford *in prep.*). Such practices are inversely correlated with the structural diversity of the vegetation (Sydes and Miller 1988), and reduce both nest site availability and prey abundance. Similarly, the 'improvement' of rough grazing and marginal agricultural land is likely to be detrimental to harriers (Bignal *et al.* 1988; Cadbury 1992). Factors that are thought to have a local effect on harrier numbers and breeding success include predation by foxes and crows (I. Williams, *pers. comm.*), collisions with overhead lines (Rose and Baillie 1989), and human disturbance. The construction of aero-generators in the uplands may pose a further risk for some populations (Madders 1995).

Hen harriers are protected under Schedule 1 of the United Kingdom Wildlife and Countryside Act 1981, Annex I of the European Union Birds Directive, and Appendix II of the Berne Convention. Batten *et al.* (1990) considered that the hen harrier was a species of special conservation concern in Britain, due to a perceived decline in population size and range.

THE UPLANDS OF BRITAIN

The British uplands are characterised by open landscapes of unenclosed heaths, grasslands, peat bogs and rocky terrain lying above the limits of cultivation (Ratcliffe 1990). About 7.7 million ha. (30%) of Britain is covered by upland vegetation. This comprises 3.1 million ha. of agricultural grassland and commercial forestry, and 4.6 million ha. of 'semi-natural' habitat (i.e. upland grassland, bog and moorland), where the vegetation has been partially modified by human activity (Bunce and Barr 1988). These semi-natural habitats are used mainly for sheep-grazing, although in large parts of northern England and central and east Scotland they are managed for red deer *Cervus elaphus* and grouse (Sydes and Miller 1988).

Changes in land-use

Three principal phases of land-use change can be identified. Firstly, the extensive climax woodland that once covered much of the uplands was progressively cleared by humans from around 3900BP until (in the remoter parts of west Scotland) about 1400BP (Birks

1988). The second major change was the widespread introduction of sheep between the late 1700s and the middle of the 19th century. Sheep numbers have subsequently remained more or less stable, at approximately 69 million (MAFF 1968), although stocking densities in many upland areas have increased due to the loss of grazing land to forestry (Sydes and Miller 1988). Lastly, there has been extensive afforestation with coniferous trees since 1919, assisted by government funding to the state-owned Forestry Commission and (more recently) private landowners and forestry companies. As a result, approximately 1.5 million ha. of predominantly coniferous woodland has been established in Britain, mainly in Scotland (Balfour and Steele 1980; Locke 1987).

Less dramatic changes include the conversion of marginal agricultural ground to grazing and arable land, and the reclamation of hill ground for sheep and cattle *Bos taurus* pasture (Anderson and Yalden 1981; Bibby 1986, 1988; Sydes and Miller 1988). In the Scottish uplands, insufficient culling of red deer has led to the population rising to levels higher than at any time since records began (Clutton-Brock and Albon 1989). In many areas, grazing pressure by sheep and deer has caused woodland and scrub to be replaced by dwarf shrub and (on wet and acid soils) grasslands. Furthermore, heavy grazing of perennial grassland has encouraged the spread of bracken (Sydes and Miller 1988).

UPLAND AFFORESTATION

The amount of new forest planted in Scotland increased each decade during 1910-1980, and since 1960 has been more than twice that in England and Wales (Fig. 1). By 1980 the total woodland cover in Britain was estimated to be 2.1 million ha., of which 1.3 million ha. (62%) was coniferous high forest (i.e. stands of trees having a canopy density ≥20% or, in the case of pre-canopy closure stands, occupying ≥20% of the ground at normal spacing) and most of the remainder was lowland broad-leaved woodland (Forestry Commission 1984). In Scotland, total woodland cover was estimated to be 0.9 million ha., of which 0.8 million ha. (89%) was coniferous high forest (Forestry Commission 1983). More recently, Thompson *et al.* (1988b) reported that over 1 million ha. (14% of the total land area) had been afforested in Scotland. The amount of new planting since 1990 has declined to ca. 25,000ha per year, approximately 75% of the current target set by the Forest Authority (the government body charged with regulating forestry in Britain) (Avery and Leslie 1990). However, it is likely that forest expansion will continue into the 21st century.

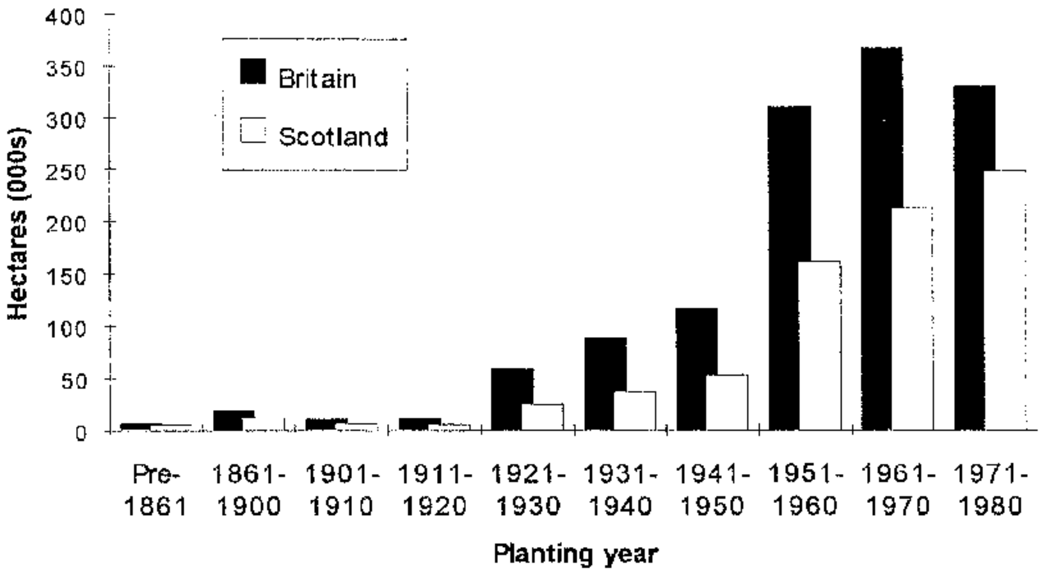

Fig. 1: Area (000s of hectares) of coniferous high forest in Britain and Scotland by planting year.

Britain's forests are predominantly young. In 1980, 77% of coniferous high forest was less than 30 years old and only 3% were established before 1910 (Forestry Commission 1984). More than half of these forests are a decade away from completing their first rotation (Avery and Leslie 1990). The principal species planted is Sitka spruce *Picea sitchensis*, which grows on a wide range of soil types and yields a high volume of industrial quality timber (Petty and Avery 1990). Sitka spruce are the most abundant trees in Britain, and in Scotland cover nearly 0.4 million ha., i.e. almost half of the total forest area. Other species planted include Scots pine *Pinus sylvestris*, which covered approximately 240,000ha of Britain in 1980, lodgepole pine *Pinus contorta* (ca. 130,000ha), Norway spruce *Picea abies* and larch *Larix* spp. (ca. 115,000ha each) (Forestry Commission 1984).

Most forestry has been established on agriculturally unproductive land, which is relatively inexpensive to purchase. Since about 1950, improved silvicultural techniques and the declining quality of land available to forestry have encouraged planting on poorer soils, such as blanket bog. In Argyll, for example, 30% of blanket bog on the Kintyre peninsula has been planted since 1945 (NCC 1986), and substantial areas of bog in the Inner Hebrides have also been planted (Bramwell and Cowie 1983). This shift has favoured the establishment of Sitka spruce above other species, and the proportion of this species is therefore greater in recent plantings.

An increasing number plantations are reaching commercial maturity. Annual felling programmes of coniferous woodland during the decade 1988/89 to 1998/99 are expected to rise from 9,700 ha. to 16,300 ha. (Tabbush 1988). Second rotations (i.e. the replanting of conifers on sites harvested of similar plantations) are therefore becoming increasingly common.

Forest management

Selection of tree species. Soil type and exposure are the most important influences on tree performance (Worrell 1987; Petty and Avery 1990). Commercial forests in the uplands have been established mainly on peaty soils and bogs. Apart from the less fertile unflushed peats, where lodgepole pine are generally more appropriate, these soils are most suitable for growing Sitka spruce (Hibberd 1986). Relatively small numbers of other tree species have been planted, although some Japanese larch *Larix kaempferi* have been established in areas where brown earths and podzols occur. Mixtures of Sitka spruce and larch or pine are sometimes used on nitrogen deficient soils (Petty and Avery 1990). Broad-leaved trees are generally not considered to be commercially viable in the uplands and have been established mainly for landscaping and conservation purposes. Most planting since 1985 has included at least 5% broad-leaved species, including birch *Betula* spp., oak *Quercus* spp., rowan *Sorbus* spp. and, on non-peaty soils, alder *Alnus* spp.

Site preparation and planting. Previously unafforested ground is fenced prior to planting to exclude herbivorous animals such as deer, sheep, goats *Capra hircus* and cattle. The ground is then ploughed to drain waterlogged soils and provide weed-free turves in which to plant trees. In some soil-types ploughing also helps break-up and mix impeded soil layers such as ironpans, thereby increasing rooting depth (Petty and Avery 1990). Plough lines are usually around 2m apart and trees are planted on the side or top of the upturned furrows. Trees are more closely-spaced in commercial plantations than natural forests, and planting densities for spruce plantations are typically around 2500 trees per ha. (Low 1987).

The trees are generally grown in a nursery seed bed (Aldhous 1972), and transplanted into rows after 1-2 years. At 2-4 years old they are taken to the planting sites as bare-rooted stock and planted by hand, usually in spring. Those that fail to survive are normally replaced in the early part of the establishment phase.

Forest fertilisation. Nitrogen deficiency on moorland soils can severely inhibit the growth of Sitka spruce, to the extent that development may virtually cease. Until recently, this was thought to be solely attributable to the effects of competition from heather, and unflushed bogs and peaty gleys dominated by heather were generally either left unplanted, or were planted with lodgepole pine (Taylor and Tabbush 1990). However, it has been shown subsequently that although heather suppresses micorrhizal development in spruce (Laing 1932; Handley 1963; Malcolm 1972), nitrogen deficiency can also occur where heather is absent, presumably due to low mineralisation rates (McIntosh 1983). Furthermore, on sites with little available nitrogen, the control of heather is ineffective in increasing forest productivity. In such situations, the application of nitrogen during the pre-thicket stage greatly increases Sitka spruce growth rates. Urea and ammonium nitrate are the most commonly used nitrogen fertilisers (Binns 1975), applied either by hand or from a helicopter. Each application usually results in a growth response lasting 3-4 years (Dickson and Savill 1974) and several applications may be required if full canopy closure is to occur. After canopy closure, the demand for nutrients is reduced (Miller 1981) and further nitrogen application is unnecessary. An alternative to nitrogen application on less fertile uplands soils is to plant mixtures of spruce and pine or larch. Depending on soil-type, other fertilisers (e.g. phosphorous and potassium) may need to be applied during the establishment phase to counteract mineral deficiencies (Taylor 1991).

The use of fertilisers, together with improvements in cultivation and weeding techniques, has increased the productivity of forests established on nutrient-poor soils and encouraged the cultivation of high yielding Sitka spruce on sites previously considered unplantable (Taylor 1991). In much of the uplands, however, logistical difficulties and cost considerations have generally resulted in less than ideal levels of fertiliser application and other remedial treatment. As a result, trees sometimes suffer from severe growth check and forests in many upland areas (including those investigated in the present study) have patchy development, leading to incomplete canopy closure.

Post-thicket stage management. Upland forest management after canopy closure is largely passive. Thinning of the crop to increase the trunk diameter of the remaining trees is desirable, but rarely practised in the uplands since it renders the standing crop more susceptible to wind throw (i.e. the blowing over of trees by strong winds) (Low 1987). Wind throw is a serious problem in west Scotland, where winds are stronger and more frequent than other parts of Britain and trees have been established in exposed upland areas, often on soils which limit the development of a wind firm root architecture (Miller 1985). Other silvicultural operations, such as the removal of lower branches (brashing) to improve access and produce knot free timber are generally impractical and unnecessary (Petty and Avery 1990).

Harvesting. Most commercial spruce forests are felled at 45-55 years of age (Busby 1974; Helliwell 1982), well before they reach their maximum size. However, wind throw hazard increases with stand height and trees in high risk areas are often harvested earlier. Large areas of upland forest are usually harvested at a time (clear felled), since piecemeal felling increases the risk of wind throw and is costly to operate. However, in areas of geomorphic shelter, selective felling may be used to create gaps where tree planting and natural regeneration can occur (Helliwell 1982). In this way, forests of mixed age or species may eventually be formed.

Trees are felled and have their branches removed (snedded) with a chain saw. They are crosscut into suitable lengths either at the felling site, or after removal to the nearest forest road. Timber extraction is usually achieved using either a skidder, which drag trees along the ground, a forwarder, which take loads of timber in a trailer pulled by a tractor unit, or a cable crane, which can winch timber off steep ground.

Re-stocking. Clear-fell sites are usually re-planted promptly after felling in order to maximise capital investment in the land and to reduce competition from the rapidly regenerating ground flora (which must otherwise be suppressed by the use of herbicides) (Avery and Leslie 1990). An important characteristic of re-stock sites is the presence of cut stumps and piles of brashings (i.e. tree branches and top pieces of no commercial value) from the previous crop. These debris impede deep cultivation techniques such as ploughing, which is therefore only done on sites where ironpan soils were inadequately cultivated prior to afforestation (Tabbush 1988). In recent years, mechanised scarifiers and mounders have been used to break up brash and provide scoops of soil suitable for tree planting without major site disturbance (Nelson and Quine 1990). Otherwise, trees are generally planted shallowly against the stumps of the former crop.

Clear-felled sites are generally more hostile environments for establishing trees than newly ploughed moorland. Sturdier transplants, with a high root growth potential, are therefore used. Prior to planting, trees are usually dipped in gamma HCH to provide some protection against root and bark damage by *Hylobius* and *Hylastes* beetles, which breed in the stumps of the former conifer crop (Scott and King 1974). The cut stumps are usually treated with urea to prevent spores of the fungus *Heterobasision annosum*, responsible for root and butt rot (Forestry Commission 1970), becoming established.

Restructuring. The concept of re-designing forests based on an integrated approach to forest management and environmental factors was developed in the late 1970s (Hibberd 1985). Until then, the most influential non-economic consideration in upland forest management had been landscape design, although wildlife probably benefited from many of the changes that this introduced (Avery and Leslie 1990). Forest restructuring provides a mechanism for implementing broad recommendations on wildlife management (e.g. Buckham *et al.* 1982) alongside those relating to operational and silvicultural requirements, landscape design and recreational concerns. Perhaps the most important consequence of restructuring in conservation terms has been the trend towards greater forest diversity, brought about mainly through the individual management of smaller stands of timber.

Changes in birdlife

Afforestation leads to great ecological changes (Petty and Avery 1990), and its effects on upland bird assemblages have given rise to much concern (Ratcliffe and Thompson 1988; Ratcliffe 1990). The diversity of wildlife in each successional stage of the forest rotation has been widely reviewed (e.g. Newton 1983; Staines 1983, 1986; Ratcliffe and Petty 1986; Petty and Avery 1990), and therefore only the principal changes associated with each stage are presented here.

Establishment. The majority of afforested ground in the uplands was previously subject to (often intense) grazing by deer and sheep, and their exclosure (together with drainage and fertilising operations) inevitably leads to a flush in plant growth. A rich ground layer develops, generally dominated by the moorland grasses and heathers present before afforestation. Greater structural diversity (Newton 1985) and insect productivity (Reed 1982) result in increases in both the number and variety of birds, although species associated with short grassland, such as wheatear *Oenanthe oenanthe*, skylark *Alauda arvensis* and most waders, decline rapidly (Batten and Pomeroy 1969; Williamson 1975; Moss 1978; Moss *et al.* 1979).

Where the ground flora is dominated by grasses, numbers of field vole *Microtus agrestis* increase dramatically, usually by a factor of around 10 but sometimes by as much as 200 (Charles 1956, 1981). Field vole populations are cyclical, with peaks every 4-6 years (Chitty 1952), and 2-3 population cycles are therefore possible before canopy closure. Short-eared owl *Asio flammeus* readily exploit this resource (Godard 1935; Lockie 1955), although they are scarce or absent in years when voles are not numerous. Hen harrier, kestrel *Falco tinnunculus* and barn owl *Tyto alba* may also benefit from increased vole abundance (Watson 1977; Village 1980; Shawyer 1987).

Canopy closure. Developing trees increasingly dominate the new habitat, forming a thicket around 10-15 years after planting. These conditions favour scrub-dwelling birds such as willow warbler *Phylloscopus trochilus*, whitethroat *Sylvia communis*, grasshopper warbler *Locustella naevia*, sedge warbler *Acrocephalus schoenobaenus*, reed bunting *Emberiza schoeniclus* and redpoll *Carduelis flammea*. Sitka spruce develop dense branches as they mature which, combined with the high density of planting, severely curtail the amount of light reaching the ground. Ground vegetation therefore declines, along with associated species such as meadow pipit *Anthus pratensis* and field vole. By the time the forest is 20 years old, the ground is generally bare except for mosses (Hill 1979), and canopy-feeding birds such as goldcrest *Regulus regulus*, chaffinch *Fringilla coelebs*, wren *Troglodytes troglodytes*, coal tit *Parus ater* and siskin *Carduelis spinus*, predominate. Predatory birds such as sparrowhawk, buzzard *Buteo buteo* and tawny owl *Strix aluco* are generally present, while goshawk *Accipiter gentilis* and long-eared owl *Asio otus* colonise some forests.

Re-stocking. Clear-felling and re-stocking forests at the end of the first rotation creates conditions superficially similar to those of new afforestation. However, not all the events of forest establishment are repeated during the 2nd rotation. Brash and debris from the clear-felled timber initially dominates the site, although vegetation such as grasses, heather, bramble, bracken and herbs soon grows through. Field voles re-colonise, and in peak years are abundant (Petty 1987, 1989), attracting predators such as buzzard, tawny owl, short-eared owl and kestrel. Leslie (1981) and Currie and Bamford (1981) found that bird density and diversity was greater on re-stock sites than first rotation plantings of equivalent age, although these studies compared relatively small areas of forest, and differences in soil type between plots may have influenced the results (Petty and Avery 1990). However, in an extensive study of re-stocked plantations in Wales, Bibby *et al.* (1985) also found high densities (>1800km^{-2}) of birds, and recorded a wider range of species than has been found in studies of first rotation plantations (e.g. Moss *et al.* 1979; Currie and Bamford 1981; Leslie 1981).

An evaluation of the effects of forestry on moorland birds

Afforestation has been largely beneficial to birdlife, although some species have declined regionally (Newton 1983). Despite this, Thompson *et al.* (1988a) considered that at least 34 bird species were at some risk from afforestation, due to a reduction in open ground for foraging, increased numbers of predators, and changes in hydrology and water chemistry.

The loss of open ground in the uplands to plantation forestry leads to the permanent displacement of several bird species perceived to be of high conservation importance, e.g. red grouse, ring ouzel *Turdus torquatus*, wheatear and skylark (Thompson *et al.* 1988a). The very large scale of planting in some areas (e.g Galloway), has caused regional declines in the population or productivity of scavenging and predatory birds that are unable or unwilling to forage among closely-spaced trees, e.g. raven *Corvus corax* (Marquiss *et al.* 1978; Newton *et al.* 1982; Mearns 1983) and golden eagle *Aquila chrysaetos* (Marquiss *et al.* 1985; Watson *et al.* 1987). Declines in the number of buzzard in southern Scotland between 1946 and 1981 have similarly been attributed to afforestation (Mearns 1983), although Newton *et al.* (1982) found no association between afforestation and buzzard occupancy or productivity in Wales. Some raptors (e.g. hen harrier and short-eared owl) have benefited from the increased abundance of live prey during the early stages of afforestation. However, these species depend largely upon capturing prey within the ground vegetation, and have declined in many areas as forests have matured (Watson 1977; Galloway and Meek 1978; O'Flynn 1983). Although passerine diversity and abundance increase with forest age (Moss *et al.* 1979, Newton 1985), the general effect of afforestation is to replace 'open country' birds with woodland species (Lack and Lack 1951) that are largely inaccessible to moorland raptors.

Several species of wading birds, e.g. golden plover *Pluvialis apricaria*, dunlin *Calidris alpina* and greenshank *Tringa nebularia* have been adversely affected by the loss of open ground to forestry or the effects of drainage prior to planting (Nethersole-Thompson and Watson 1981, Stroud *et al.* 1987). Waders nesting in the vicinity of forests are also vulnerable to higher levels of predation by crows, foxes and other predators that find sanctuary within plantations (Thompson *et al.* 1988a). Furthermore, widespread coniferous afforestation can result in the acidification of soils and water run-off, leading to lower invertebrate productivity in many upland streams (Harriman and Morrison 1982; Stoner *et al.* 1984). This may have contributed to the recent decline of dipper *Cinclus cinclus* in some areas (Omerod **et al.** 1985).

Many moorland species (e.g. black grouse *Tetrao tetrix*, meadow pipit, stonechat *Saxicola torquata* and whinchat *Saxicola rubetra*) are able to occupy open ground within forests (Thompson *et al.* 1988a). Newton (1985) reported that 24/68 (35%) of bird species that breed regularly in Scottish woodlands depend on open land, either within or adjacent to the forest, and Leslie (1981) and Ratcliffe (1984) considered this to be one of the most crucial influences on the wildlife of commercial forests. The extent of open ground within forests varies both temporally and spatially, depending on the growth stage of the trees, planting design, and level of crop failure. Recent management practices, including the restructuring of forests to improve landscape quality, creation of glades for efficient control of deer numbers (Ratcliffe 1985), and the habit of leaving areas immediately adjacent to watercourses unplanted, have encouraged the creation of greater open space within forests, although in many areas this has been offset by programmes to replace trees with poor or zero growth.

Incremental felling and judicious restructuring should help diversify the age and structure of upland forests, and therefore its bird community. Assuming canopy closure after 10 years and forest rotations of 40 years, Petty and Avery (1990) estimated that about a quarter of the forest area is likely to remain open at any one time. However, this is unlikely to be of use to birds that have extensive foraging ranges and require large tracts of open land, e.g. golden eagle and raven. Even upland species that benefited from the early stages of afforestation, e.g. hen harrier and short-eared owl, may find the fragmented distribution of suitable habitat within the forest less conducive than first rotation plantings, which are generally extensive and surrounded by moorland.

AIMS OF THE PRESENT STUDY

Further afforestation, the maturation of existing forests, and the re-stocking of clear-felled forests are likely to have profound effects on hen harrier populations in Britain. Although harriers in many areas appear to site their nests among developing conifers in preference to grazed moorland, the value of forestry as a foraging habitat is poorly understood. Yet the extent and proximity of foraging areas are likely to be crucial in determining most aspects of harrier reproduction. In order to manage harrier populations effectively we therefore need to (1). determine the relative use made by foraging hen harriers of various types of forest and moorland, (2). relate foraging habitat preferences to measures of vegetation cover and structure and estimates of prey abundance, and (3). relate the frequency of occupation of breeding sites, and breeding success, to the composition of land used for foraging. The current study aims to resolve these questions. Subsidiary objectives are detailed in the introduction to each chapter.

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CHAPTER 2

STUDY AREA AND CHRONOLOGY

Contents:

INTRODUCTION

Fieldwork was conducted in the district of Argyll and Bute, West Scotland, between 1992 and 1994. Argyll was selected for study because:

(1). A variety of upland habitats were present, including examples of commercial forest that spanned the entire cycle of forest development (i.e. newly planted forests through to clear-felled and restocked forests).

(2). Few areas were managed for moorland gamebirds and there was consequently little illegal persecution of hen harriers.

(3). The distribution of breeding hen harriers within a substantial part of Argyll had been established during survey work in 1988-89 (Madders unpubl.).

STUDY AREA

Four widely separated sites, known to support a total of around 30 breeding pairs of hen harrier, were selected for study. These were located in the Cowal peninsula, Isle of Islay, Kintyre peninsula and Lorn (Fig. 1). Each contained a range of upland habitats representative of west Scotland and were used as replicates in studies of harrier foraging and assessments of habitat and prey. The location, terrain and habitat characteristics of each study site are summarised below and in Table 1.

Cowal

The study site was located in the south-west of the Cowal peninsula, bordered by Loch Fyne to the west, the Kyles of Bute to the south, and Glendaruel to the east. A broad ridge of hills, including the summits of Beinn Bhreac (454m), Cruach nan Caorach (458m) and Cruach Chuilceachan (435m), bisected the site from north to south. In the east lay another ridge, dominated by Beinn Bhreac (507m). The fertile lowland ground (e.g. between Melldalloch and Ballimore, at Millhouse, and in Glendaruel) was occupied by enclosed pastures, where grazing, regular re-seeding, and the application of fertilisers had resulted in grassland improvement. The higher ground comprised blanket bog and dwarf shrub heath, which were mostly given over to sheep grazing, and coniferous forest. Forest-types ranged from recently established first rotation plantations to developing restocks.

Islay

This was the least typical of the sites studied, due mainly to the island's complex geology (with soils frequently influenced by limestone and other base-rich rocks; Bignal *et al.* 1988) and maritime climate (Boyd 1983). The study site was located in

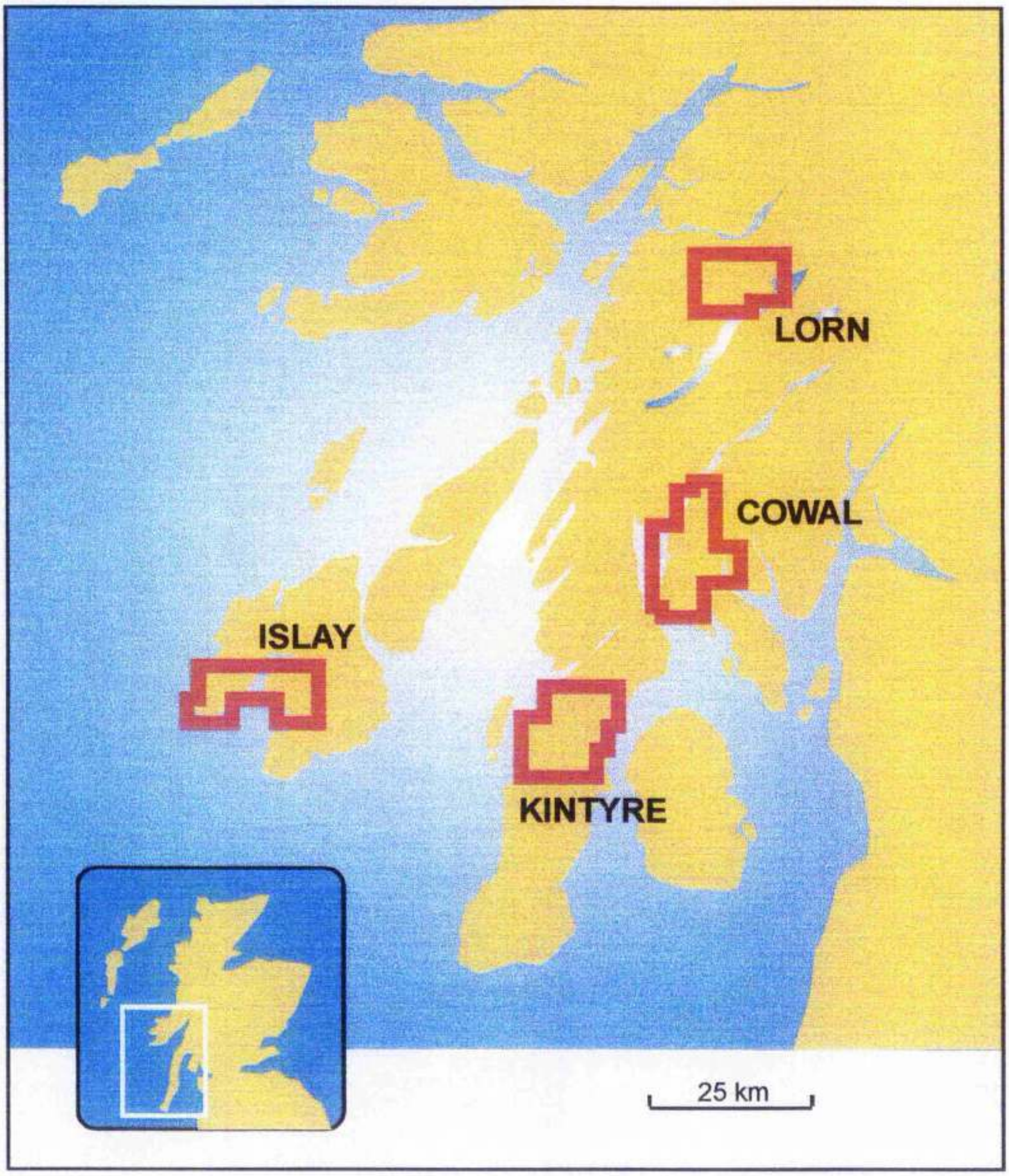

Figure 1: Location of study sites.

the western part of the island and included a substantial part of the Rinns peninsula and Laggan estate lands, separated by a broad sea loch (Loch Indaal). In the west, a ridge of ground rose to a peak of 232m and comprised mostly low-lying bog and heath habitats, interspersed with rough pastures and rushy fields used for sheep and beef cattle *Bos taurus* grazing. Plantation forestry was established on the eastern slopes of this ridge between 1982 and 1988. East of Loch Indaal, the ground rose slowly to the summit of Beinn Bhan (450m). This area was dominated by unproductive bogs and mires, heaths and rough grazings for sheep, and an area of even-aged conifer forest established during the 1960s. However, there were also several areas of improved, semi-improved and arable habitat, located on the meander plains of the Laggan and Duich rivers, and an extensive dune system bordering the coast at Laggan Bay.

Kintyre

The study site spanned the Kintyre peninsula, a continuous ridge of hills containing several summits in excess of 400m, and extended roughly from a line between Clachan and Escairt in the north, to one between Muasdale and Carradale in the south. The highest point was Cruach nan Gabhar (354m) and the majority of the study site was more than 200m above sea level. Bogs, heaths and rough grazings for sheep dominated the open hill ground. There was extensive afforestation, with plantations ranging from newly established first rotations to restocks. Elsewhere, e.g. the floor of the Carradale valley and the fertile coastal plain between Rhunahaorine and Muasdale, the ground was enclosed and used for arable and pastoral farming. Kintyre is subject to an oceanic climate, with precipitation levels exacerbated by high relief.

Lorn

The study site was bounded by Loch Etive to the north, Loch Awe to the east, and the Beinn Ghlas - Beinn Dearg massif to the west. It was located on the eastern part of the base-rich andesitic plain that underlies much of northern Lorn. There were several summits in excess of 200m, including Carn Gaibhre (462m), Cruach Airdeny (396m), Cruach Achadh na Craoibhe (277m) and Creag Thulach (222m). The northern part of the site was bisected by Glen Nant, a wooded ravine that led north towards Loch Etive. The remainder of the site drained into Loch Awe, mainly via Kilchrenan Burn. A complex of freshwater lochs occupied the centre of the site, the largest of which (Loch Nant) was used for hydro-electricity generation. The lower-lying ground (e.g. Kilchrenan valley and around Loch Awe) was enclosed and contained improved and partially improved pastures. Much of the upland vegetation was subjected to continuous heavy grazing by sheep, although stocking densities were lower than previously. Small patches of heather occurred on some knolls, whilst other areas of dry ground had been artificially treated with lime to increase grass yield. Otherwise the hill ground consisted mainly of poorly drained slopes and boggy hollows and was dominated by heath/ grassland mosaics. There were 3 areas of extensive coniferous forest, centered on Glen Nant, Hayfield, and Loch Nant. These covered the entire spectrum of forest development, from newly established first rotation crops to clear fells and restocks.

Table 1: Amounts (ha.) of the principal moorland and forest habitats in the 4 study sites. Data from a Geographic Information System (GIS, ARC / INFO package, copyright 1987,1988, 1989 Environmental Systems Research Institute Inc., USA) containing information interpreted from 1:24,000 scale black and white aerial photographs taken in 1988.

Habitat	Cowal	Islay	Kintyre	Lorn
MOORLAND				
Heaths and bogs	4,614	5,608	4,294	2,656
Acidic grasslands	4,095	1,537	1,722	2,916
Neutral grasslands	2,129	2,309	1,290	550
Other open habitats	227	703	253	998
FORESTRY				
Land recently ploughed for afforestation	1,788	1,109	3,923	583
Open canopy young plantation	3,749	0	1,722	613
Closed canopy woodland	5,395	598	3,787	1,572
Recently felled woodland	159	0	63	11
TOTAL LAND	22,147	11,864	17,055	9,900

CHRONOLOGY

An important aspect of the current study was to investigate the responses of hen harriers to forest succession. In the time available it was not feasible to study this process at a single site. A chronosequence (Hill 1986) was therefore used, whereby forest sites at different successional stages were sampled simultaneously. This method has been employed in studies to investigate mammalian responses to forest succession (e.g. Hansson 1978; Wolk and Wolk 1982) and has been shown to produce trends similar to those from long-term single site studies (Twigg *et al.* 1989; Fox 1990).

Fieldwork was carried out during April-August each year. Harrier foraging activity, prey abundance, and vegetation cover and structure were assessed in Cowal in 1994, Isle of Islay in 1993, Kintyre in 1992 and Lorn in 1992-4. Harrier nesting density, breeding success and diet were monitored in each study site in all 3 years.

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CHAPTER 3

BROAD-SCALE FORAGING HABITAT PREFERENCES

Contents:

"'Unting is all that's worth living for....."

Robert S. Surtees (1843). Handley Cross.

INTRODUCTION

Vegetation cover and structure are important variables in determining raptor foraging distribution (Southern and Lowe 1968, Wakeley 1978, Baker and Brooks 1981, Bechard 1982, Janes 1985). The measurement of associations between foraging activity and habitat is therefore an important part of raptor research and management. However, few studies have attempted to quantify the use of habitat by foraging hen harriers, especially during the breeding season. For example, Nieboer (1973), Schipper (1973, 1977) and Watson (1977) discuss habitat use by hen harriers by comparing their behaviour with other, sympatric, harrier species. Boedeltje and Zijlstra (1981) and Preston (1990) investigated habitat use by hen harriers wintering in predominantly agricultural habitats. The only studies of foraging habitat selection by breeding hen harriers are those of Martin (1987), conducted in the Snake River Birds of Prey Area, Idaho, and Redpath (1989), who investigated habitat selection in relation to prey abundance on heather moorland in north-east Scotland. The objective of the current study was to determine the relative use made by foraging harriers of broad categories of forest and moorland habitat, and to identify the vegetative and abiotic components of these environments that were influential on harrier use.

Definitions used in this study follow those of Mosher, Titus and Fuller (1987). *Availability* of a habitat component is its accessibility to a harrier. *Use* is a measure of the quantity of a component utilised over a fixed period of time. *Selection* occurs when a harrier uses a component disproportionately in relation to its availability. *Preference* for a component is reflected in the likelihood of that component being chosen if its availability is equal with that of other components.

METHODS

Previous studies of foraging hen harriers (e.g. Temeles 1987, Bildstein and Collopy 1985) have continuously tracked territorial individuals over relatively large areas and for long periods of time. This technique was unsuitable for the present study due to the rugged terrain and complex vegetation in some areas, which limited long-range visibility. Instead, all harrier foraging activity was recorded in sample 1x1km observation squares, which were small enough to enable comprehensive visibility from a single vantage point. Observation squares were selected from those of the national grid. Hen harriers generally commence foraging immediately upon leaving the nest vicinity (Watson 1977) and habitat adjacent to nesting sites is therefore used disproportionately. To maximise the efficiency of foraging watches, and help control for the effects of nest distance, observation squares were constrained to lie adjacent to 1x1km grid squares containing a harrier nest. In cases where breeding failure caused this condition to be violated, observations of the square were curtailed. To investigate the effects of the number and proximity of harrier nests on square use, the distance between observation squares and each occupied nest within 5 km was measured. Since the area available for hunting increases exponentially with nest distance, the influence of nest proximity on the use of each observation square was calculated thus:

$$\sum {}^{1}/_{D^2}$$

where D = the distance between the centre of the square and each harrier nest within 5 km.

Habitat stratification

Candidate observation squares were stratified across 7 broad habitat-types, defined by plant communities and vegetation structure. These were: heath/bog, acid grassland, neutral grassland, coniferous forest less than 3 years old (new forest), developing first rotation forest (pre-thicket), closed canopy forest (post-thicket), and developing second rotation forest (restock) (Table 1). Habitat evaluations were made by overlaying 1:24,000 aerial photographs of each observation square with a grid, the cells of which represented 100m x 100m. The principal habitat in each cell was determined and squares were classified according to the habitat that occupied the greatest number of cells. Within each study site and year a random sample of observation squares, constrained by nest distance and stratified by habitat, was selected. One square of each available habitat was selected per study site/year. Thus 6 habitats were represented in Kintyre (1992), 5 in Islay (1993), 6 in Cowal (1994), and 7 in Lorn (1992-4). Annual re-selection in Lorn led to 5 squares being used twice and 2 squares being used in all 3 years. A hypothetical example of square selection is shown in Fig. 1.

Because of planned forestry operations adjacent to the pre-thicket square selected in Kintyre, the heath/bog square in Islay and the post-thicket square in Lorn 1992, duplicates of these squares were chosen in the relevant study sites as insurance against the possibility of observations in the original squares being disrupted. Forty-one squares were thus selected.

Table 1: Habitats used to classify study area.

Habitat	Description
Heath/bog	Wet and dry dwarf shrub heathland with >25% *ericoids* (characterised by species such as *Calluna vulgaris, Vaccinium myrtillus,* and *Molinia caerulea*), plus blanket bog (characterised by *Calluna* and *Erica spp., Eriophorum angustifolium, Tricophorum cespitosum, Molinia caerulea* and *Sphagnum spp*).
Acid grassland	Typically, unenclosed hill-land with <25% *ericoids*, used for grazing sheep. Characterised by species such as *Deschampsia flexuosa, Nardus stricta* and *Juncus squarrosus*, plus some fine grasses such as *Agrostis tenuis* and *Festuca ovina.* Stands of *Juncus spp.* and *Pteridium aquilinum* may occur.
Neutral grassland	Typically, enclosed and usually more intensively managed than acid grasslands. Characterised by species such as *D. cespitosa, Festuca spp., Lolium perenne.* Includes waterlogged and neglected pastures (typified by stands of *Juncus spp.*) and hay meadows.
New forest	Newly established forest plantations, fenced less than 3 years previously. Characterised by prolific herb layer. Planted trees <1m tall.
Pre-thicket forest	First rotation forest plantations (excluding new forest) before canopy closure. Characterised by prolific herb layer with varying shrub layer development. Trees >1m tall; much open space between lines of planting.
Post-thicket forest	Closed-canopy forest plantations. Characterised by absence of herb or shrub layer, except in rides between stands of trees and in small patches of unplanted ground or failed crop
Restock forest	Second rotation forest plantations before canopy closure. Characterised by varying herb and shrub layer development, and brash and tree root-plates from the previous crop. Much open space between lines of planting

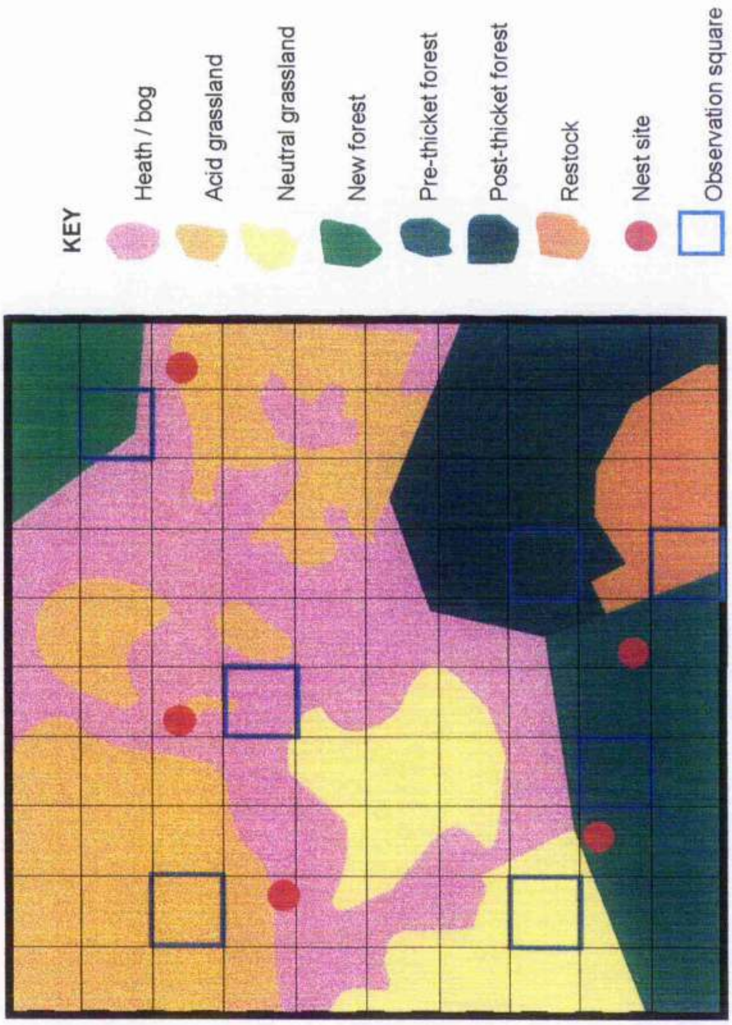

Figure 1: Diagramatic representation of observation square selection. A fictitious study site is shown in order to preserve nest site confidentiality. Grid cells represent 1 x 1 km. squares.

Habitat measurement

Measurements of topography and vegetation structure and cover were made at randomly located points in each observation square. Measurement points were selected from the centre points of each 100m x 100m cell. A sample of 30 points per habitat per square were selected. In cases where fewer than 30 points were available, the maximum possible were selected. Measurements were made within a 5m radius around each point. Following suggestions in Mosher *et al.* (1986), variables were selected that described the vegetation in terms that were both ecologically meaningful and useful to forest managers (Table 2). Habitat measurements were undertaken in August.

Foraging observations

Each observation square was watched for a total of 15 hours (defined as an *assessment*). Watches commenced between 0900 and 1800 hours and were of a maximum of 3 hours duration. Repeat observations of any one square were made only after an interval of 7 or more days. Observations were not made in conditions of poor visibility, or during rain. Care was taken not to disturb harriers. Habitat use by some raptors has been shown to vary seasonally (e.g. Marquiss and Newton 1982). To help control for this possibility, each assessment was divided equally between 2 stages of the breeding cycle. The 'early' stage corresponded to the incubation and close-brooding period (i.e. clutch initiation to day 14 after hatch), whilst the 'late' stage corresponded to the post close-brooding period (i.e. day 15 after hatch to fledging). The division between these stages was defined by reference to the median laying date for nests in each study site/year, and assuming a 35 day interval between clutch initiation and hatching. Observations during the early period ranged from May 6 to July 15, and those in the late period from June 25 to July 31.

With the aid of photographs of each square taken from the vantage points used for observations, the visible area of each habitat was plotted onto 1:10,000 maps and measured with a planimeter. The time spent foraging by harriers in each habitat in each square was recorded. Time spent in flight behaviour that was clearly not aimed at detecting or capturing prey (e.g. territorial soaring and display, agonistic interactions, and prey transit) was excluded. Whether or not a harrier was hunting was inferred from the manner of its flight. When foraging, harriers generally make frequent direction changes and follow terrain contours (Schipper *et al.* 1975). Following Redpath (1992), birds flying >10m above the ground were recorded separately and later excluded from analysis. Harriers were searched for by continual scanning with 10x binoculars. Individual harriers were selected as they flew into view, and observed using focal-

Table 2: Habitat variables recorded at randomly located points within 1x1km observation squares.

Variable	Measurement method and precision
Topographic	
Altitude	From 1:25,000 scale maps. To nearest 50m.
Angle of slope	Using field inclinometer. To nearest 5°
Vegetation structure	
0-0.5 m. height	Percent volume of foliage, estimated by eye to nearest 10%
0.6-2.0 m. height	
2.1-5.0 m. height	
5.1-15 m. height	
Vegetation cover	
Heather (*Calluna* and *Erica spp.*)	Percentage cover, estimated by eye to nearest 5%
Other dwarf shrub (mainly *Myrica* and *Vaccinium spp.*)	
Upland grasses (mainly *Molinia, Nardus, Agrostis* and *Festuca spp.*)	
Rushes (*Juncus spp.*)	
Bracken (*Pteridium spp.*)	
Bare ground	
Tree canopy	
Tree characteristics	
Height	Mean of 3 trees nearest point. Measured with telescopic rod to nearest 10cm.
Trunk diameter at breast height	Mean of 3 trees nearest point. Measured with callipers to nearest 1cm.

animal sampling (Altmann 1974), until they left the square or ceased foraging. Observations were recorded on a dictophone, set to run continuously for the duration of each foraging bout.

In order to compare the use made by harriers of different habitats, it must be assumed that the likelihood of their detection is equal in each. However, due to differences in vegetation cover and structure, harriers may be more difficult to detect in some habitats than others. This was investigated by comparing the distances at which harriers were initially detected in each habitat. For each foraging bout the distance to the point at which harriers were initially located, regardless of whether this was in the observation square, was estimated to the nearest 10m. Wherever possible, these distances were checked by reference to prominent ground features whose distance from the vantage point was known, or could be later measured. Detection rates may have also varied due to differences between squares in the sex or age of the harriers present. For example, we might expect female and one year old male harriers ('brown-plumaged birds') to be more difficult to detect than adult males ('grey-plumaged birds') because their appearance was more cryptic. A higher proportion of foraging time by brown-plumaged harriers in a particular square could occur if a one year old male harrier bred nearby, or if polygamous matings caused an increase in the amount of foraging time by female harriers. To investigate these effects, the plumage-type of the bird involved in each foraging bout was also recorded.

Analytical procedures

Foraging preferences were investigated by comparing habitat selection probability functions (Manly *et al* 1993), calculated for each study site/year. This function is defined as the proportion of available units in a particular category that are used. In this case, it is estimated by dividing the proportion of the observed time that harriers spent foraging in a particular habitat by the proportion of that habitat in the observed area, i.e.

$$w_i = (u_i/u_+) \Big/ (\mathrm{A}_i/\mathrm{A}_+)$$

where w_i is the sample selection ratio, u_i is the observed time harriers spent foraging in habitat i, u_+ is the total observed harrier foraging time, A_i is the area of habitat i observed, and A_+ is the total area of all habitats observed. These ratios were standardised so that they summed to one for each study site/year. The standardised selection ratio for each habitat (*Bi*) can be interpreted as being the estimated probability that it would be the next one selected if each habitat could be made equally available to a foraging harrier.

In order to identify which habitat variables were most influential on harrier use, a least squares multiple regression model was built relating harrier foraging activity (the continuous dependent variable) to the various measures of topography and vegetation (the independent variables) within each observation square. Foraging activity was determined by calculating the time that harriers were recorded foraging per time the square was observed per area of square visible. Two models were developed using the SPSS/PC REGRESSION procedure (Norusis/SPSS Inc. 1993). Model I included variables representing the means of habitat measurements, whereas model II included variables representing the percentage of points at which each vegetation class was present (or, in the case of topographical features, the percentage within defined categories of measurement). In squares with more than one habitat, these values were weighted according to the area of each habitat observed.

The term $\Sigma^{1}/_{D^{2}}$, representing the proximity of harrier nests to observation squares, was included in both models because it was expected *a priori* to be a nuisance variable with an important effect on harrier use. Variables used in the development of each model are shown in Table 3.

Following recommendations in Wilkinson and Dallal (1981), forward selection of variables was specified, with selection stopping when the significance level of the *F*-to-enter for the next variable exceeded .05. The robustness of the selected model was tested by including study site as a factor. Dummy variable coding was used to create variables X1 to X3, representing the 4 study sites, which were then entered as a group into the regression equation. *Ad hoc* evaluations of assumptions regarding the distribution of the data were carried out by the examination of residuals scatter plots. Plots of independent variables against residuals were inspected for systematic differences in residual variance.

Table 3: Candidate variables used in the development of a multiple regression model to predict the use of observation squares by foraging hen harriers from measurements of topography, vegetation and nest proximity. • Denotes model in which variable used.

Variable type	**Description of variable**	**Variable**	
		Model I	**Model II**
DEPENDENT	Use of observation square by foraging harriers **(HH)**	•	•
INDEPENDENTS:			
Topographic	Mean altitude **(AL)**	•	
	Percentage of points over 200 m. **(AL200)**		•
	Mean angle of slope **(SL)**	•	
	Percentage of points with slope > 15° **(SL15)**		•
Vegetation structure	Mean foliage volume 0-0.5 m. height **(mVS1)**	•	
	Percent points with foliage 0-0.5 m. height **(%VS1)**		•
	Mean foliage volume 0.6-2.0 m. height **(mVS2)**	•	
	Percent points with foliage 0.6-2.0 m. height **(%VS2)**		•
	Mean foliage volume 2.1-5 m. height **(mVS3)**	•	
	Percent points with foliage 2.1-5.0 m. height **(%VS3)**		•
	Mean foliage volume 5.1-15 m. height **(mVS4)**	•	
	Percent points with foliage 5.1-15 m. height **(%VS4)**		•
Vegetation cover	Mean cover of heather **(mHEA)**	•	
	Percent points with heather **(%HEA)**		•
	Mean cover of other dwarf shrub **(mSHR)**	•	
	Percent points with other dwarf shrub **(%SHR)**		•
	Mean cover of upland grasses **(mGRA)**	•	
	Percent points with upland grasses **(%GRA)**		•
	Mean cover of rushes **(mRUS)**	•	
	Percent points with rushes **(%RUS)**		•

Table 3 cont.'

Variable type	Description of variable	Variable Model I	 Model II
	Mean cover of bracken **(mBRA)**	•	
	Percent points with bracken **(%BRA)**		•
	Mean cover of bare ground **(mBGD)**	•	
	Percent points with bare ground **(%BGD)**		•
	Mean of cover trees **(mTREE)**	•	
	Percent points with trees **(%TREE)**		•
Tree characteristics	Mean height of trees **(mHT)**	•	•
	Mean trunk diameter at breast height **(mDBH)**	•	•
Harrier nest proximity	$\sum {}^{1}/_{\mathrm{D}^{2}}$, where D = the distance between the centre of each observation square and each harrier nest within 5 km **(NP)**	•	•

RESULTS

A total of 40 assessments in 32 observation squares were completed. One assessment was abandoned due to nest failure. In 600 hours of observation, harriers were recorded foraging 166 times for 11.69 hours (1.95% of total). Foraging activity totalled 5.97 hours in the early stage of breeding (grey harriers 4.81 hours, brown harriers 1.16 hours) and 5.72 hours in the late stage (grey harriers 3.23 hours, brown harriers 2.49 hours). Foraging time ranged from 0-79.7 minutes per assessment (mean 17.5 minutes). Summary data for each assessment are shown in Appendix 1.

Detection of foraging harriers

The mean initial location distance of harriers in each habitat ranged from 414-953m (Table 4). Location distance distributions were slightly positively skewed in unafforested habitats, new forest and pre-thicket forest, and moderately positively skewed in post-thicket forest and restock. Data were therefore square root transformed to improve normality. The means of the transformed distances differed significantly between habitats (one way ANOVA, $F_{6,159} = 2.62$, $P = 0.019$). However, when data from restock habitat were excluded there was no significant difference (one way ANOVA, $F_{5,149} = 1.04$, $P = 0.40$). No restock habitat was available to harriers at a distance >950m from the vantage points, and closer detection distances in restock may have been an artifact of habitat availability. There was no significant difference in the mean initial location distances of grey and brown birds (independent samples *T*-test, $t = 0.87$, df 164, $P = 0.39$).

Table 4: Mean initial location distances (+/-*S.E.*) of hen harriers foraging in 7 habitats. N = number of observations.

Habitat	**N**	**Mean initial location distance (m)**	***±S.E.***
Heath/bog	36	801	*70.5*
Acid grassland	22	766	*83.1*
Neutral grassland	12	650	*192.5*
New forest	6	692	*106.8*
Pre-thicket	61	843	*51.8*
Post-thicket	18	953	*146.6*
Restock	11	414	*79.2*
All squares	**166**	**788**	***35.4***

These analyses suggest that, with the exception of restock habitat, the likelihood of detecting foraging harriers did not vary between squares.

Habitat selection

The calculation of selection functions for each habitat in each study site/year is shown in Appendix 2. Standardised selection ratios for each habitat (Table 5) were compared using Friedmann's Test for related samples. New forest and restock were not available in all sites, and these habitats were therefore excluded from analysis. Lorn assessments for all 3 years were included in some analyses, although it is appreciated that these data were not strictly independent. Selection indices were re-calculated for each combination of study sites and years compared. When all 6 sites/years were compared, no significant difference was found between the median ranks of the 5 habitats tested ($\chi^2_4 = 7.23$, $P = 0.12$). However, when Lorn 1992 assessments were excluded, there was a highly significant difference ($\chi^2_4 = 12.76$, $P<0.01$). This difference was also significant when Lorn data from 1993 only, or 1994 only, were included ($\chi^2_4 = 10.35$, $P<0.05$, and $\chi^2_4 = 10.85$, $P<0.05$, respectively). Examination of the data revealed anomalies in the selection functions for pre- and post-thicket forests in Lorn 1992, compared with other years.

Table 5: Standardised selection indices for the use of 7 habitats by foraging hen harriers.

Study site/year	Heath/ bog	Acid grass.	Neutral grass.	New forest	Pre-thicket	Post-thicket	Restock
COWAL	.09	.16	0	.40	.35	0	-
ISLAY	.17	.15	.29	-	.26	.12	-
KINTYRE	.09	.19	.21	.03	.44	.05	-
LORN 1992	.27	.05	.10	-	.02	.16	.40
LORN 1993	.02	.13	.10	.26	.31	.04	.15
LORN 1994	.16	.04	.10	.48	.21	0	0
TOTALS *	.80	.72	.80	-	1.59	.37	-

* Totals are shown only for those habitats present in all study sites.

Selection ratios within Lorn were also compared, in order that data from restock forest could be included; there was no significant difference between the medians of the 6 selection ratios ($\chi^2_5 = 1.33$, $P = 0.92$).

The selection indices show that foraging harriers prefer pre-thicket forest more, and post-thicket forest less, than other habitats. Overall, the probability of selection for the 3 unafforested habitats was similar. Harriers showed a strong preference for new forest habitat in 3 out of 4 assessments, and for restock in one out of 3 assessments.

Table 6: Matrix of Pearson correlation coefficients for variables used in the development of multiple regression model I. Correlations significant at the 1% level are shown in **bold**.

	HH	AL	SL	mVS1	mVS2	mVS3	mVS4	mHEA	mSHR	mGRA	mRUS	mBRA	mBGD	mTREE
AL	0													
SL	-.01	**+.42**												
mVS1	**+.49**	+.25	+.12											
mVS2	-.03	-.04	**-.43**	+.06										
mVS3	-.26	-.13	-.34	-.34	**+.81**									
mVS4	-.31	-.19	-.34	**-.48**	**+.66**	**+.91**								
mHEA	+.21	**+.60**	+.32	**+.55**	+.10	-.18	-.38							
mSHR	**+.48**	+.18	+.04	**+.41**	-.08	-.25	-.35	+.21						
mGRA	+.08	-.25	-.02	+.18	**-.45**	**-.45**	**-.46**	-.38	+.07					
mRUS	+.13	-.38	+.04	+.13	-.38	**-.43**	-.33	-.31	-.08	+.28				
mBRA	+.03	-.20	+.18	+.15	-.01	0	-.08	+.13	+.15	-.14	-.10			
mBGD	-.29	-.14	**-.41**	**-.45**	**+.57**	**+.76**	**+.90**	-.35	-.35	**-.53**	-.35	-.13		
mTREE	-.11	+.01	-.35	-.12	**+.93**	**+.90**	**+.84**	0	-.18	**-.54**	**-.43**	-.11	**+.74**	
NP	+.39	-.09	+.06	+.26	+.02	-.13	-.07	+.13	+.04	-.23	+.20	+.23	+.03	-.10

Table 7: Matrix of Pearson correlation coefficients for variables used in the development of multiple regression model II. Correlations significant at the 1% level are shown in **bold**.

AL200	+.06															
SL15	+.08	+.01														
%VS1	+.27	+.29	+.01													
%VS2	+.27	-.14	-.26	-.31												
%VS3	-.07	0	-.24	**-.43**	**+.70**											
%VS4	-.29	-.30	-.21	**-.67**	**+.48**	**+.73**										
%HEA	+.19	**+.57**	+.07	**+.42**	-.16	+.01	**-.41**									
%SHR	+.16	+.21	-.08	+.34	+.07	-.13	-.36	+.36								
%GRA	+.26	+.08	+.38	**+.66**	**-.41**	**-.73**	**-.87**	+.24	+.40							
%RUS	+.10	-.16	+.22	+.31	-.12	**-.42**	**-.47**	-.30	0	**+.53**						
%BRA	+.05	-.13	**+.56**	-.05	-.18	-.24	-.24	-.09	+.02	+.26	+.30					
%BGD	-.30	+.08	-.31	**-.59**	+.33	**+.47**	**+.76**	**-.43**	-.28	**-.70**	-.24	-.36				
%TREE	+.17	+.11	-.23	-.33	**+.79**	**+.85**	**+.56**	+.04	+.01	**-.56**	-.29	-.37	**+.54**			
mHT	-.33	-.24	+.01	**-.55**	+.09	**+.44**	**+.62**	**-.49**	**-.52**	**-.58**	-.16	-.01	**+.53**	+.26		
mDBH	-.30	-.11	-.08	**-.44**	-.12	**+.46**	**+.54**	-.38	**-.48**	**-.57**	-.18	+.01	+.35	+.20	**+.88**	
NP	+.39	-.05	+.08	+.03	+.21	+.07	-.05	+.04	-.08	-.01	**+.28**	+.10	-.01	+.12	-.13	-.18
	HH	**AL 200**	**SL15**	**%VS1**	**%VS2**	**%VS3**	**%VS4**	**% HEA**	**% SHR**	**% GRA**	**% RUS**	**% BRA**	**% BGD**	**% TREE**	**mHT**	**m DBH**

Habitat features influencing harrier foraging activity

Correlation matrices for the variables used in models I and II are shown in Tables 6 and 7, respectively. With the variable representing harrier nest proximity forced into the equation, the forward multiple regression based on model I selected 2 further variables, representing foliage volume <0.5m height and dwarf shrub cover. With all significant independent variables in the equation, R = .65, $F_{3,36}$ = 8.84, P = 0.0002. This model explained 38% of the variance in harrier use. Similarly, model II selected variables representing the volume of foliage 2-5m tall and the cover of bare ground and trees. After entry of all IVs, R = .70, $F_{4,35}$ = 8.26, P = 0.0001 (Table 8). Model II explained a greater amount (43%) of the variance in harrier use than model I and was therefore chosen for further development.

Table 8: Statistical regression of habitat and nest proximity variables on use of observation squares by foraging hen harriers, based on model II. The table shows the unstandardised regression coefficients (*β*) and intercept, standardised regression coefficients (*Beta*), semi-partial correlations (sr^2), squared multiple correlations (R^2), incremental *F* ratio, and R, R^2 and adjusted R^2 after entry of all IVs. NP = harrier nest proximity, %BGD = percentage of points with bare ground, %TREE = percentage of points with trees, %VS3 = percentage of points with foliage 2.1-5m. height.

	β	***Beta***	***T***	***sr²*** **(a)**	***P***	***R²*** **(b)**	***F*inc**	
NP	2.17	.27	2.18	.12	.036	.12	5.24	*
%BGD	-1.26	-.55	-3.82	.11	.000	.23	5.18	*
%TREE	1.50	1.01	4.14	.13	.000	.36	7.24	**
%VS3	-1.15	-.68	-2.94	.13	.006	.49	8.67	**
Intercept	14.12							

R	.70	***
R²	.49	
Adj. *R²*	.43	

(a). = incremental. **(b).**= cumulative. * P <0.05, ** P <0.01, *** P <0.001.

The addition of bare ground resulted in a significant improvement in R^2. The addition of tree cover and the volume of foliage 2-5m tall each resulted in highly significant improvements in R^2. The frequency distribution of the residuals for the selected model did not depart significantly from normal (Kolmogorov-Smirnov one sample test: z = 0.974, $P = 0.30$). Using Mahalanobis distance with $P < 0.001$, the assessment for square NR 17/52 was identified as a multivariate outlier. Examination of the data revealed a raw score on the harrier use variable 4 times greater than that predicted by the model.

When model II was re-selected with variables representing study site (X1-3) forced into the equation, the same 3 habitat variables were selected. With study site included in the model, the explained variability in harrier use was 53%. Nest proximity was not significant in this model.

It was hypothesised that the magnitude and direction of the effect of the presence of trees might be dependent upon their characteristics. This dependence was tested by introducing variables representing the interaction terms %TREE*mHT (mean tree height for points at which trees were present) and %TREE*mDBH (mean trunk diameter for points at which trees were present). However, when model II was re-selected with the 2 interaction terms included amongst the candidate variables, neither were chosen. Mean tree height and mean trunk diameter were strongly and positively correlated with both the percentage of points with foliage 2-5m tall and the percentage of points with bare ground. Why then did they not have a significant effect in the model? To investigate this, the tree characteristics analysis was repeated, except that the variables relating to vegetation structure (%VS1-4) and bare ground (%BGD) were excluded. Again, neither of the interaction terms were selected. The inference of this analysis is that the variables representing bare ground and the volume of foliage 2-5m tall were better at describing the effect of tree development on foraging activity than were measures of tree height and trunk diameter.

When model II was re-run with foraging activity by either grey- or brown-plumaged birds only as the dependent variable, no topographic or habitat variables were selected. Nest proximity had a significant effect on the foraging time of grey, but not brown, birds ($P = 0.04$ and 0.07, respectively). This may have been because brown birds included one year olds, some of which did not breed.

DISCUSSION

The strong positive correlation between tree cover and the volume of foliage 2-5m tall would normally lead us to be cautious about which one the model selected, since it would be expected that a positive effect could have been identified with either variable. However, tree cover had a positive effect in the model, whilst the volume of foliage 2-5m tall had a negative effect. This suggests that harriers prefered foraging in locations with trees, but only if the trees did not have much foliage between 2-5m height. Bare ground was strongly and positively correlated with tree cover and height, presumably because the ground vegetation was suppressed by the shading effects of tree foliage. Bare ground had a negative effect on harrier foraging activity, again suggesting that harriers avoided areas which had greatest tree development. These preferences are consistent with the finding that harriers prefer newly afforested and pre-thicket forests more, and post-thicket forests less, than other habitats. Commercial forests aim to have a tree stocking density of approximately 2,500 trees ha^{-1} (Petty and Avery 1990), and canopy closure starts to occur when the trees reach about 3m height (Ratcliffe and Petty 1986). Major changes in the composition and availability of prey occur at this stage (Moss *et al.* 1979, Lack and Lack 1951, Petty and Avery 1990, Avery and Leslie 1990), and woodland raptors such as buzzard *Buteo buteo*, sparrowhawk *Accipiter nisus* and tawny owl *Strix aluco* are increasingly favoured over those of open country, such as hen harriers and short-eared owls *Asio flammeus*.

The density and distribution of harrier nests had a major influence on foraging activity. Examination of the raw data for each observation square (Appendix 1) indicated that variation in nest proximity was able to explain many of the discrepancies in habitat selection between study sites and years. For example, the anomalous selection indices for pre- and post-thicket habitats in Lorn 1992 can be explained by reference to the relatively low nest proximity score (0.94) for the pre-thicket forest square NN 06/24, and relatively high score (2.12) for the post-thicket forest square NN 01/22. High nest proximity scores can also be used to explain the relatively strong selection for heath/bog in Lorn 1992 and 1994, acid grassland in Lorn 1993 and Cowal 1994, and restock in Lorn 1992. Conversely, low nest proximity scores may explain the relatively low probability of selection for heath/bog in Lorn 1993 and neutral grassland in Cowal 1994. Habitat selection probabilities must therefore be treated with caution, and conclusions drawn only where there is clear consensus between study sites and years.

New forest was a highly preferred habitat in Cowal and Lorn, but not Kintyre. Examination of the raw scores for those variables found to have a significant effect on foraging activity showed that this discrepancy could not be explained by differences between observation squares in nest proximity, tree cover or volume of foliage 2-5m tall. However, the extent of bare ground in the Kintyre observation square was 4 times greater than that in any other new forest square. This difference was probably because the Kintyre new forest square had been ploughed more recently than those elsewhere, and vegetation re-colonisation was therefore less advanced. Although the negative effect of bare ground on foraging activity was thought to have been largely an artifact of tree foliage density, harriers may have avoided areas of bare ground even where there was little tree development, since prey were probably scarce.

Preference for restock habitat varied considerably between years. Thus restock was the highest ranked habitat in 1992, yet was ranked equal lowest in 1994. Differences in nest proximity help explain the relatively strong selection in 1992, but not the low value for selection in 1994. Habitat varied between years mainly as a result of tree growth, but on their own these differences were probably insufficient to account for the magnitude of the shift in preference. It is possible that tree felling adjacent to the restock observation square had an adverse effect on foraging activity; sporadic felling began in 1993, and was regular in 1994. Although foraging observations were not undertaken whilst felling was in progress, overall disturbance may have caused harriers to avoid the area generally in years that felling occurred.

Martin (1987) found that harriers' preference for foraging over croplands declined when the vegetation reached a height of around 0.5m., and concluded that this was because prey were less vulnerable to capture in the longer vegetation. In the present study, harriers foraged preferentially in afforested habitats until there was much foliage 2-5m tall. Foliage volume at this height was strongly and negatively correlated with foliage volume below 0.5m. It is possible that harriers within forests hunted for prey mainly within the ground vegetation, and that afforested habitats therefore became less attractive as tree development caused the amount of foliage <0.5m tall to decline. The strength of this effect may have been further increased by the difficulty of manoeuvering amongst taller trees.

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CHAPTER 4

FINE-SCALE FORAGING HABITAT PREFERENCES

Contents:

"All time is lost what is not spent in 'unting - it is like the hair we breathe - if we have it not we die."

Robert S. Surtees (1843). Handley Cross.

INTRODUCTION

Several raptor studies (e.g. Wakeley 1979; Bechard 1982; Janes 1985) have stressed the importance of vegetation cover and structure to raptor foraging patterns. This may be because suitable prey is more abundant in some habitats than others, or more vulnerable to capture, or both. Hen harriers are highly agile and manoeuvrable birds (Schipper 1973; Nieboer 1973), and typically forage low over the ground with frequent changes of direction and pace (Watson 1977). They make extensive use of variation in terrain and vegetation relief, such as ditches, shrubs and habitat edge (Schipper 1977; Bildstein 1987; Redpath 1992). These behaviours suggest that harriers are able to respond acutely to fine-grained variation in habitat and prey.

At a landscape scale, foraging hen harriers exhibited a strong preference for young plantation forestry (Chapter 3). Harriers' use of forests declined as the trees developed, to the extent that they avoided areas where canopy closure had occurred. However, the scale at which observations and measurements are made can have an important effect on the interpretation of relationships between foraging activity and habitat, and associations found at one scale may be absent or different at another (Wiens 1985). Thus, in the current study, the way in which harriers use afforested and other habitats is largely unknown, and we can therefore only speculate upon which aspects of land cover are most influential to harrier foraging. The main objective of this part of the study, therefore, was to examine the route decisions made by harriers foraging within the various types of forest and moorland, and relate these to fine-scale variation in habitat.

METHODS

The flight-paths used by harriers foraging within 1x1km observation squares were recorded from vantage points overlooking each square. Routes were initially plotted onto enlarged colour photographs taken from each vantage point, then later transferred onto 1:10,000 scale maps. Where observation squares were selected in more than one year, foraging routes were plotted in the first year only.

Table 1: Variables measured around points (1). over-flown by harriers, and (2). located randomly, within 1x1km observation squares.

Variable-type	Description, method of measurement, and precision	Variable
DEPENDENT	Habitat measurement **point-type**: route or random	P_TYPE
INDEPENDENTS:		
Topographic	**Altitude:** from 1:25,000 scale maps. To nearest 50m	AL
	Angle of slope: using field inclinometer. To nearest 5^0	SL
	Aspect of slope: (zero, N/NE, E/SE, S/SW,W/NW)	ASP(0-4)
	Topographic exposure: sum of the angles of inclination of the skyline at the 8 cardinal compass points (Pyatt 1977, Wilson 1984),	TOPEX
	Distance to nearest linear feature: e.g. streams, forest rides, tracks & walls. Measured on 1:10,000 scale maps, to nearest 10m.	LIN
Vegetation structure	Percent volume of foliage, estimated by eye to nearest 10%.	
	Foliage within **0-0.5m height**	VS1
	Foliage within **0.6-2.0m height**	VS2
	Foliage within **2.1-5.0m height**	VS3
	Foliage within **5.1-15m height**	VS4
Vegetation cover	Percentage cover, estimated by eye to nearest 5%	
	Heather (*Calluna* and *Erica spp.*)	HEA
	Dwarf shrub (mainly *Myrica* and *Vaccinium spp.*)	SHR
	Upland grasses (mainly *Molinia, Nardus, Agrostis* and *Festuca spp.*)	GRA
	Mosses (mainly *Sphagnum* and *Polytrichum spp.*)	MOSS
	Rushes (*Juncus spp.*)	RUS
	Bracken (*Pteridium spp.*)	BRA
	Bare ground	BGD
	Tree canopy	TREE

Table 1 cont.'

Variable-type	Description, method of measurement, and precision	Variable
Tree characteristics	Mean of 3 trees nearest measurement point	
	Height, measured with telescopic rod to nearest 10cm	mHT
	Trunk diameter at breast height, measured with callipers to nearest 1cm	mDBH

Within each observation square, plotted routes were divided into sections representing 10m on the ground. Following sample size guidelines given by Morrison (1984), a random sample of 30 sections per habitat per square (or maximum possible if less than 30 were available) were selected, and measurements of topography and vegetation made at the mid-point of each section. In order to compare the habitat over-flown by harriers with that available generally, measurements were also made at a sample of randomly located points in each habitat in each square (see Chapter 3).

Measurement points were located on the ground with the assistance of an observer positioned at the vantage point for each square. Habitats were measured within a radius of 5m around each point. This area was considered to be similar to that scanned by a harrier foraging at typical elevation of ca 3m. Variables measured at each point are shown in Table 1.

Analytical procedures

The probability that a sample point was overflown by a foraging harrier was estimated using the SPSS/PC LOGISTIC REGRESSION procedure (Norusis/SPSS Inc. 1993). Logistic regression is a more useful means of modelling probabilities than multiple regression, since it forces estimated probabilities to lie within the range zero to one. Moreover, it has the advantage over discriminant function analysis that the assumptions and sample size requirements necessary for valid application are less restrictive. The logistic model has the form:

$$Prob(y) = \frac{\exp\,(b_0 + b_1x_1 + b_2x_2 + \ldots + b_px_p)}{1 + \exp\,(b_0 + b_1x_1 + b_2x_2 + \ldots + b_px_p)}$$

where *Prob(y)* is the probability of an event occurring, b_0 and b_1 are coefficients estimated from the data and x_1, x_2, etc. are values of the independent variables.

The dichotomous dependent variable was the measurement point-type (i.e. whether located on a foraging route or randomly) and the covariates were the various measures of habitat. Data from all observation squares were pooled. Frequency distributions of the scores of habitat variables were examined and, if necessary, transformed to improve skewness. In order to prevent the effects of the point characteristics from being obscured by gross differences in the amounts of the habitats and numbers of random and route measurement points between observation squares, dummy indicator variables were used to represent different squares, and habitats within squares. These were forced into the model as nuisance factors, regardless of whether or not they were significant. Tree characteristic variables were set to zero for points at which no trees were present. Forward stepwise selection of habitat variables was specified and a likelihood ratio test used to determine entry ($P <.05$) and removal ($P <.10$) of variables. A potential problem of this approach is that of pseudoreplication (Hurlbert 1984), since it assumes that each habitat measurement point is statistically independent of every other point. This is unlikely to be the case, since many points were closely spaced along foraging routes and, given the patchiness of the habitat within observation areas, it would be expected that many points would have had similar habitat characteristics. The model is therefore likely to be 'optimistic' in that estimates of the statistical significance of variables will probably be inflated. As a result, variables may be included which would not have been selected by a more stringent approach.

In order to improve the significance testing procedure, those habitat variables selected by the initial analysis were then fitted to data from each observation square separately. Dummy variables were included, where necessary, to represent different habitats within each square. All variables were entered as a single block. Variables were deleted from models for squares in which they showed no variation. The significance of each habitat variable was then assessed by calculating the mean regression coefficient (across squares) and standardising this value by dividing by its standard error. The resultant *t*- value was large for those habitat variables that had consistent effects across squares.

A model containing the habitat variables initially selected, together with the observation square / habitat dummy indicator variables, was then re-fitted to the pooled data from all squares. A backwards elimination procedure was used to remove the least significant habitat variable at each step. Using this approach, it is the data for the observation squares, rather than habitat measurement points, that are regarded as statistically independent of one another.

Validation of foraging route plotting accuracy

The accuracy with which the position of a raptor can be plotted is important in determining the scale of habitat measurement (Mosher, Titus and Fuller 1987). It was accepted that a high degree of accuracy in placing a flying harrier was unrealistic, and that accuracy might decline as distance from the observer increased (due to the effects of parallax). Furthermore, accuracy might have varied between the different habitats, since features enabling the correspondence between bird and landscape to be checked were scarce in homogenous environments such as heath/bog and acid grasslands.

In order to estimate route plotting errors, tests were carried out in 3 observation squares of contrasting habitat: heath/bog, neutral grassland and pre-thicket forest. A radio-controlled model helicopter was fitted with a remotely operated video camera, angled to record the ground directly below. The dimensions of the helicopter (rotor blade length ca. 120 cms.) were similar to those of a harrier, and it was flown at heights and speeds typical of a foraging bird. Helicopter routes were chosen that meandered across the width and breadth of each square. The ground vegetation over-flown by the helicopter was recorded at 15 second intervals using 2 independent methods: (1). by an observer positioned at a vantage point over-looking the square, and (2). from video-tape showing the ground over-flown. A visual cue, recorded on the video and simultaneously signalled to the observer, ensured that the 2 sets of observations were synchronised. Vegetation nearest the central point of the video screen was recorded. Six vegetation-types were recognised: heather, other dwarf shrub, grassland, rushes, bracken, and bare ground. In the squares observed, these vegetation-types were patchily distributed with respect to the distance between helicopter sampling points. The correspondence between the vegetation classified by each method therefore provided a useful measure of route plotting accuracy.

RESULTS

Foraging activity was recorded in 28 of the 32 squares observed. Habitat measurements were made at 918 randomly located and 835 foraging route points, this discrepancy being attributable to fewer route than random points being available for selection (since harriers did not use all habitats in all squares). In one square (NR 76/50) the length of foraging route recorded permitted only 3 habitat measurement points to be placed, and data from this square were therefore excluded.

Route plotting accuracy

There was a high level of agreement between the ground vegetation classified from vantage point watches and video-tape within all 3 observation squares tested (Table 2). This is reassuring since it shows that, in terms of vegetation-type, it was possible to accurately plot ca 90% of the points overflown by the helicopter (and therefore, by implication, those overflown by a harrier). Vegetation classification did not differ significantly between the 3 habitats tested ($\chi^2_2 = 0.48$, $P = 0.79$).

Table 2: Percentage agreement between classifications of ground vegetation over-flown by a radio-controlled helicopter, made from (1). vantage point observations, and (2). video-tape recorded by a camera fitted to the helicopter. Classifications were made every 15 seconds following a synchronised start time.

Habitat	No. of vegetation classes present	No. of classifications	Agreement between recording methods
Heath/bog	5	36	86%
Neutral grassland	4	22	86%
Pre-thicket	4	33	91%
Overall	6	91	88%

Foraging route selection

Using data from all habitat measurement points, 6 variables were selected by the initial model. These represented altitude, distance to nearest linear feature, volume of foliage 0.6-2m tall, and cover of grasses, bracken and trees. These variables were then fitted to data from each observation square separately, and the means of the resultant coefficients and their departure from zero calculated (Table 3). This analysis shows that tree cover had a consistently large effect on point-type relative to other variables, and that distance to linear features and the cover of grasses were also important.

Table 3: Means, standard errors, and *t* values (indicating the significance of the departure of means from zero), for logistic regression coefficients of habitat variables identified as having an important effect on determining the routes of foraging hen harriers. Coefficients were calculated for 32 observation squares.

Variable	**Mean**	***S.E.***	**N**	***t* value**
VS2*	.08	*.29*	27	.28
BRA*	-.30	*.61*	21	.49
AL	.01	*.02*	27	.50
GRA	-.01	*.01*	27	1.00
LIN	-.01	*.01*	27	1.00
TREE*	-.99	*.51*	15	1.94

* log transformed.

Table 4 shows details of logistic regression models using these variables re-fitted to pooled data from all observation squares, with the least significant variable removed at each step of a backward elimination procedure. In logistic regression analysis, the probability of the observed results (i.e. the *likelihood*) is a small number less than one, and is it customary to use minus twice the log-likelihood ($X_L{}^2$) as a measure of how well the model fits the data. A good model is one that results in a small value for $X_L{}^2$. The difference between the value of $X_L{}^2$ for successive steps of the model can be tested for significance by comparison with the chi-squared distribution to indicate whether a particular model provides a significant improvement over the previous one in terms of fitting the data (Manly *et al.* 1993). This is comparable to the *F*-change test in multiple regression. Inter-correlations between habitat variables are shown in Table 5.

Table 4: Results of logistic regression models predicting the likelihood of a measurement point lying on a hen harrier foraging route. The columns give details of -2 times the log-likelihood (X_L^2), model chi-square improvement and significance, and the percentage of points correctly classified as either randomly located or on a foraging route. Each step of a backward selection procedure to eliminate variables is shown. 1 = log TREE, 2 = LIN, 3 = GRA, 4 = AL, 5 = log BRA, 6 = log VS2.

Variables	**X_L^2**	**Model improvement**	**df**	***P***	**Correct classification (%)**		
					Random	Route	Overall
1-6	2188.68	25.13	1	.0000	70.70	63.35	67.20
1-5	2213.81	29.14	1	.0000	68.30	60.24	64.46
1-4	2242.92	20.44	1	.0000	69.93	55.93	63.26
1-3	2285.67	4.53	1	.033	71.02	47.43	59.78
1-2	2290.20	2.76	1	.097	75.27	44.91	60.81
1	2292.96	113.18	1	.0000	52.51	70.18	60.92
Constant	2406.14	20.10	32	.949	28.10	79.04	52.37

Table 5: Matrix of Pearson correlation coefficients between variables used in the development of a logistic regression model to predict the likelihood of a measurement point lying on a hen harrier foraging route.

BRA*	+.06				
AL	-.03	-.09			
GRA	-.15	-.04	-.16		
LIN	-.18	-.08	-.01	+.04	
TREE*	+.71	-.14	+.15	-.24	-.11
	VS2*	**BRA***	**AL**	**GRA**	**LIN**

* log transformed.

The model containing all 6 variables correctly classified 63% of foraging route and 71% of random points. Removal of the variable with the smallest *t*-value (volume of foliage 0.6-2m tall), resulted in only a small decline in the accuracy with which points were classified. Of the remaining variables, those representing bracken cover and altitude each had similarly small *t*-values. Removal of both variables resulted in a small improvement in the classification of random points. However, foraging route point classification declined by almost 13%, and overall classification by nearly 5%. It was therefore decided to retain 5 variables. Summary statistics for this model are shown in Table 6. Tree cover made the largest individual contribution to the model, followed by bracken, altitude, and distance to linear feature. The extent of grass cover had only a weak effect. Altitude was the only variable to have a positive effect on foraging route selection.

This analysis shows that harriers selected foraging routes mainly so as to avoid trees. They preferred foraging over patches with least bracken, and appeared to avoid those with much grass cover. Routes tended to traverse the higher parts of study sites, and were biased towards linear landscape features.

Table 6: Regression coefficients, Wald statistic (and associated significance *P*), partial correlations (*R*) and changes in the odds of a point being on a foraging route (Exp [B]) for a logistic regression model to estimate the probability of a habitat measurement point lying on a hen harrier foraging route. The Wald statistic tests the null hypothesis that a coefficient is zero. The value for Exp [B] is the factor by which the odds of a point lying on a harrier foraging route change when an independent variable is increased by one unit. Variables marked with an asterisk have been log transformed.

Variable	**B**	***S.E.***	**Wald**	**df**	***P***	***R***	**Exp[B]**
TREE*	-.861	*.097*	78.97	1	.0000	-.178	.423
BRA*	-.327	*.062*	27.26	1	.0000	-.102	.721
AL	.012	*.003*	19.61	1	.0000	.085	1.012
LIN	-.005	*.001*	10.83	1	.0010	-.060	.995
GRA	-.005	*.002*	5.12	1	.0236	-.036	.995
Constant	-.873	*.457*	3.64	1	.0563		

Therefore $Prob(y) = a / 1 + a$,

where $a = e^{-0.873 - 0.861\log TREE - 0.327\log BRA + 0.012AL - 0.005LIN - 0.005GRA}$.

Foraging route selection over trees

When the model was re-selected using only the 892 measurement points (462 randomly located and 430 foraging route) in afforested habitats, 4 variables were retained by the initial model. These represented altitude, and cover of grass, bracken, and trees. These were fitted individually to data from the 15 squares containing points with trees. This analysis indicated that the cover of bracken and trees had the largest consistent effects on point-type (Table 7).

Table 7: Means, standard errors, and t values for the logistic regression coefficients of habitat variables identified as having an important effect on determining the routes of hen harriers foraging over trees. Coefficients were calculated for 15 observation squares.

Variable	Mean	*S.E.*	N	*t* value
GRA	.02	*.03*	15	.67
AL	.70	*.84*	15	.83
TREE*	-15.96	*12.89*	15	1.24
BRA	-.70	*.42*	11	1.67

* log transformed.

Table 8 shows summary statistics for models containing the 4 variables, re-fitted to pooled data from all observation squares, at each step of the backwards elimination procedure. Inter-correlations between variables are shown in Table 9.

The model containing all variables correctly classified 58% of foraging route and 78% of random points. Removal of the variables with the smallest *t*-values (grass cover and altitude) resulted in only minor change in point classification accuracy. However, when the next least significant variable (tree cover) was removed, there was a decline of 15% in overall point classification. The model containing the variables representing bracken cover and tree cover was therefore retained. Summary statistics for this model are shown in Table 10.

Table 8: Results of logistic regression models predicting the likelihood of a measurement point lying on the route of a hen harrier foraging over trees. Each step of a backward selection procedure to eliminate variables is shown. Details as per Table 4, except 1 = BRA, 2 = log TREE, 3 = AL, 4 = GRA.

Variables	**X_L^2**	**Model improvement**	**df**	***P***	**Correct classification (%)**		
					Random	Route	Overall
1-4	1081.32	13.48	1	.0003	78.35	58.37	68.72
1-3	1094.80	3.73	1	.0682	77.71	56.05	67.26
1-2	1098.53	124.97	1	.0000	75.32	59.77	67.83
1	1223.50	3.81	1	.0561	35.93	70.47	52.58
Constant	1227.31	8.11	16	.9454	28.57	76.74	51.79

Table 9: Matrix of Pearson correlation coefficients between variables used in the development of a logistic regression model to predict the likelihood of a measurement point lying on a harrier foraging route over trees.

AL	+.08		
TREE*	-.38	-.18	
BRA	-.04	-.11	-.03
	GRA	**AL**	**TREE***

* log transformed.

Table 10: Summary statistics for a logistic regression model to estimate the probability of a habitat measurement point lying on a hen harrier foraging route over trees. Variables marked with an asterisk have been log transformed.

Variable	**B**	***S.E.***	**Wald**	**df**	***P***	***R***	**Exp[B]**
TREE*	-.620	*.061*	101.99	1	.0000	-.284	.538
BRA	-.036	*.010*	13.46	1	.0002	-.096	.965
Constant	1.929	*.378*	26.01	1	.0000		

Therefore $Prob(y) = a / 1 + a$,

where $a = e^{1.929 - 0.620\log TREE - 0.036BRA}$

Tree cover made by far the largest individual contribution to the model. To test whether the strength of this effect was dependent on the characteristics of the trees, the model was re-selected with the interaction terms TREE*mHT (representing mean tree height at points with trees) and TREE*mDBH (representing mean trunk diameter at points with trees) included amongst the candidate variables. However, neither of these interaction terms were significant in the resultant model. This analysis suggests that harriers foraging in afforested habitats selected routes with least tree cover, regardless of the dimensions of the trees, and that they tended to avoid locations with much bracken.

DISCUSSION

Investigation of the selection process by which a harrier came to be in a particular habitat-type (Chapter 3) showed that harriers foraged preferentially in areas with small trees (e.g. pre-thicket forests). However, the present study shows that the flight paths followed by foraging harriers avoided trees, even if these were small. This suggests that harriers' preferred young forests because of factors other than trees. One explanation for this might be that more prey were available to harriers in young forests than other habitats, but that these prey were associated with the ground vegetation rather than the trees. Harriers hunt predominantly for open country species, and capture these mainly on the ground (Watson 1977). Their long legs and ability to locate prey acoustically (Rice 1982) appear to be adaptations for securing prey within rank vegetation. Preference for hunting over ground vegetation within young forests would therefore be unsurprising, since the exclusion of sheep and lack of rotational burning mean that the ground flora in these habitats is particularly well developed. Trees are generally planted about 2m apart in commercial forests. In the early growth stages, we would therefore expect harriers (wingspan 1-1.2m) to be able to access prey occupying the ground vegetation between trees with relative ease. Later in the forest rotation, however, access is likely to be limited to areas of failed or checked tree growth and linear gaps such as rides and stream corridors.

This shift in the interpretation of the relationship between trees and harrier foraging behaviour demonstrates the importance of scale in studies of habitat association, as emphasised by Wiens (1985) and Mosher, Titus and Fuller (1987), and underlines the value of a hierarchical approach to studying resource selection (Johnson 1980).

Harriers avoided selecting routes over locations with much bracken, both generally and when foraging over trees. Bracken stands tend to be poor floristically and generally support limited fauna (Pakeman and Marrs 1992; Stillman and Brown 1994). Furthermore, the dense foliage readily forms a closed canopy, and this is likely to make prey detection difficult. Thus Collopy and Bildstein (1987), and Martin (1987) found that harrier foraging success was relatively poor in structurally dense vegetation and concluded that this was because prey vulnerability in such habitats was low.

Higher ground was used more than low-lying ground overall. This may have been an artifact of the distribution of sparsely afforested ground, since we would expect tree development to be both slower and less complete at higher altitude. In general, foraging routes tended to be associated with linear habitat features. During foraging observations, harriers sometimes disappeared from view as they flew behind walls and ditch embankments, or followed stream valleys. Schipper (1977) found a similar preference for prominent landscape features in agricultural land, and suggested that this behaviour increased their chances of surprising prey. Furthermore, features such as walls, fences and ditches often formed habitat boundaries, which have been shown to be used disproportionately by harriers (Redpath 1992). Why did harriers not appear to be influenced by linear features in forests? Many such features (e.g. streams, tracks, and fences) were distinguished by an absence of trees, and it therefore possible that their effects were masked by that of tree cover.

The avoidance of grassy habitats is puzzling. Areas with much grass were generally less structurally diverse than those elsewhere, and this may have limited the opportunities for surprising prey. If true, this would be consistent with harriers' preference for areas of heterogeneous tall vegetation (Schipper 1977), where prey occupying relatively isolated stands of vegetation appear to be more vulnerable to harrier predation (Collopy and

Bildstein 1987). However, grasslands are a preferred habitat of field voles *Microtus agrestis*, an important harrier prey species in Argyll (Chapter 6), and we might therefore have expected the distribution of grasses to have had a positive effect on foraging route choice.

This study demonstrates the importance of trees and other vegetation on the behaviour of foraging hen harriers. Preston (1990) suggested that harriers responded to variation in foraging profitability, i.e. the interaction between prey abundance and its vulnerability to capture. Thus, in the present study, harriers may have selected foraging routes over open ground because these areas held suitable prey that were relatively easy to detect and capture. Open ground within forests is likely to be particularly profitable, since the ground layer is well developed and may hold relatively high densities of prey, and the trees may prevent prey from easily detecting approaching harriers, thereby reducing the time available for escape. Harriers in forests foraged over areas of least canopy cover, suggesting that they continued to hunt for prey within the ground vegetation until prevented from doing so by the developing trees.

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CHAPTER 5

FORAGING BEHAVIOUR AND SUCCESS

Contents:

".....and 'dilly dilly', calls the loft hawk, 'Come and be killed,' "

Dylan Thomas (1949) Over Sir John's Hill.

INTRODUCTION

Hen harriers are found in a wide variety of open and semi-open habitats (Tucker and Heath 1994). In Britain, they mainly occupy undulating moorlands and young conifer plantations during the breeding season, but generally frequent coastal and lowland agricultural areas in autumn and winter (Watson 1977, Cramp and Simmons 1980). Differences in vegetation and prey composition between these environments mean that harriers need a wide repertoire of foraging strategies in order to locate and capture food. Moreover, harriers may exploit a wide range of vegetation-types within each environment, and frequent shifts in foraging behaviour are therefore required as they move from one habitat to another. Thus, previous studies (e.g. Schipper *et al.* 1975, Bildstein 1978, Temeles 1986, Collopy and Bildstein 1987) have described a high degree of plasticity in harrier foraging behaviour, with tactical approaches ranging from methodical quartering of the ground to aerial pursuits of prey.

In order to better understand the use of habitat and food resources by hen harriers in Argyll, I studied their flight behaviour and foraging performance over various upland habitats. Specifically, I wanted to know how these variables differed between afforested and moorland habitats and, within forests, how they were affected by tree development. For example, we might expect flying elevation to increase as forests matured, due to the difficulty of manoeuvring between larger trees. Flying height might also need to be proportionately greater over taller trees in order to maintain sufficient insight into the vegetation (Schipper *et al.* 1975). Prey are likely to detect harriers at much shorter distances in structurally complex habitats such as forests, and may be easier to surprise. We might therefore expect harriers to fly more slowly over forests than moorland habitats (where they are relatively conspicuous). Furthermore, harriers are unlikely to detect prey in tall vegetation until they are almost directly over it and, in such situations, faster flying speeds may be too demanding of a harrier's agility.

Repeated measures of an individual's behaviour cannot be assumed to be independent (Martin & Bateson 1986), even when records are separated by a specified interval of time (e.g. Morrison 1984, Porter *et al.* 1985). In the rugged terrain studied, I was seldom able to follow individual harriers for more than a few minutes, and earlier trials (Madders 1991) had indicated that it was not possible to sequentially sample the data within each foraging bout at intervals far enough apart in time for records to be independent. The most obvious way to obtain independent records is to select new areas with new individuals for each observation. However, in the present study, it would have been possible to gather only a very small sample of observations in this way. A less extreme approach is to use only initial observations from each bird located. Initial observations have been used in several previous studies of avian foraging (e.g. Gibb 1954, Morse 1970, Lewke 1982, and Franzreb 1985), and have been shown to be more independent than those made sequentially (Hejl *et al.* 1990). However, despite their limitations, sequential observations none-the-less provide important information on prey encounter and capture rates. Accordingly, I used initial location observations to compare foraging techniques, and (continuous) sequential observations for the purpose of calculating prey strike and capture rates.

METHODS

The behaviour of harriers apparently searching for prey was recorded in areas dominated by one of 7 habitats (see Chapter 3). Observations were made principally from 32 vantage points over-looking 1x1km squares used to investigate habitat use by foraging harriers. Details of the selection of these squares is given in Chapter 3. These data were supplemented by watches made opportunistically during the course of other fieldwork routines. Observations were therefore widely spread across the study sites and through time.

Individual harriers were selected as they flew into view and observed using focal-animal sampling (Altmann 1974), until they were lost from sight or ceased foraging. Time spent in non-foraging activities, e.g. loafing, feeding, agonistic interactions, and prey transit was not recorded. However, *contra* Schipper *et al.* (1975), harriers flying at high elevations were not excluded. A tape recorder, set to run continuously for the duration of each foraging bout, was used to record observations. I used a 'continuous talk-over' technique to record the following details:

(1). Habitat over-flown by the harrier.

(2). Estimated flying height above ground, classified as <2m, 2-5m, 5.1-10m, and >10m. In post-thicket forests, where harriers were not able to fly between trees, height above the tree canopy was estimated.

(3). Flying speed, classified according to Schipper *et al.* (1975), i.e. 'slow' (ca. 20 km hr^{-1}), 'normal' (ca. 30 km hr^{-1}) and 'fast' (ca. 40 km hr^{-1}).

I was unable to reliably sex every harrier observed, due to similarities in plumage between females and one year old males. The plumage-type of each harrier observed was therefore recorded, scored as either 'brown' or 'grey', corresponding to females / first year males, and adult males, respectively. Observations were not made in conditions of poor visibility or during rain.

The reliability with which I classified harrier flying height and speed was tested in 3 habitats (heath/bog, neutral grassland and pre-thicket forest) by a second observer, linked by 2-way radio, who simultaneously tracked the same harriers from a different vantage point. We independently recorded the height and speed of specified harriers at 15 second intervals (prompted by a digital timer), following a synchronised start time.

The number of prey strike attempts and prey captures made by harriers in each habitat was recorded. Three strike methods were recognised (modified from Collopy and Bildstein 1987): pounces, touch downs (where the bird gently alights rather than pounces on the ground), and bird chases. Each strike was considered an independent capture attempt. Prey strike success was usually apparent from the harrier's subsequent behaviour, with failed capture attempts resulting in immediate resumption of foraging. In the few cases where the outcome of a prey strike was unclear, strike sites were thoroughly searched for evidence of prey capture (e.g. plucked feathers, fur and viscera). Prey remnants were collected following all successful strikes, and later identified to the lowest level possible.

Analytical procedures

Foraging behaviour was described, and relationships between flying height, flying speed and habitat explored, using data sampled at the instant harriers were initially located in each foraging bout. Foraging bouts recorded during a particular watch often related to the same harrier hunting over the same habitat. Dependency between observations was therefore checked prior to analysis by testing for randomness in the order of the records, using a one-sample runs test (Norusis / SPSS Inc. 1993).

Although both flying height and speed were measured on ordinal scales, neither the Kruskal-Wallis one-way analysis of variance nor the Jonckheere test for ordered alternatives was suitable for analysing these data. This was because the small number of categories for each behaviour resulted in a high proportion of tied observations (and, in the case of flying height, many of these ties occurred at a single value). It would be expected for this to have a large effect on the variance of the test statistic, leading to difficulties in interpreting the result (Siegel and Castellan, 1988). Accordingly, observations of flying height and speed in each habitat were compared using chi-square contingency tests. Categories of behaviour were combined, as necessary, to ensure that fewer than 20% of the expected frequencies ≤ 5.

Time spent foraging by harriers was used to calculate the frequency with which harriers made prey strike attempts and captures. Variation in strike and capture rates was analysed in relation to (1). flying height and speed, as recorded immediately prior to each strike, (2). harrier plumage-type, and (3). habitat. In each case, differences between categories were tested by calculating the number of strikes and captures per hour for each observation (i.e. per category in each foraging bout), then comparing strike/capture rates between 2 categories (or groups of categories) using a Wilcoxon-Mann-Whitney test. All probabilities quoted are for 2-tailed tests.

RESULTS

Reliability of flying height and speed classification

There was a high degree of agreement between the classifications of harrier foraging behaviour made by 2 observers (Table 1). Levels of agreement did not differ significantly between the habitats tested (flying height: $\chi^2_1 = 1.35$, $P = 0.25$; flying speed: $\chi^2_1 = 0.88$, $P = 0.40$; heath/bog and neutral grassland combined). Although consistency between observers does not necessarily mean that either has classified foraging behaviour correctly, these results are none-the-less reassuring.

Table 1: Agreement (%) between simultaneous classifications of hen harrier flying height and speed made independently by 2 observers (n = number of classifications).

Foraging behaviour	Heath/bog (n = 24)	Pre-thicket (n = 55)	Neutral grassland (n = 15)	Overall (n = 94)
Height	79%	91%	93%	88%
Speed	87%	93%	87%	90%

Foraging behaviour

Foraging harriers were seen 227 times for a total of 17.44 hours (grey birds 170 times, 13.66 hours; brown birds 57 times, 3.78 hours) during observations on 67 days and in 65 localities. Foraging bouts lasted from 0.25 mins. to 25.65 mins. (mean 2.33 mins.).

Flying height and speed

Initial location observations may have been biased toward harriers flying at greater height. This was tested using measurements of the distance at which harriers were initially located during observations of habitat use (chapter 3). There was no significant difference in the mean initial location distances (transformed to improve slight positive skewness) of harriers flying in different height categories (one way ANOVA: grey birds $F_{4,117} = 1.77$, $P = 0.139$; brown birds $F_{4,39} = 1.73$, $P = 0.164$, *ns.*). This suggests that high- and low-flying harriers were equally conspicuous.

There was a highly significant difference in the distribution of foraging observations between flying height categories (grey birds $\chi^2_3 = 209.50$, $P < 0.0001$, brown birds $\chi^2_3 = 131.83$, $P < 0.0001$). Harriers were observed most frequently at low flying elevations, and only 10% of observations were of harriers flying above 5m (Table 2). There was no significant difference in flying height between grey and brown birds ($\chi^2_2 = 2.89$, $P = 0.235$, heights above 5m combined).

Harriers were observed more frequently at 'slow' and 'normal' than 'fast' flying speeds (grey birds $\chi^2_2 = 56.34$, $P < 0.0001$, brown birds $\chi^2_2 = 24.37$, $P < 0.0001$). The flying speed of grey and brown birds did not differ significantly ($\chi^2_2 = 0.17$, $P = 0.919$). There was a positive association between flying height and speed, although this was significant only for grey birds (Goodman and Kruskal *gamma*, grey birds: $G = 0.464$, $P = 0.03$; brown birds $G = 0.602$, $P = 0.06$).

Table 2: Number and percentage of initial location observations of hen harriers foraging in various categories of flying height and speed (n = number of occurrences).

Foraging behaviour	**Grey birds** n	(%)	**Brown birds** n	(%)	**Overall** n	(%)
Flying height						
<2m	117	*(74%)*	59	*(84%)*	176	*(77%)*
2-5m	22	*(14%)*	5	*(7%)*	27	*(12%)*
5.1-10m	14	*(9%)*	1	*(1%)*	15	*(7%)*
>10m	4	*(2%)*	5	*(7%)*	9	*(4%)*
Flying speed						
Slow	75	*(48%)*	35	*(50%)*	110	*(49%)*
Normal	74	*(47%)*	31	*(44%)*	105	*(46%)*
Fast	8	*(5%)*	4	*(6%)*	12	*(5%)*
Overall	**157**	***(100%)***	**70**	***(100%)***	**227**	***(100%)***

Foraging behaviour in relation to habitat

It was predicted that harrier flying height and speed were dependent on vegetation height and density. Habitats were therefore arranged in order of increasing vegetation height and structural complexity, i.e. neutral grassland < acid grassland < heath/bog < new forest < pre-thicket forest < restock < post-thicket forest. Only 8 (3%) observations were of harriers foraging in restock habitat, and this habitat was therefore combined with pre-thicket forest. Observations in neutral grasslands were excluded from this analysis because of unrecorded changes in vegetation height during the breeding season as a result of the growth and harvest of grass for silage. To maintain adequate sample sizes, data from grey and brown birds were pooled. This was justified because the overall flying height and speed of the 2 groups were similar.

There was a highly significant difference between habitats in the proportion of harriers flying at <2m height above the ground or tree canopy (χ^2_4 = 14.37, P = 0.006). Partitioning of the χ^2 statistic revealed that the use of low flying heights differed mainly with respect to new forest (acid grassland and heath/bog : new forest, χ^2_1 = 4.17, P = 0.044; acid grassland + heath/bog + new forest : pre-thicket forest + restock, χ^2_1 = 4.91, P = 0.032) (Fig. 1).

Flying speed also differed significantly between habitats (χ^2_4 = 33.48, P = <0.0001). There were significant differences between chi-square partitions comparing acid grassland + heath/bog : new forest (χ^2_1 = 15.66, P < 0.001), acid grassland + heath/bog + new forest : pre-thicket forest + restock (χ^2_1 = 12.41, P < 0.001), and all 4 habitats : post-thicket forest (χ^2_1 = 5.25, P < 0.027). Speed differed mainly in respect of new forest, where harriers mainly flew at 'slow' speed (Fig. 2).

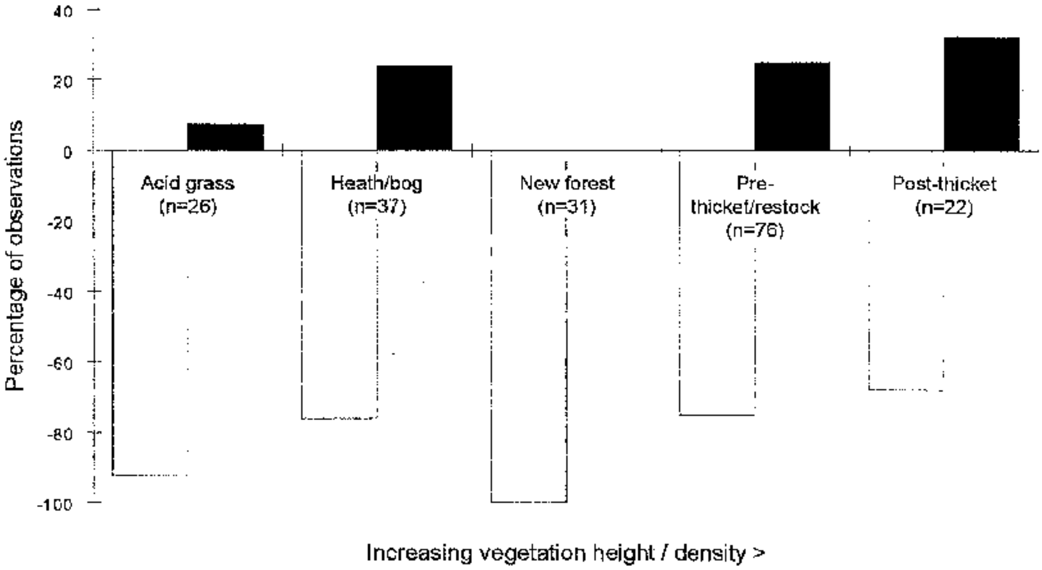

Figure 1: Hen harrier flying height in relation to habitat. The graph shows the percentage of initial location observations involving harriers flying >2m (solid bars), and <2m (open bars), above the ground. In post-thicket forests, height above the tree canopy was measured. (n = the number of observations in each habitat).

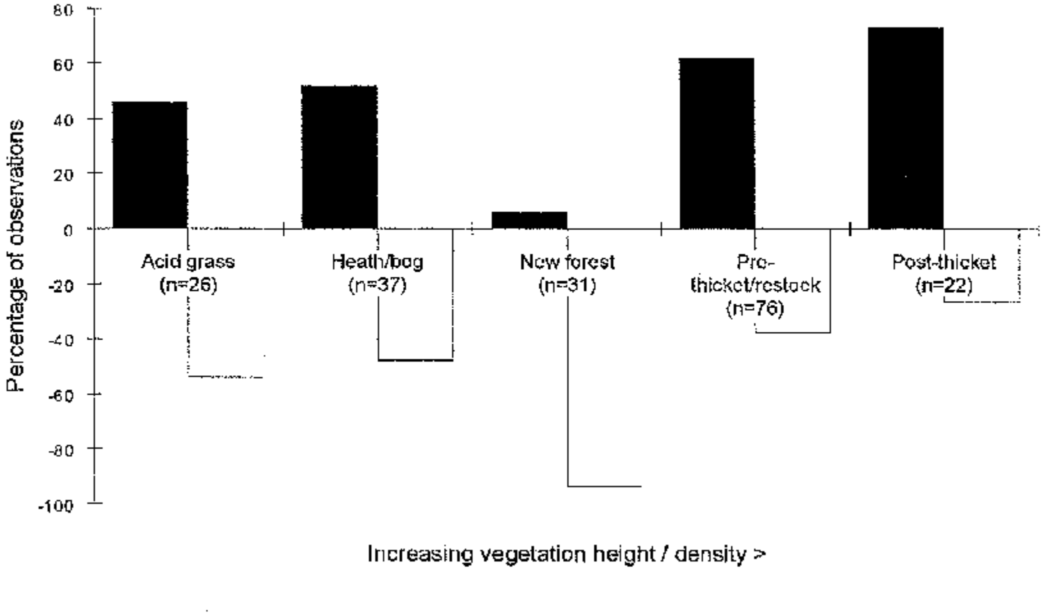

Figure 2: Harrier flying speed in relation to habitat. The graph shows the percentage of initial location observations involving harriers flying at 'fast' and 'normal' speeds (solid bars), and 'slow' speeds (open bars). (n = the number of observations in each habitat).

Foraging success

A total of 186 prey strike attempts were observed, of which 32 (17%) were successful. Captured prey included 23 passerines (72% of total), 6 field voles *Microtus agrestis*, 2 waders *Charadrii spp.*, and a single rabbit *Oryctolagus cuniculus*. Passerines were caught by both grey and brown birds, and in all habitats except restock. Most were nestlings or recently-fledged young. Meadow pipit *Anthus pratensis* was the most frequently taken species. Field voles were captured by grey birds only, in new and pre-thicket forests. The rabbit was caught by a brown bird in neutral grassland habitat.

Most (94% of total) prey strikes were pounces onto prey on the ground, 31 (18%) of which resulted in prey capture. Touch downs and bird chases were each observed on 6 (3% of total) occasions. Touch downs were made by both grey and brown birds, and involved harriers flying at slow speed less than 2m above the ground. Harriers invariably remained on the ground after touching down, sometimes for up to a minute, and looked around intently before making prey capture attempts. These typically involved pounces onto prey hidden in thick ground vegetation, accompanied by much wing-flapping. Only one touch down resulted in prey capture. Bird chases were made by grey birds only, and were initiated during fast flights less than 2m above the ground / tree canopy. No birds were captured in this way. Grey birds made more prey strike attempts and captures per hour of foraging than brown birds (Table 3). These differences were significant for strike, but not capture rate (Wilcoxon test: z = -2.66, P = 0.008 and z = -1.42, P = 0.155, respectively). There was no significant difference in prey strike success between the 2 groups ($\chi^2_1 = 0.14$, $P = 0.71$).

Table 3: Observed foraging time, number and frequency of prey strike attempts and prey captures, and prey strike success (percentage of strike attempts that resulted in prey capture) of hen harriers, grouped by plumage-type.

Plumage-type	Foraging time (hrs.)	No. of strikes	Strikes hr^{-1}	No. of captures	Captures hr^{-1}	Prey strike success (%)
Grey	13.66	157	11.49	28	2.05	18
Brown	3.78	29	7.67	4	1.06	14
Overall	17.44	186	10.66	32	1.83	17

Foraging success in relation to flying height and speed

No strike attempts were made by harriers flying >10m above the ground / tree canopy. Overall, harriers flying <2m height made prey strikes and captures less frequently than those flying at 2-10m (Table 4). These differences were tested using data from the 90 foraging bouts recorded acid grassland and heath/bog habitats, which had vegetation of similar height. This analysis showed that there was a significant difference in strike rate ($z = -2.65$, $P = 0.008$), but not capture rate ($z = -1.70$, $P = 0.089$), between the 2 height categories. There was some indication that overall strike success declined with increasing flying height (Table 4), although this was not statistically significant ($\chi^2_2 = 2.93$, $P = 0.28$).

Table 4: Observed foraging time, number and frequency of prey strike attempts and prey captures, and prey strike success of hen harriers flying in various categories of speed and height.

Foraging behaviour	**Foraging time (hrs.)**	**No. of strikes**	**Strikes hr^{-1}**	**No. of captures**	**Captures hr^{-1}**	**Prey strike success (%)**
Flying height						
<2m	11.42	87	7.62	19	1.66	22
2-5m	3.69	67	18.16	10	2.71	15
5.1-10m	1.65	32	19.39	3	1.82	9
>10m	.68	0	0	0	0	-
Flying speed						
Slow	6.28	82	13.06	17	2.71	21
Normal	9.23	65	7.04	10	1.08	15
Fast	1.93	39	20.21	5	2.59	13

Harriers made prey strikes and captures least frequently when flying at 'normal' speed (Table 4). However, within acid grassland and heath/bog habitats, this difference was not significant (strikes hr^{-1}.: $z = -0.46$, $P = 0.648$; captures hr^{-1}.: $z = -1.57$, $P = 0.116$). Overall prey strike success did not decline significantly with speed ($\chi^2_2 = 1.61$, $P = 0.47$).

Foraging success in relation to habitat

Overall, prey strikes and captures were made most frequently in new forests (Table 5). This difference was tested after first controlling for the effects of flying height by excluding data from foraging bouts in which harriers flew ≥2m above the ground. Neither strike nor capture rates differed significantly between new forest and other habitats (strikes hr^{-1}.: $z = -1.553$, $P = 0.120$; captures hr^{-1}.: $z = -1.854$, $P = 0.064$, n = 195). However, harriers flying below 2m made significantly more strikes hr^{-1} in afforested habitats than in those without trees ($z = -2.659$, $P = 0.008$, n = 195).

Table 5: Observed foraging time, number and frequency of prey strike attempts and prey captures, and prey strike success of hen harriers, grouped by habitat. With the exception of neutral grassland (see text), habitats are arranged in order of increasing vegetation height and density. Harriers were watched for only 0.32 hours in restock habitat, and this habitat was therefore combined with pre-thicket forest.

Habitat	**Foraging time (hrs.)**	**No. of strikes**	**Strikes hr^{-1}**	**No. of captures**	**Captures hr^{-1}**	**Prey strike success (%)**
Acid grass.	2.50	35	14.00	5	2.00	14
Heath/bog	3.54	26	7.34	4	1.13	15
New forest	1.85	42	22.70	5	2.70	12
Pre-thicket / Restock	5.28	51	9.66	12	2.42	23
Post-thicket	2.71	19	7.01	3	1.11	16
Neutral grassland	1.56	13	8.33	3	1.92	23

There was no significant difference in prey strike success between habitats ($\chi^2_3 = 2.64$, $P = 0.46$, post-thicket forest and neutral grassland excluded), nor was there evidence to suggest that strike success tended to vary as a result of increasing vegetation height and density. However, the sample size of capture observations in each habitat was too small for these tests to have much power.

When these data were related to foraging habitat preferences (Chapter 3), significant correlations were found between the median selection indices for each habitat and both prey strike rate and (especially) prey capture rate (Spearman rank correlation coefficients, strike rate: $r_s = 0.89$, $P = 0.019$; capture rate: $r_s = 0.94$, $P = 0.005$; $n = 6$, pre-thicket and restock forest combined) (Fig. 3). However, there was no significant correlation between habitat preference and strike success ($r_s = -0.46$, $P = 0.35$).

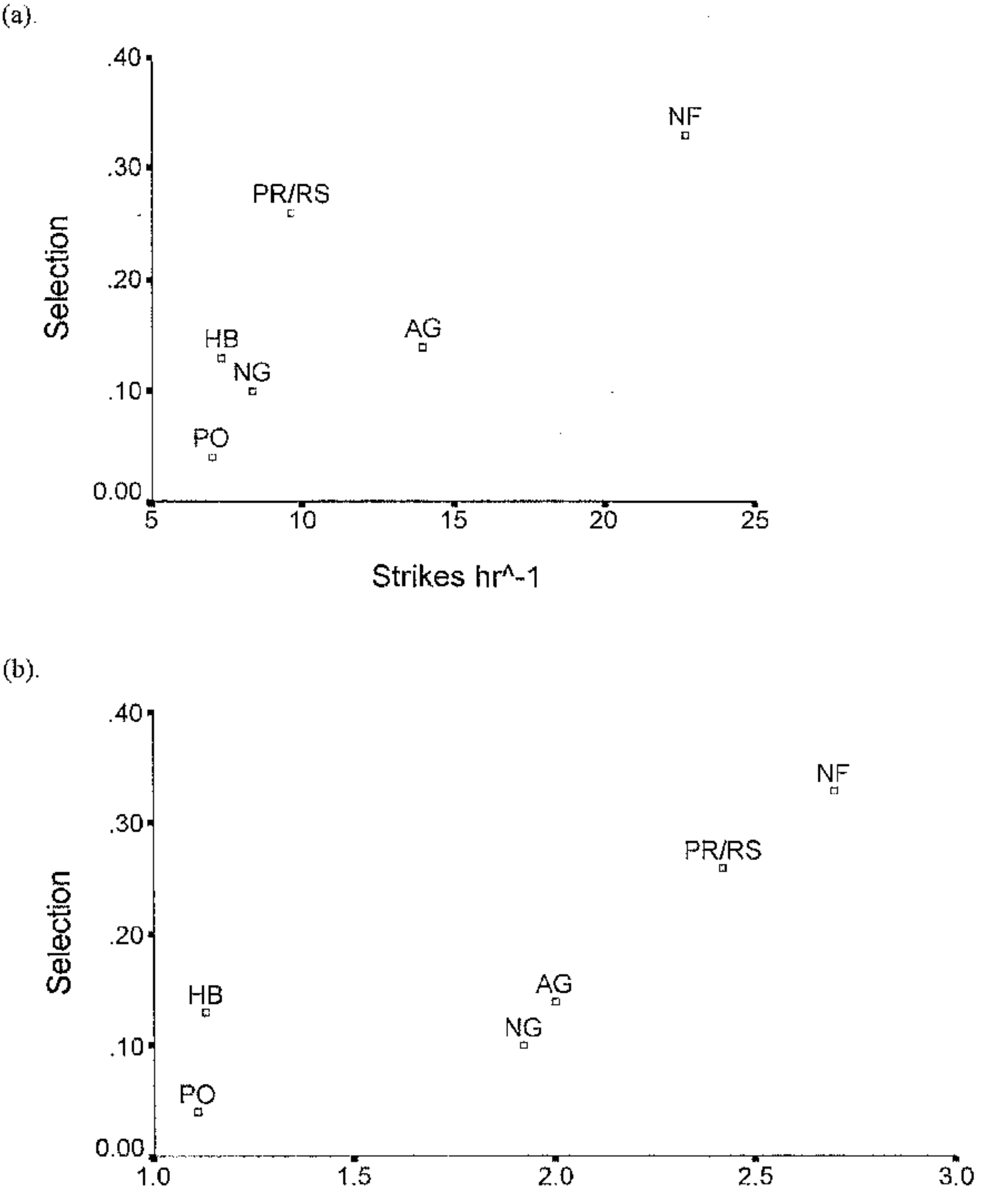

Figure 3: Relationship between habitat selection and (a). prey strike rate, and (b). prey capture rate. The graphs show the median selection index for each habitat plotted against the number of prey strikes and captures per hour of foraging. HB = heath/bog, AG = acid grassland, NG = neutral grassland, NF = new forest, PR/RS = pre-thicket + restock forest, PO = post-thicket forest.

DISCUSSION

Hen harriers breeding in Argyll mainly hunted low over the ground and avoided fast flying speeds. Low flying reduces the probability of detection by prey, but may be incompatible with fast flying speeds because it is too demanding of a harrier's manoeuvrability (Schipper *et al.* (1975). This may explain why adult male harriers used greater speed when flying at higher elevations, although it is also possible that they flew high and fast simply to move between locations in which they foraged more intensively.

The observed behaviours suggest that harriers were searching the vegetation thoroughly for prey which they expected to be able to capture without a great need for surprise. We might expect harrier foraging behaviour to be geared to capturing prey-types that occurred most frequently in their diet (searching image; see Tinbergen 1960, Croze 1970). The evidence from this study, and more detailed work carried out later (Chapter 6), was that a high proportion of the prey taken by harriers in Argyll comprised nestling and recently-fledged meadow pipits, together with smaller numbers of field voles. Both prey-types are generally well concealed in (typically rank) ground vegetation, and harriers must therefore search meticulously in order to find them. At close range (3-4m), harriers are able to locate the vocalisations of voles (Rice 1982), and this may have further encouraged low and slow foraging techniques. Young songbirds are neither highly mobile, nor well equipped to detect approaching predators (although they may be alerted by the calls of their parents), and consequently there may have been little advantage to harriers in using fast flying speeds in order to maximise the effects of surprise. If much of the prey sought by harriers was relatively easy to catch, once detected, why were more than 80% of strike attempts unsuccessful? A possible explanation is that harriers made opportunistic strikes at more mobile prey, e.g. adult songbirds. Field voles were most abundant in young plantation forests (Chapter 7), where the ground vegetation was particularly well developed. This may explain why harriers made more frequent prey strike attempts in afforested than moorland habitats.

The ease with which harriers detected prey presumably varied with the density of cover. Thus, we might expect harriers to have to search more diligently for prey in forests than open habitats. This may explain why harriers foraged at consistently low elevations and slow speeds in new forests. However, in older forests it was presumably harder for harriers to quarter the ground methodically due to the difficulty in manoeuvring between the trees, and this may be why they tended to use higher and faster flights. Although harriers generally avoided post-thicket forestry (Chapter 3), they nonetheless made prey strike attempts and captures in this habitat, indicating that it had some value to foraging birds.

Prey were captured on the ground, and were rarely pursued. It was my impression that harriers generally ignored birds flushed from the vegetation, even when these broke cover only a short distance ahead. The use of touch downs differed from that observed by Collopy and Bildstein (1987), who did not witness any subsequent hunting on the ground. However, ground hunting has been described by Geyr (1959), Wassenich (1968), Schipper *et al.* (1975) and Schipper (1977). Harriers probably hunted on the ground for prey that they had detected from the air, and which they expected to re-appear.

No prey strike attempts were made by harriers flying above 10m, suggesting that these birds were in transit rather than foraging. It is possible that harriers above 10m sometimes detected prey movements, and then investigated these more thoroughly during low level passes. Moreover, it may have been possible for harriers to see scent marks made by field voles, as has been demonstrated for kestrels *Falco tinnunculus* by Viitala *et al.* (1995). This ability would have enabled high-flying harriers to screen large areas for voles, in order to locate unusual concentrations. Below 10m, the frequency with which harriers made prey strikes increased with flying height, presumably because at higher elevations they were able to scan larger areas and therefore detect more prey. However, there was some indication that prey strike success tended to decline with height. If so, this may have been because high-flying harriers were more conspicuous to prey, which consequently had more time to escape. In addition, it may have been more difficult for high-flying harriers to assess the likelihood of strike success, leading to a higher proportion of futile attempts.

The harriers in this study used slow flying speeds significantly more than those studied by Schipper (1977) in the Netherlands and France ($\chi^2_2 = 87.88$, $P < 0.0001$ and $\chi^2_2 = 128.85$, $P < 0.0001$, respectively). This suggests that harriers in Argyll made greater use of searching, rather than prey ambush, techniques. The diversity of vegetation cover in the habitats studied by Schipper was probably similar to that in upland Argyll. However, as a result of more intensive land use, habitat patch-size is likely to have been considerably smaller, and the landscape criss-crossed by features such as dikes, ditches and field boundaries. This finer-grained habitat may have encouraged harriers to make greater use of fast flying speeds in order to ambush prey. Caution is necessary when comparing the studies, however, since both Schipper and I categorised flying speed subjectively, and it was not possible to standardise estimation techniques. Differences in recorded flying speed may therefore be an artifact of systematic errors in recording accuracy between the studies. Furthermore, 2 other species of the genus *Circus* bred within the areas studied by Schipper, and this may have encouraged hen harriers (the most agile species) to exploit niches as far removed as possible from those of the others, including the use of faster flying speeds.

Temeles (1986) observed that male harriers wintering in California foraged at fast speeds more often than females, and found that male flying speed increased with vegetation height, whereas that of females decreased. Sexual differences in the speeds of wintering hen harriers, due mainly to the use of faster speeds by high-flying males, were also reported by Schipper *et al.* (1975). However, Schipper (1977) found that flying speeds were similar in the breeding season, as was the case in the present study. Faster flying speeds might be expected of males, since they are the more agile and manoeuvrable sex (Nieboer 1973). However, it is possible that males have less need to exploit this advantage during the breeding season, when easily caught bird fledglings are abundant. In Argyll, brown birds made prey strikes less often than grey birds, suggesting that strike rate may have differed between males and females. If true, this is consistent with the conclusions of Nieboer (1973) and Schipper (1973), that females compensate for their relatively poor agility by specialising in larger and less abundant prey.

The frequency with which harriers made prey strikes is identical to that reported by Redpath (1992) for harriers foraging on heather moorland in north-east Scotland. However, 46% of the prey strikes observed by Redpath were successful, and this was significantly higher than in the present study ($\chi^2_1 = 35.28$, $P < 0.0001$). Variation in strike success would be expected if harriers hunted for different prey-types, or if prey were more vulnerable to predation in one area than the other. The diet of harriers in the 2 studies differed mainly with respect to the number of red grouse *Lagopus lagopus scoticus* taken, which in Redpath's study accounted for almost a quarter of the prey captured. However, Redpath's results do not indicate that harriers were any more successful in capturing grouse than other prey. Many of the prey attacks I observed occurred in habitats characterised by tall and dense ground vegetation, where we might expect prey to be least vulnerable to capture (Collopy & Bildstein 1987, Martin 1987). This hypothesis is not supported by the data, however, since there was no evidence that prey strike success was lower in habitats with more structurally complex ground vegetation. One explanation for the differences between the 2 studies might be that strike success was dependent on habitat heterogeneity. Thus, the harriers studied by Redpath foraged over monotypic habitat with relatively little variation in vegetation structure, whereas those in the present study foraged over a wide range of contrasting vegetation-types. Harriers in Argyll are therefore faced with a much a broader range of capture situations than those in north-east Scotland, and may consequently rely on less specialised (and by implication, less successful) strike techniques.

Preston (1990) suggested that preferences for different habitats probably reflected foraging profitability, i.e. the function of prey abundance and its vulnerability to capture. Thus, in the present study, harriers appeared to forage according to the frequency with which they captured prey. However, only a small number of prey captures were observed in each habitat, and this result must therefore be interpreted with caution. It is possible that the most profitable foraging habitats were used by the fittest harriers, in which case it is unsurprising that this resulted in relatively high capture rates in habitats such as young forests. This could be tested by examining nest site selection by wing-tagged harriers over successive years to see whether individuals breeding in areas of young forestry (a). continued to breed in the same localties as the forest matured and the habitat became less profitable, or (b). moved locality in order to maximise the availability of young forest.

The frequency with which harriers encountered prey was not directly measured (e.g. by recording the number of hesitations made whilst foraging), but this may also have had an important effect on foraging behaviour. Prey strikes are probably not a good measure of encounters, since an unknown proportion of the prey encountered may have taken cover before harriers were within striking range, and some strikes may have been 'mistakes' by harriers.

Summary

This study suggests that hen harriers mainly employed foraging techniques aimed at detecting and capturing concealed and relatively immobile prey. Flying elevation and speed varied between habitats, mainly as a result of consistently low and slow foraging techniques in new forests. Harriers only attempted to catch prey whilst flying below 10m. Strikes were more frequent, but less successful, between 2-10m height than below 2m. No sexual differences in flying height and speed were found, but adult males struck at prey more often than females and one-year old males. Comparison of the results from this study and those of Chapter 3 suggest that harriers' preference for different habitats may be explained by variation in prey capture rates.

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CHAPTER 6

DIET

Contents:

"Dis-moi ce que tu manges, et je te dirai ce que tu es."

Anthelme Brillat-Savarin 1755-1826

INTRODUCTION

Studies of hen harrier diet have been comprehensively reviewed by Watson (1977) and MacWhirter and Bildstein (1996). In Scotland, passerines (notably meadow pipit *Anthus pratensis*) appear to be the principal prey during the breeding season, although birds with nidifugous young (mainly red grouse *Lagopus lagopus scoticus*), lagomorphs, and small mammals (especially voles *Microtus spp.*) are important in some areas (Balfour and MacDonald 1970; Watson 1977; Picozzi 1978, 1980; Redpath 1991). Elsewhere, the contribution of birds and mammals to diet in the breeding season has been shown to vary both annually and geographically. Hagen (*in* Bannerman and Lodge 1956) found that voles were the single most important prey group in Norway, and formed over 95% of diet in some years. Schipper (1973) studied harrier diet over several years in the Netherlands and France and found that passerines pre-dominated in all but one area, where waders *Charadriformes* and gamebirds *Galliformes* were of equal importance. Mammalian prey comprised common voles *M. arvalis* and rabbits *Oryctolagus cuniculus*, the relative importance of which varied between study areas. In Flevoland, the Netherlands, Schipper noted a shift towards voles when these were numerous. Craighead and Craighead (1956) showed that meadow mice *M. pennsylvanicus* were the main prey of harriers in Michigan, whilst Randall (1940) found juvenile birds to be the most important items in Pennsylvania. Similarly, Errington and Breckenridge (1936) reported that harriers in Wisconsin took mainly mammals (especially ground squirrels *Citellus spp.* and young cotton-tail rabbits *Sylvilagus spp.*), whilst those in Iowa took more or less equal numbers of birds and mammals. MacWhirter (1985) found that harriers in New Brunswick, took greater numbers of passerines in years of low vole abundance.

The objectives of the current study were to (1). describe the range of prey taken by hen harriers in Argyll during the breeding season, (2). determine the relative importance of the main prey-types, and (3). investigate variation in diet in relation to study sites and years.

Several approaches are available to researchers wishing to study avian diet (see Rosenberg and Cooper 1990 for a review). Raptor diets have generally been investigated by (1). analysis of pellets of indigestible matter periodically regurgitated by raptors (e.g. Errington 1930), (2). identification of uneaten prey remnants (e.g. Newton and Marquiss 1982), and (3). direct observations of prey captured or delivered to nests (e.g. Collopy

1983). Direct observations have been shown to be the most reliable of these methods (Marti 1987), despite some bias towards larger, more identifiable prey (Newton 1986, Sonerud 1989). However, they are also the most time consuming, particularly if data are collected from foraging birds. For example, during 600 hours of observation in the present study I recorded less than 12 hours of foraging activity by harriers and only 32 prey captures (Chapter 3). Observations of prey deliveries to nestlings are more time-efficient, but logistical constraints generally mean that diet can only be sampled at a few nests.

In contrast to direct observations, collections of pellets and prey remains allow the diet of a large number of individuals / nests to be sampled simply and quickly. Both methods suffer from potentially serious biases, however. Some prey may be poorly represented in pellets because they do not survive the pellet forming process well (see Short and Drew 1962). Frogs *Rana temporaria*, for example, are usually completely digested by harriers and traces are therefore seldom found in pellets (Schipper 1973). Pellets regurgitated by harriers contain few bones (Craighead and Craighead 1956) and prey are generally represented only by fur and fragments of feathers. It is therefore both tedious and difficult to identify prey, and impossible to enumerate individual items. Furthermore, estimating the proportions of each prey class in the diet is complicated by the possibility that some items are represented in more than one pellet (Craighead and Craighead 1956, Smith and Richmond 1972, Lowe 1980). This may be a result of prey items, especially if large, appearing in 2 or more pellets produced by the same harrier or, in the case of pellets collected from nests, by 2 or more siblings that have shared the item. Finally, once egested, pellets which are loosely formed (e.g. those comprising feathers), may deteriorate more rapidly than those in which the remains are compacted (such as those composed of mammalian fur), resulting in a greater numbers of the latter being collected (Schipper 1973).

Similarly, larger prey are likely to be over-represented in skeletal remains because the bodies of most small prey are wholly consumed (Tinbergen 1946, Newton 1986). In addition, some prey remains may deteriorate more rapidly than others. Newton and Marquiss (1982), for example, found that very small species seemed to be under-represented in the older prey pluckings of Sparrowhawk *Accipiter nisus*.

Simmons *et al.* (1991), studying the diet of African marsh harrier *Circus ranivorus*, found that biases in pellets and prey remains followed opposite trends and that an accurate estimate of overall diet could be achieved by combining results from the 2 methods. This approach was also adopted by Arroyo (1995) in her study of the diet of

Montagu's harrier *Circus pygargus*. The sources of bias are different for the 2 techniques, however, and it is difficult to see how combining estimates from each can increase reliability. Accordingly, in the present study, I analysed pellets and prey remains separately, and used periodic direct observations to correct for biases in prey representation.

METHODS

Prey remains and pellets were collected from harrier nests in each study site in each year. Direct observations of chick provisioning were made at 4 nests, located in Kintyre (1992), Islay (1993) and Cowal and Lorn (1994).

Pellets and prey remains

At least 30 harrier nests (and perching posts nearby) were searched annually for pellets and prey remains during visits to monitor breeding success (see Chapter 8). Intact or partially eaten prey were identified *in situ*, and not collected. Care was taken not to record these items on subsequent visits. No attempt was made to distinguish between pellets produced by adult and young harriers.

Identification of prey fragments within pellets was undertaken by R. Clarke. Pellets were dissected and prey parts washed and dried. Avian prey were identified mainly from feather remains, with assistance from bone and bill parts, matched to a reference collection. Where necessary, feathers were identified using x125 magnification of the downy barbules, using the key devised by Brom (1986). Mammalian prey were identified from teeth (using the key by Yalden and Morris, 1990), and x125 magnification of guard hair outlines (shrews) and medullae (lagomorphs and rodents) using a reference collection and the key by Teerink (1991). However, it was not possible to discriminate between lagomorph species, owing to similarities in medullar patterns. Prey were identified to the lowest level possible. Data from invertebrate species were excluded, since it was assumed that these were present in the crops of prey, or had entered pellets after egestion. Even had this not been the case, their contribution to diet would have been negligible.

Skeletal prey remains and pluckings generally presented few difficulties in identification. Where necessary, reference was made to Lawrence and Brown (1967) and Brown *et al.* (1987).

Direct observations

Observations were made from hides placed 5-10 m. from harrier nests. Prey provisioning rate varies according to the number of chicks in the nest and increases with chick age (Redpath & Thirgood *in prep.*). In order to improve the efficiency of watches, and help control for possible variation in prey as a result of differences in chick age or brood size, nests were selected that contained 3-4 chicks of at least 21 days age. Within these constraints, nests were chosen from as wide a range of habitats as possible. All 4 selected nests were the result of monogamous pairings. Nests were watched from 0600 hours until 2100 hours on consecutive days until at least 50 identifiable prey items had been recorded. Seven prey-types were distinguished: (1). passerines, (2). waders and gamebirds, (3). other birds, (4). lagomorphs, (5). small mammals, (6). reptiles and amphibians, and (7). unidentified items. Nest observations were carried out by experienced birdwatchers, each given similar training in prey recognition.

Pellets and prey remains were cleared from nests prior to the start of the first watch, and then collected at the end of each day's observations. It was accepted that not every pellet or prey remnant was found, either because they had disintegrated as a result of the effects of rain and trampling by chicks, or because they had been removed by the breeding female and could not be located. However, collection efficiency was similar to that used more generally.

Analytical procedures

Non-parametric statistical tests were used throughout. Diet composition in different study sites and years was compared using chi-squared contingency tests. Expected frequencies were examined to check that fewer than 20% were less than 5. When the obtained value for χ^2 was significant, contingency tables were partitioned to help determine the location of differences. Since there was no obvious *a priori* way of ordering partitions, the significance of each was tested *a posteriori*, using a critical value for χ^2 based on $\alpha = 0.05$ divided by the number of partitions (see Seigel and Castellan 1988). Partitioning was complemented by analysing the residuals (i.e. the discrepancies between observed and expected values) in order to determine which were larger than expected by chance.

RESULTS

A total of 497 pellets were collected and 76 prey remains identified. Few pellets or prey remains were found prior to hatching, and most (96% and 84%, respectively) were found when the young were >15 days old. Pellets and remains occurred at a similar number of nests (35 and 32, respectively), but pellets were found during a greater number nest visits (116 compared with 51).

Each pellet contained between one and 6 prey species (mean = 1.99). In total, 31 bird and 6 mammal species were identified. In 92 (18%) pellets it was not possible to identify the remains of all bird species present, due to severe deterioration in feather parts. However, in all but 30 (6% of total) cases, prey were identified to order level. Eight (2%) pellets contained small mammal remains that could be identified only to order level, whilst 4 (1%) contained small mammals, represented by underfur only, which were impossible to further classify. Of the prey identified to species level, 49% of passerines were meadow pipits and 80% of small mammals were field voles.

Twelve bird and 3 mammal species were identified from prey remains. Of these, 7 meadow pipits or skylarks (9% of total) , a gamebird and a lagomorph (1% each of total) could not be further classified.

Range of prey taken

Data from each study site and year were pooled to describe the overall range of prey taken. Passerines, waders and gamebirds, lagomorphs, and small mammals together accounted for 95% of prey occurrences in pellets, and 96% of prey remains (Table 1). A wider range of species were sampled by pellets than prey remains. Despite this, 5 species (including 11 red grouse) were represented by prey remains but not in pellets. Weights of individual prey were estimated to range from 9-400g.

Table 1: Frequency with which prey occurred in 497 pellets and 76 prey remains found at hen harrier nest sites 1992-94. The estimated mean weight of each prey class is shown.

	Frequency in		Mean
	Pellets	Remains	weight*(g)
Birds			
Passerines			
Meadow pipit *Anthus pratensis*	300	28	20
Stonechat *Saxicola torquata*	47	2	15
Song thrush *Turdus philomelos*	39	1	76
Unidentified songbirds *Passeriformes*	39	0	20
Skylark *Alauda arvensis*	34	2	40
Wren *Troglodytes troglodytes*	30	0	9
Wheatear *Oenanthe oenanthe*	18	0	25
Starling *Sturnus vulgaris*	15	0	75
Siskin *Carduelis spinus*	13	2	15
Grasshopper warbler *Locustella naevia*	11	0	13
Reed bunting *Emberiza schoeniclus*	11	0	18
Whinchat *Saxicola rubetra*	9	2	15
Pied wagtail *Motacilla alba*	8	0	18
Whitethroat *Sylvia communis*	6	0	16
Robin *Erithacus rubecula*	5	0	19
Mistle thrush *Turdus viscivorus*	4	1	130
Unidentified tits *Parid spp.*	4	0	15
Blue tit *Parus caeruleus*	3	0	13
Chaffinch *Fringilla coelebs*	3	0	20
Linnet *Carduelis cannabina*	3	0	15
Redpoll *Carduelis flammea*	3	0	12
Dunnock *Prunella modularis*	2	0	21
Greenfinch *Carduelis chloris*	2	0	28
Blackbird *Turdus merula*	1	0	95
Bullfinch *Pyrrhula pyrrhula*	1	0	22
Great tit *Parus major*	1	0	19
Twite *Carduelis flavirostris*	1	0	15
Unidentified chats *Saxicola spp.*	1	0	15

Table 1, cont'.

	Frequency in		Mean
	Pellets	**Remains**	**weight*(g)**
Willow warbler *Phylloscopus trochilus*	1	0	9
Meadow pipit / skylark	0	7	30
Waders & gamebirds			
Unidentified *Charadrii spp.*	12	0	100
Unidentified *Tetraonid & Phasianid spp.*	7	1	180
Snipe *Gallinago gallinago*	2	0	60
Curlew *Numenius arquata*	1	0	150
Pheasant *Phasianus colchicus*	1	1	180
Redshank *Tringa totanus*	1	0	65
Red grouse *Lagopus lagopus*	0	11	180
Lapwing *Vanellus vanellus*	0	1	105
Other birds			
Unidentified birds	30	0	20
Cuckoo *Cuculus canorus*	12	0	114
Water rail *Rallus aquaticus*	0	1	110
Feral pigeon *Columba livia*	0	1	300
Mammals			
Lagomorphs			
Unidentified *Lagomorph spp.*	92	1	225
Rabbit *Oryctolagus cuniculus*	0	4	150
Unidentified hares *Lepus spp.*	0	2	300
Small mammals			
Field vole *Mictotus agrestis*	153	6	25
Common rat *Rattus norvegicus*	12	1	100
Unidentified shrews *Sorex spp.*	8	0	10
Common shrew *Sorex araneus*	6	0	10
Bank vole *Clethrionomys glareolus*	5	0	10
Unidentified small mammals	4	0	20
Pygmy shrew *Sorex minutus*	1	0	10
Wood mouse *Apodemus sylvaticus*	1	0	20

Table 1, cont'.	Frequency in		Mean
	Pellets	**Remains**	**weight*(g)**
Reptiles / Amphibians			
Unidentified lizards *Lacerta spp.*	10	0	10
Common frog *Rana temporaria*	0	1	20
TOTALS	**973**	**76**	

* Taken from Cramp & Simmons (1982), Underhill-Day (1985), Dunning (1993), Picozzi (1978) and Schipper (1973). Weights of waders, gamebirds and lagomorphs are based on the estimated size classes taken by harriers.

Biases in pellet and prey remains data

A total of 247 prey deliveries were observed during nest watches. Of these, 36 (15%) items could not be classified and were therefore excluded from analysis. These were invariably small items which were rapidly eaten. A total of 84 pellets and 26 prey remains were collected concurrent with nest observations. All species identified by direct observation were also recorded in pellets, but 3 species did not feature as prey remains: willow warbler, a shrew *spp.*, and wood mouse.

Table 2: Observed prey deliveries, pellets collected and prey remnants identified at 4 hen harrier nests, 1992-4.

Nest	Study site	Year	No. of prey deliveries*	No. of pellets	No. of prey remains
1	Kintyre	1992	52	20	9
2	Islay	1993	55	24	5
3	Cowal	1994	54	21	6
4	Lorn	1994	50	19	6
	TOTALS		**211**	**84**	**26**

* excluding unidentified prey.

The sample size of pellets and prey remains from each nest was rather small, and data from all 4 nests were therefore pooled. A potential problem of this approach is that variation in the numbers of pellets and remains collected at each nest may bias the way in which prey are represented. For example, small mammals might feature highly in pellets simply because most pellets came from a nest where small mammals were the main prey. In fact, the sample size of pellets varied little between nests (Table 2) and bias due to combining the data is therefore likely to be minor. However, the number of prey remains collected fluctuated more widely between nests, and caution is therefore required when interpreting the relationship between prey deliveries and remains.

Pellet and prey remains data were collapsed into the same prey-type categories used for direct observations, and the percentage occurrence of each prey-type calculated. When the percentages of each prey-type recorded by pellet analysis were compared with those determined from direct observations, the 2 methods were found to give similar results for passerines. However, pellets grossly over-estimated lagomorphs, and under-estimated waders and gamebirds, and small mammals (Table 3). Likewise, prey remains grossly over-estimated lagomorphs and waders and gamebirds, and under-estimated passerines and small mammals. There was no statistically significant agreement between the 3 methods of estimating diet (Kendall coefficient of concordance, W = 0.724, df 3, P = 0.09).

Table 3: Comparison of 3 methods of determining hen harrier diet. The contribution of the 4 main prey-types is shown. Data are pooled from 4 nests. Observations of prey deliveries and collections of pellets and prey remains were made concurrently.

Prey-type	Direct observations (n = 211)	Pellets (n = 215) *	Prey remains (n = 26)
Passerines	65%	68%	48%
Waders & gamebirds	9%	4%	30%
Lagomorphs	3%	11%	11%
Small mammals	22%	17%	11%

* Number of occurrences in 84 pellets.

Age of prey taken

Of the bird prey remains that could be aged, 20/24 (83%) passerines and 6/9 (67%) waders and gamebirds were juveniles. All young passerines were more or less fully grown, whereas young waders and gamebirds ranged in size from 1/4 to 3/4 grown. Based on measurements of hind feet, 5/6 (83%) lagomorphs found as prey remains were juveniles, ranging in size from 1/2 to nearly full grown. Of the prey recorded by direct observation that could be aged, 60/72 (83%) passerines were more or less fully grown juveniles, and all waders, gamebirds and lagomorphs were part-grown young (n = 13).

Contribution of main prey-types to diet

Pellets were more consistently available than prey remains and consequently sampled diet more thoroughly. They were therefore used to estimate the overall contribution of the 4 main prey-types, and to investigate spatial and temporal variation in diet. To correct for biases in prey representation, the frequency with which each prey-type occurred in pellets was adjusted to a predicted direct observation value by multiplying by a correction factor. These factors were calculated from Table 3, by dividing the percentage of occurrences according to direct observations by those derived from pellets.

Passerines were the most frequently taken prey-type, accounting for 65% of overall items. These were followed by small mammals (26%), waders and gamebirds (6%), and lagomorphs (3%). In order to evaluate the relative contribution of prey-types in terms of biomass, the occurrence of each component species and prey class was multiplied by the estimated mean weight of an individual of that species / class (see Table 1). These data were then re-grouped into the 4 main prey-types and the proportion of biomass contributed by each calculated and adjusted for detection bias. Prey weights of waders, gamebirds and lagomorphs were based on the estimated size classes taken (see above). This analysis showed that passerines accounted for 43% of prey by weight, small mammals 19%, waders and gamebirds 19%, and lagomorphs 18%.

Variation in diet between study sites

Few pellets were collected in Kintyre because of the small number of harrier nesting attempts. Data from this study site were therefore excluded from analysis. To maintain adequate sample sizes in statistical tests, prey weighing ≥60g (i.e. lagomorphs, waders and gamebirds) were combined to form a single group, termed 'large prey'.

Within each site, the contribution to diet of each prey-type varied between years (Table 4). Dietary differences between study sites were therefore investigated year by year. The distribution of large prey, passerine, and small mammal occurrences differed significantly between sites in 1992 and 1994 ($\chi^2_4 = 12.06$, $P = 0.02$ and $\chi^2_4 = 42.52$, $P < 0.00001$, respectively), but not 1993 ($\chi^2_4 = 8.16$, $P = 0.09$, *ns*). Data from 1992 and 1994 were further analysed, using partitioning procedures and examination of the standardised residuals, in order to determine the loci of the differences. A significance level of $\alpha = 0.01$ was used to test partition χ^2 values.

Table 4: Percentages of large prey, passerine, and small mammal prey occurrences in pellets (adjusted for detection biases) within each study site, grouped by year. (n = total number of prey occurences).

Year	Study site	n	Prey-type (%)		
			'Large'	Passerine	Small mammal
1992	**Cowal**	82	2.4	72.0	25.6
	Islay	58	8.6	56.9	34.5
	Lorn	120	6.7	78.3	15.0
1993	**Cowal**	91	9.9	70.3	19.8
	Islay	202	10.4	76.7	12.9
	Lorn	34	0	73.5	26.5
1994	**Cowal**	112	6.3	42.0	51.8
	Islay	92	21.7	63.0	15.2
	Lorn	69	5.8	36.2	58.0

In 1992, the occurrence of small mammals relative to other prey differed significantly between Lorn and non-Lorn sites ($\chi^2_1 = 7.52$, $P < 0.01$), with fewer small mammals taken in Lorn. Similarly, small mammal occurrence in 1994 differed significantly between Cowal and Islay ($\chi^2_1 = 26.47$, $P < 0.001$). When Cowal and Islay data were pooled and compared with Lorn, this difference remained significant ($\chi^2_1 = 11.60$, $P < 0.001$). Analysis of the residuals revealed that the observed value for small mammals in Islay 1994 was significantly less than that expected ($z = -4.1$, $P < 0.0001$), whereas the observed value for large prey in Islay 1994 was significantly greater than expected by chance ($z = 3.4$, $P < 0.001$).

This analysis indicates that diet differed significantly between sites in 2 out of the 3 years of study. The difference was greatest in 1994, when harriers in Islay took proportionately more large prey, and proportionately fewer small mammals, than harriers in other study sites.

Large differences were apparent in the estimated contribution by weight of each prey-type between study sites in all 3 years (Fig. 1). In 1992, these differences were due mainly to harriers in Cowal and Islay eating proportionately more lagomorphs, and fewer waders and gamebirds, than those in Lorn. Passerines contributed more to dietary biomass in Cowal and Lorn than in Islay, where lagomorphs predominated. In 1993, passerines were the most important prey-type in all 3 sites. However, lagomorphs, waders and gamebirds formed over 40% of dietary biomass in Cowal and Islay, yet were absent from the diet of harriers in Lorn. In 1994, small mammals predominated in Cowal and Lorn, but accounted for less than 10% of overall biomass in Islay, where lagomorphs, waders and gamebirds were the most important prey. In all 3 years, harriers consumed more lagomorph biomass in Islay than other sites.

Variation in diet between years

Annual differences in diet composition were investigated within each study site. There was a significant difference in the distribution of large prey, passerine, and small mammal occurrences between years within each site (Cowal: $\chi^2_4 = 31.00$, $P = <0.00001$; Islay: $\chi^2_4 = 23.24$, $P <0.001$; Lorn: $\chi^2_4 = 41.84$, $P = 0.00001$).

Partitioning procedures indicated that the distribution of prey occurrences in Cowal was similar between 1992 and 1993. However, 1994 differed significantly from other years with respect to the occurrence of small mammals relative to other prey ($\chi^2_1 = 25.89$, $P <0.001$). Analysis of the residuals showed that the observed value for small mammals in 1994 was significantly greater than expected by chance ($z = 3.2$, $P <0.01$), whereas that for passerines in 1994 was significantly less ($z = -2.4$, $P <0.05$).

In Islay, prey occurrences differed significantly between all 3 years. When 1992 and 1993 were compared, the occurrence of small mammals relative to other prey differed significantly ($\chi^2_1 = 14.88$, $P < 0.001$), with more small mammals than expected being taken in 1992 ($z = 3.2$, $P <0.01$). When 1992 and 1993 were pooled and compared with 1994, the relationship between large prey and passerines differed significantly ($\chi^2_1 = 7.95$, $P <0.01$), with more large prey than expected being taken in 1994 ($z = 2.3$, $P < 0.05$).

In Lorn, prey distributions were similar between 1992 and 1993. However, when 1992 and 1993 were pooled and compared with 1994, the occurrence of small mammals relative to other prey differed significantly ($\chi^2_1 = 37.07$ $P < 0.001$). The observed value for small mammals in 1994 was significantly greater than expected ($z = 4.2$, $P <0.0001$), whereas that for passerines in 1994 was significantly less ($z = -2.9$, $P <0.01$).

This analysis shows that harrier diet differed significantly between years in the 3 study sites tested. Differences were greatest in Cowal and Lorn, where harriers took a higher proportion of small mammals and a lower proportion of passerines in 1994 than in other years. Islay was the only study site where passerines comprised a larger proportion of diet than small mammals in all 3 years. Harriers in Islay took more small mammals in 1992, and more large prey in 1994, than in other years.

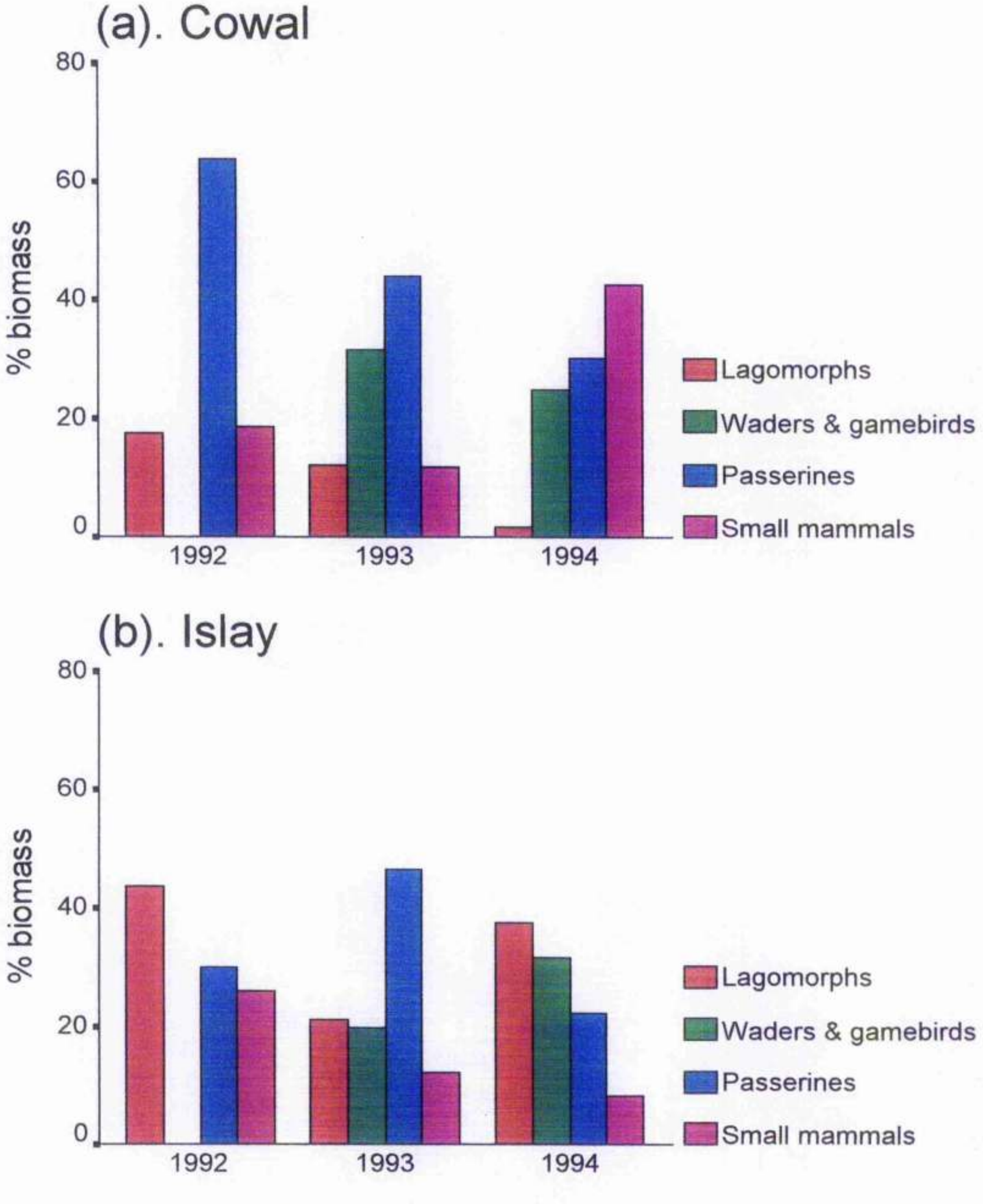

Figure 1: Relative importance to hen harrier diet of the 4 main prey-types in terms of weight. The graphs show the contribution of each prey-type as a percentage of the combined biomass within each year for (a). Cowal and (b). Islay.

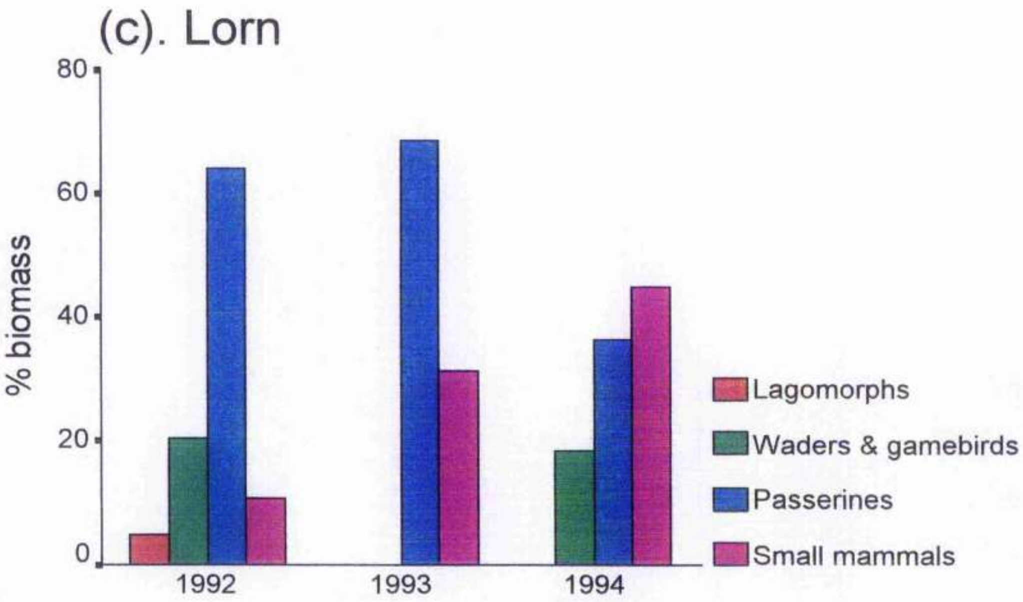

Figure 1 (c).: Relative importance to hen harrier diet of the 4 main prey-types in terms of weight. The graph shows the contribution of each prey-type as a percentage of the combined biomass within each year for Lorn.

Diet composition by weight appeared to vary between years in all 3 sites (Fig. 1). Small mammals contributed more to dietary biomass in 1994 than other years in Cowal and Lorn, but not Islay. Passerines contributed less in 1994 than other years in all 3 sites, but especially Cowal and Lorn. In Cowal and Islay, waders and gamebirds were important in 1993 and 1994 but not in 1992, whilst the opposite was true in Lorn. Lagomorphs were important in all 3 years in Islay, whereas their contribution varied between years in Cowal and Lorn.

DISCUSSION

Evaluation of analysis

The data were biased towards prey delivered to nests during the later stages of the harrier breeding period. This may have over-emphasised the importance of passerine prey, many of which were at least partially migratory and therefore likely to be scarce in the uplands early in the season. Prey sampling during harrier courtship and the incubation and close-brooding periods could have been improved by collecting a greater number of pellets from locations other than nests. One method of increasing the efficiency of these collections would have been to provide territorial harriers with perch posts fitted with wire baskets to catch regurgitated material (e.g. Simmons *et al.* 1991). I was reluctant to adopt this approach because the posts might have been used as vantage points by potential nest predators, such as hooded crow *Corvus corone* and raven *Corvus corax*.

It was not possible to discriminate prey taken by male and female harriers. Adult females are largely nest-bound until ca. 15 days after hatch, and the period that they were most active therefore coincided with the period in which most pellets were collected. Although females caught prey less often than males (Chapter 5), they are capable of taking larger items (Schipper 1973). Consequently, they may have contributed disproportionately to prey biomass in areas where large prey were available.

It is possible that the prey delivered to nestlings was not representative of overall harrier diet. For example, foraging constraints may have caused harriers not to take all of the largest or smallest prey back to nests (Simmons *et al.* 1986). However, a wide range of prey sizes were delivered to nests, and both the largest and smallest prey captured during observations of foraging birds (rabbit, ca. 150g, and willow warbler, ca. 9g, respectively; Chapter 5) were transported towards harrier nests. These observations suggest that bias as a result of some prey being caught and eaten *in situ* is unlikely to be serious.

The proportion of prey uneaten by harriers, such as large bones, tends to increase with prey size. No attempt was made to correct for this in calculations of biomass, and it is accepted that the importance of larger prey may therefore have been over-estimated.

It is recognised that the application of a factor to correct for bias in the way prey was represented in pellets also affects the sample size of observations, and that this change will have influenced the chi-square statistic used to test variation in diet. The problem is most serious in cases where a correction factor greater than one has been used (i.e. wader / gamebird and small mammal prey categories), since this will have inflated the significance of the test result. A better approach would have been to test for differences in diet between study sites and years using the uncorrected data, assuming bias in the way prey are represented in pellets to be similar in each site and year, and then assess diet corrected for bias. Confidence intervals surrounding each estimate of diet would have given a useful indication of the accuracy of the adjusted figures.

Bias in pellets and prey remains

Pellets and prey remains estimated the numbers of passerines and small mammals recorded by direct observation more accurately than they did larger prey. As expected, prey remains greatly over-estimated large prey, presumably because they were less likely to be entirely consumed. It was also predicted that large prey would be over-estimated in pellets, since they were more likely to be consumed by more than one harrier, and by each harrier more than once. However, whilst this was true of lagomorphs, waders and gamebirds were under-estimated by pellets. Although unexpected, this is consistent with the findings of Simmons *et al.* (1991), who found that large avian species were more likely occur as prey remains than in pellets.

Contra Simmons *et al.*, biases in pellet and prey remain data did not follow opposite trends. However, the current study collected a smaller proportion of pellets and remains from adult harriers, and this may have affected both the magnitude and direction of the various biases.

Diet composition

Harriers hunted virtually all of the common species of suitable size present in the study area (see Chapter 7), and many of the less common ones (e.g. linnet, greenfinch, water rail, bank vole and pygmy shrew). Young birds featured strongly in harrier diet, presumably because they were abundant and less able to evade capture than adults. They also have relatively high fat reserves (Welty 1975), making them particularly rewarding prey. Most lagomorphs taken were also juvenile. Large prey are energetically costly to transport, and harriers may therefore have found it more efficient to capture part-grown individuals.

Variation in diet between study sites presumably reflected differences in prey availability. Thus, large prey may have featured more in the diet of harriers in Islay than elsewhere because lagomorphs were relatively abundant (Chapter 7). This is consistent with the greater preference for neutral grasslands (where most lagomorphs were observed) in Islay than elsewhere (Chapter 3). Marquiss (1980) found that lagomorphs comprised 54% of prey items in pellets collected from a winter roost in Islay, compared with only 13% in pellets collected from mainland Scotland. Based on counts of grey- and brown-plumaged birds at the roost sites, he suggested that greater numbers of lagomorphs were taken on Islay because the wintering harrier population comprised mainly females, and these hunted in habitats where large prey were most available. However, sex ratio bias does not explain the differences observed in the current study, as there is no reason to expect that Islay females provisioned nests more than those on the mainland.

Harrier diet varied between years mainly as a result of differences in the contribution of small mammals. Populations of field voles, the principal small mammal taken, oscillate synchronously over large areas on a broad 3-4 year cycle (Middleton 1930, Elton 1942), leading to large differences in their abundance between harrier breeding seasons. Thus, in the present study, voles were less abundant in 1992 than 1993-94 (Chapter 7), and this may explain much of the variation in the contribution of small mammals to harrier diet. The importance of small mammals to harrier diet increased mainly at the expense of passerines. This shift is consistent with the assertion by Korpimaki (1984) and others that voles are a highly profitable prey species in energetic terms.

Comparison with studies elsewhere in Britain

Watson (1977) found that hen harriers breeding in mixed moorland and forest habitats in south-west Scotland took mainly avian prey. The majority of these were passerines, although many grouse were also taken. The only mammal of significance were field voles, which accounted for less than 10% of overall prey. Harriers breeding on heather moorland managed for red grouse in north-eastern Scotland also fed mainly on birds, of which 56% were passerines (notably meadow pipit) and the remainder mostly red grouse (Picozzi, 1978). About 13% of overall prey were mammals, comprising mainly mountain hares *Lepus timidus* and rabbits. In Orkney, Balfour and MacDonald (1970) studied harrier diet at a single nest and found that similar proportions of birds (mainly passerines) and mammals (mainly Orkney voles *M. arvalis orcadensis* and rabbit) were taken. However, in a more comprehensive study, Picozzi (1980) found that bird prey predominated. Most of the birds taken were passerines, especially meadow pipit and starling, whilst most mammalian prey were young rabbits.

The present study recorded a similar range of bird species to Watson, but a more diverse range of both large and small mammals. Red grouse were considerably less important than in other mainland studies. This is unsurprising in view of the species' scarcity in west Scotland, due largely to the absence of suitable heather management. Lagomorphs contributed more to harrier diet in Argyll than in south-west Scotland, but were less important than in the north-east Scottish mainland and Orkney. High levels of polygyny in Orkney (Balfour and Cadbury 1979; Picozzi 1984) mean that females must provide a larger proportion of nestling food than elsewhere, and this may explain why greater numbers of these large prey were taken. Overall, field voles appear to contribute more to the diet of harriers in Argyll than elsewhere in Scotland.

Conclusions

Hen harriers breeding in Argyll predated a wide range of bird and mammal species. Passerines were the largest single prey group, and accounted for 65% of overall prey by number and 43% by weight. However, in some sites and years small mammals comprised over 50% of prey by number and more than 40% by weight. Meadow pipit were by far the most numerous species taken, and accounted for 49% of passerine prey. Field vole were second most numerous, and comprised 80% of small mammal prey. The proportion of small mammals taken increased mainly at the expense of passerine prey. This suggests that although harriers mostly ate meadow pipits, they may have preferred field voles.

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CHAPTER 7

FORAGING EFFORT IN RELATION TO PREY ABUNDANCE

Contents:

"Seeing is deceiving. It's eating that's believing."

James Thurber (1956) Further fables for our time

INTRODUCTION

The availability of prey is one of the most important biological parameters that affect the behaviour of animals. Steenhof and Kochert (1988) found that diet in 3 species of raptor was related only to the density of preferred prey. However, Preston (1990) argued that raptors respond to variation in foraging profitability, i.e. the interaction between prey abundance and its vulnerability to capture. Thus, birds may forage selectively in habitats that hold populations of suitable prey which they are able to detect and surprise with relative ease.

Hen harriers breeding in Argyll forage preferentially in young first rotation coniferous forests, where they search the relatively dense ground vegetation between the trees (Chapters 3 and 4). A wide range of prey is taken, including passerines, waders and gamebirds, lagomorphs, and small mammals. Two species predominate: meadow pipit *Anthus pratensis* (mainly taken as nestlings and recently fledged young) and field vole *Microtus agrestis* (Chapter 6). Prey abundance can be expected to vary between habitats, and the relationships between harrier foraging activity, habitat and prey are therefore likely to be complex. Furthermore, prey availability may vary over time. For example, field voles are subject to cyclical and synchronous population fluctuations (Charles 1981), with highs occurring about every 3 years in west Scotland (Taylor *et al.* 1988). Numbers of meadow pipit are more stable from year to year, although numbers may vary seasonally (Thirgood *et al.* 1995). We might expect such temporal variations in prey to have an important effect on harrier foraging behaviour.

The aims of the present study were to (1). estimate the abundance of usable food resources available to harriers, (2). investigate spatial and temporal variation in the abundance of harriers' principal prey, (3). relate harrier foraging activity to indices of prey abundance, and investigate the effects of vegetation structure on this relationship.

METHODS

Estimates of abundance were determined for birds and various species of mammal in each of the 1x1km squares used for observations of harrier foraging activity. Details of square selection are given in Chapter 3. Within each square, prey and foraging activity were assessed in the same year.

Avian prey abundance

Several different approaches are available to researchers wishing to estimate bird abundance (see Ralph and Scott 1981, Verner 1985 and Bibby *et al.* 1992 for reviews). In the present study, it was important to gather information on a wide range of species within a relatively large area (13-14 1x1km squares) each year. Techniques involving territory mapping were therefore inappropriate, since they are very time consuming and their main advantage, that of providing data on bird distribution, was not relevant to the aims of study. Two techniques are commonly used to sample bird populations simply and quickly: (1). line transects (Emlen 1971), which are effective in open habitats where birds may flee ahead of the observer (Bibby *et al* 1992), and (2). point counts, which are more suitable in densely-structured habitats, where walking a line transect is generally difficult. The present study required that habitats of widely differing structure were censused, and the use of either line transect or point count techniques alone may therefore have exacerbated habitat-related bias. Accordingly, I combined both techniques by recording birds from line transects connecting evenly-spaced count points.

Selection of transects and count points

Methods were adapted from those used in the *Pilot Census Project* (1992-93), administered by the British Trust for Ornithology. In each 1x1km observation square 2 parallel linear transects, each 1km long, were established 250m either side of the square's north-south axis. Five count points were located along each transect line, such that the first point was 100m from the start of each transect and the rest were spaced at 200m intervals. The start and finish of each transect line and position of each count point was marked using either canes or coloured tape attached to trees. The dominant habitat within 100m of each transect section and each count point was recorded.

Recording protocol

Two bird recording visits were made to each square, one between April 15th and May 14th ('early'), and one between May 15th and June 13th ('late'). The first visit encompassed the main period of territorial activity by resident birds, and the second was timed to include that of late migrants. Within each recording period low-lying squares were visited before those of higher elevation, in order to help control for the effects of altitude. Birds were recorded between 0600 and 0800 hours BST. Visits were not made during weather conditions likely to have a large effect on bird activity or detection, such as continuous rain, wind speeds >8ms^{-1}, or visibility <1km.

Each transect line was walked at a slow and constant pace. Birds encountered before the start and after the finish of a line were disregarded. Transect recording was suspended within 25m of each count point, and birds flushed in these areas were classified as point count records. The effective length of transects was therefore 750m each and 1.5km per observation square. At count points, birds were recorded during a 5 minute detection period. Many birds were recorded by both transect and point count techniques. However, care was taken not to record the same bird more than once using the same method.

Birds were detected by both sight and sound. Pulli were not recorded, since the likelihood of their detection may have differed from that of fledged birds. The distance to the location at which each bird was initially detected from the count point or transect line (measured perpendicularly) was estimated and attributed to one of 2 recording bands: 0-25m and >25m. The accuracy with which location distances were classified was periodically checked with a tape measure. Birds in flight that were not seen to land were recorded separately.

Analytical procedures

Data from each transect section and count point were grouped by habitat and study site/year. Within each group, an index of population density for each recorded species was determined using both transect and point count techniques. Following Bibby *et al* (1985), data for 'early' and 'late' count periods were combined by taking the higher of the 2 counts for each species at ranges 0-25m and 0m to infinity.

Transects. Densities were estimated using the linear model described by Jarvinen and Vaisanen (1975). This assumes that the probability of detecting a bird, if present, at x metres from the transect line = $1-kx$, where k is a positive species-specific constant. It can be shown that the proportion of birds recorded within the inner recording band (p) = $kw(2-kw)$, where w is the distance from the transect line to the inner recording band in metres (in this case, 25m). It follows that $k = (1-\sqrt{(1-p)})/w$. This permits the estimation of the number of birds of a particular species km^{-2} (D) thus:

$$D = 10^3 Nk/L$$

where N is the total number of birds of that species recorded and L is the transect length in km.

Point counts. Densities were estimated from point count data by assuming a half-normal decline in the probability of detecting a bird that was present as its distance from a count point increased. For each species, birds km^{-2} were estimated from:

$$D = 10^6 \log_e(n/n_2) \times n/m(\pi r^2)$$

where n is the total number of birds of that species counted at all points, n_2 is the number of birds of that species beyond the inner recording radius, m is the total number of counts and r is the inner recording band radius in metres (in this case, 25m).

For each species, transect and point count density estimates were each standardised to have zero means and unit standard deviations, and the mean of the 2 standardised scores for the various habitats within each site/year calculated to give composite density estimates.

It was assumed that species seen in only one recording band (and for which it was therefore impossible to calculate density estimates) were scarce rather than prone to recording bias. However, in order that these birds could contribute to the analysis, all sightings within the inner recording band of line transects in the various habitats in each site/year were pooled into one of 3 groups and totalled. These groups were passerines, waders and gamebirds, and other birds. It was accepted that the detection of species within these groups varied as a consequence of differences in their size and conspicuity. However, this effect was minimised by excluding the more distant records (i.e. those from the outer recording band).

Mammalian prey abundance

Four mammal species (field vole, mountain hare *Lepus timidus*, brown hare *Lepus europaeus* and rabbit *Oryctolagus cuniculus*) were of principal interest, since collectively they accounted for almost 90% of mammalian prey occurrences in harrier pellets (Chapter 6).

Field voles

The need to assess vole abundance over a wide area each year precluded the use of intensive monitoring techniques, such as those relying on continuous live trapping (Gurnell and Flowerdew 1982). Simple and quick abundance estimates using activity indices based on vole signs, such as faeces, grass clippings (characteristic of voles feeding) and the length of vole runs, have been used with success in several previous studies (e.g. Emlen *et al.* 1957; Hayne and Thompson 1965; Lidecker 1973; Tapper 1979; Petty 1992). These techniques were therefore adopted in the present study.

Relationships between sign indices and actual densities of field voles are difficult to establish (Tapper 1976), although studies by Petticrew and Sadleir (1970), Tapper (1979) and Petty (1992) have shown correlations between sign indices and densities estimated by intensive live capture or trap-out methods. However, Village and Myhill (1990) noted that it was impossible to distinguish signs produced by field and bank voles *Clethrionomys glareolus* and concluded that sign indices were appropriate only in areas where a one or the other species was present. In order to test whether sign indices would provide reliable estimate of field vole abundance in Argyll, indices derived from various vole signs were compared with an index determined by intensive trapping methods.

Vole sign indices. Within each 1x1km observation square, 25 quadrats (25cm x 25cm) were randomly located in the dominant habitat and sampled for the presence (= 1) or absence (= 0) of 5 features that could be related to vole density. These were: runways amongst the vegetation, fresh and decomposing vole faeces, and fresh and decomposing vegetation clippings. Fresh vole faeces were discrete and moist, and usually greenish in colour; fresh clippings had no evidence of weathering at the cut surface. Assessments were undertaken in April and August in order to control for changes in vole abundance between spring and summer. The presence/absence scores for each vole sign were summed across the 25 quadrats to give a maximum total score of 25 per observation square.

Vole trapping index. Trapping was undertaken concurrent with vole sign assessments in 15 1x1km observation squares during April and August 1992 (7 in Kintyre and 8 in Lorn). In each square, a trap line comprising 25 break-back traps set at 10m intervals was established in the dominant habitat. Traps were modified according to Petty (1992), so that they caught without bait and were triggered by objects weighing more than 5g. Traps were visited at 24 hour intervals over 2 days, giving a total of 50 trap nights per observation square sampled per trapping period. Sprung traps that were empty were deducted from the trap night total, since they may have been triggered by heavy precipitation rather than animals that evaded capture. A vole trapping index (*VTI*) for each observation square was calculated thus:

$$VTI = \frac{\text{number of captures}}{\text{number of adjusted trap nights}} \times 100$$

It was assumed that the *VTI* was closely related to actual field vole density, although it is accepted that trapping techniques may also be subject to error (Hansson 1975). However, Redpath *et al.* (1995) have shown that 2-night trapping methods similar to those used in the present study can generate a reliable index of field vole abundance.

The relationship between the *VTI* and each vole sign index was investigated using data from the 15 1x1km squares sampled by each technique in 1992. These data were not normally distributed, and correlations were therefore determined non-parametrically.

Lagomorphs

Lagomorphs were recorded from line transects during counts of birds in each 1x1km observation square. Similar recording protocols were used, except that recording was not suspended within 25m of bird count points. The effective transect length in each square was therefore 2km. Care was taken not to record the same individual more than once.

Variation in harrier prey abundance

Temporal and spatial variation in the abundance of the most frequently taken species (meadow pipit and field vole) and prey-type (passerines) was investigated. Prey abundance estimates were available for 3 years in Lorn. These data were therefore used in statistical comparisons of abundance between years. However, to ensure data independence, only data from Lorn in 1992 were included in analyses of between-habitat and between-site variation.

Hen harrier foraging activity in relation to prey abundance

Each observation square was watched for a total of 15 hours. Recording methods are described in Chapter 3. The total time that harriers were observed foraging per area of square visible was used as the continuous dependent variable in a multiple regression model that had estimates of abundance for various prey species in each square as the independent variables (IVs).

A variable representing the proximity of observation squares to all harrier nests within 5km was forced into the model on the grounds that it had been shown to have an important effect on foraging time (Chapter 3). Other IVs were entered into the model using a forward selection procedure, with selection stopping when the significance level of the F-to-enter for the next variable exceeded 0.05. The robustness of this analysis was tested using backward selection. It was hypothesised that the relationship between harrier foraging activity and prey abundance might vary between years. This was investigated after holding the effects of the different study sites statistically 'constant' by re-selecting the model with dummy variables X1 to X3, representing the 4 sites, entered as a single block into the regression equation.

Evaluations of assumptions regarding the distribution of the data were carried out by screening variables for normality prior to analysis and by examination of the normal probability plot for the residuals. Plots of IVs against residuals were inspected for systematic differences in residual variance. Where necessary, independent variables were transformed to reduce skewness and improve normality.

RESULTS

Avian prey

A total of 60km of line transect and 400 count points resulted in recording 75 species of bird (transects 66, point counts 70). These included all except 4 species recorded as hen harrier prey in Argyll (greenfinch *Carduelis chloris*, redshank *Tringa totanus*, water rail *Rallus aquaticus* and feral pigeon *Columba livia*; Chapter 6). Wren *Troglodytes troglodytes* was the only species recorded in all 7 habitats surveyed, although meadow pipit was recorded in 5 and whinchat *Saxicola rubetra*, skylark *Alauda arvensis* and willow warbler *Phylloscopus trochilus* in 4 each. Twelve species exceeded 5 birds km^{-2} in at least one habitat/study site/year, whether judged by transects (Table 1) or point counts (Table 2). Both count techniques ranked meadow pipit highest in unafforested, new forest and pre-thicket habitats. Skylark was ranked 2nd in unafforested habitats, but was relatively scarce in new forest and replaced in abundance by willow warbler in pre-thicket forest. In post-thicket forests, goldcrest *Regulus regulus* was ranked highest, followed by chaffinch *Fringilla coelebs*, coal tit *Parus ater*, robin *Erithacus rubecula* and wren. Chaffinch was ranked highest in re-stock.

Table 1: Summary of density estimates (birds km^{-2}) for bird species recorded from line transects, grouped by habitat. Only species with estimated densities >5 km^{-2} in one or more habitat/study site/year are shown. Hen harrier prey species (indicated by asterisk) are ranked in order of their frequency in pellets collected from nests (Chapter 6), meadow pipit being most frequent. N = number of study sites/years each habitat was studied. Blank spaces indicate that no birds were recorded. Lorn density estimates for all 3 years are included, although these data are not strictly independent.

	Heath/bog (N = 6)		**Acid grassland** (N = 6)		**Neutral grass.** (N = 6)		**New forest** (N = 4)		**Pre-thicket** (N = 6)		**Post-thicket** (N = 6)		**Re-stock** (N = 3)	
	Median	*Inter-quartiles*	Median	*Inter-quartiles*	Median	*Inter-quartiles*	Median	*Inter-quartiles*	Median	*Inter-quartiles*	Median	*Inter-quartiles*	Median	*Inter-quartiles*
*Meadow pipit	141	*132-177*	152	*68-159*	58	*27-146*	158	*152-159*	164	*129-196*				
*Song thrush *Turdus philomelos*											0	*0-14*		
*Skylark	29	*0-56*	30	*0-168*	23	*0-68*	0	*0-8*						
*Wren					0	*0-15*			0	*0-19*	13	*12-20*	18	*0-22*
*Wheatear *Oenanthe oenanthe*	0	*0-16*	0	*0-15*										
*Siskin *Carduelis spinus*											0	*0-14*		
*Whinchat									0	*0-16*				
*Robin									0	*0-6*	30	*25-53*		
*Chaffinch											50	*21-115*	45	*0-121*
*Willow warbler							7	*0-24*	20	*14-31*	6	*0-12*		
Coal tit *Parus ater*											33	*0-134*		
Goldcrest											82	*56-122*	0	*0-31*

Table 2: Summary of density estimates (birds km^{-2}) for bird species recorded from point counts, grouped by habitat. Details as per Table 1.

	Heath/bog (N = 6)		**Acid grassland** (N = 6)		**Neutral grass.** (N = 6)		**New forest** (N = 4)		**Pre-thicket** (N = 6)		**Post-thicket** (N = 6)		**Re-stock** (N = 3)	
	Median	*Inter-quartiles*	Median	*Inter-quartiles*	Median	*Inter-quartiles*	Median	*Inter-quartiles*	Median	*Inter-quartiles*	Median	*Inter-quartiles*	Median	*Inter-quartiles*
*Meadow pipit	200	*168-260*	199	*77-280*	89	*14-206*	286	*279-290*	261	*233-289*				
*Song thrush											0	*0-54*		
*Skylark	80	*0-109*	75	*0-211*	44	*0-176*	0	*0-54*						
*Wren											36	*0-124*		
*Wheatear			0	*0-5*										
*Siskin											0	*0-5*		
*Whinchat									0	*0-5*				
*Robin									0	*0-24*	54	*48-64*		
*Chaffinch											78	*24-170*	66	*0-162*
*Willow warbler							0	*0-27*	22	*0-47*				
Coal tit											68	*0-141*		
Goldcrest											182	*113-260*	0	*0-77*

Transect and point count density estimates for the 12 most abundant species in each study site/year were highly correlated in all habitats (Table 3). Composite transect and point count density estimate scores for these species are shown for each habitat and study site/year in Appendix 3.

Overall, 38 passerine species were recorded within 25m of transect lines. Habitat-specific density estimates for passerines in each site/year varied from 0-18 km^{-2} (Appendix 4). Only 11 waders/gamebirds were recorded within the 25m band. These included 7 red grouse *Lagopus lagopus scoticus*, 2 black grouse *Tetrao tetrix*, a pheasant *Phasianus colchicus* and a snipe *Gallinago gallinago*. All were recorded within Cowal and Kintyre. Twelve other non-passerine birds were recorded, including 2 mallard *Anas platyrhynchos*, 7 herring gull *Larus argentatus* and 3 raptors. These were recorded in Islay, Kintyre, and Lorn (1993).

Table 3: Spearman rank correlation coefficients for relationships between estimates of birds km^{-2} derived from transects and point counts, grouped by habitat. Data for the 12 most abundant species in each study site/year are shown. N = number of transect and point count estimates per habitat. All correlations were significant at the 0.1% level.

Habitat	**N**	r_s
Heath/bog	72	0.92
Acid grassland	72	0.98
Neutral grassland	72	0.97
New forest	48	0.93
Pre-thicket forest	72	0.87
Post-thicket forest	72	0.96
Restock	36	0.80

Mammalian prey

Small mammal community

A total of 63 small mammals of 5 different species were trapped during 500 trap nights. Field vole was the most frequently caught species in both April and August, followed by common shrew *Sorex araneus,* a small number of wood mouse *Apodemus syvaticus* and pygmy shrew *Sorex minutus*, and a single bank vole (Table 4). Between April and August, the number of small mammals caught declined by nearly 50% in Kintyre, whereas there was a 3-fold increase in Lorn. However, the proportion of small mammals that were field voles did not differ significantly between trapping periods (Fisher's exact tests, Kintyre: $P = 1.00$; Lorn: $P = 0.13$).

Small mammals were caught in all habitats except heath/bog and neutral grassland. Overall, 94% of small mammals were trapped in afforested habitats (Fig. 1). Field vole was the most frequently trapped species in all habitats.

Table 4: Number (and percentage of totals) of small mammals caught in each study site and trapping period during 1992. N = no. of trap nights.

Species	**Kintyre**				**Lorn**			
	April		August		April		August	
	N = 350		N = 350		N = 400		N = 400	
Field vole	8	*(57%)*	4	*(50%)*	9	*(90%)*	19	*(61%)*
Bank vole	0	-	0	-	0	-	1	*(3%)*
Wood mouse	2	*(14%)*	0	-	0	-	1	*(3%)*
Common shrew	4	*(29%)*	2	*(25%)*	1	*(10%)*	9	*(29%)*
Pygmy shrew	0	-	2	*(25%)*	0	-	1	*(3%)*
Totals	**14**		**8**		**10**		**31**	

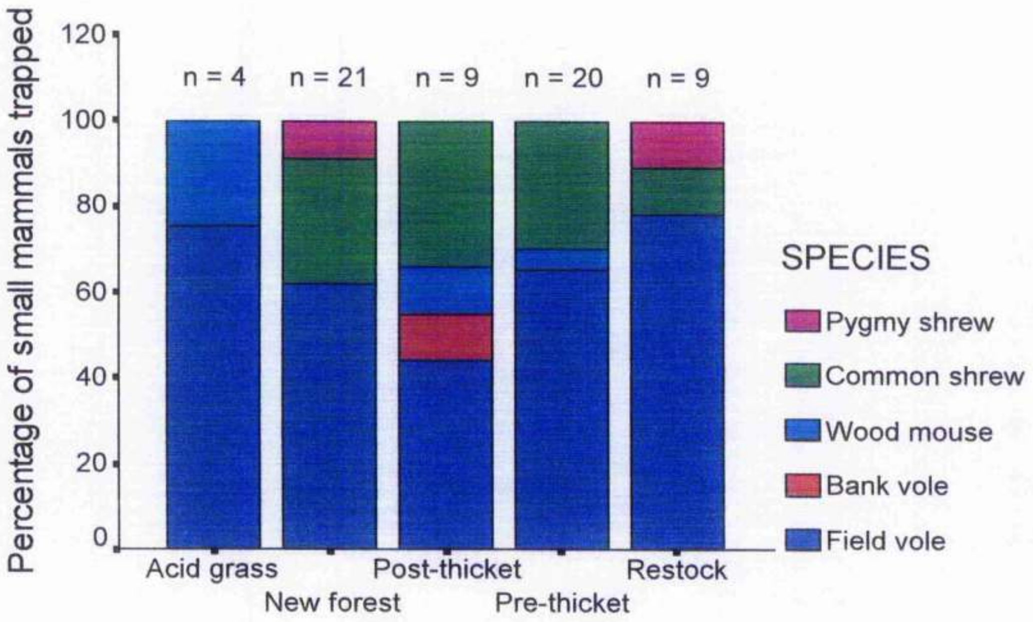

Figure 1: Species composition of small mammals trapped in Kintyre and Lorn in 1992, grouped by habitat (data from April and August trapping periods pooled). Within each habitat, species are shown as a percentage of the total trapped. N = number of animals caught.

Relationships between vole signs and the trapping index

All 5 vole sign indices were significantly inter-correlated, with the strongest relationships (r_s >0.90) occurring between those measuring old clippings, old droppings and vole runs (Table 5a). Overall, the fresh clippings index (*FCI*) and fresh droppings index (*FDI*) were more strongly correlated with the *VTI* than were other indices (Table 5b). However, in each study site and trapping period, the *VTI* was tracked more consistently by the *FDI* than it was by the *FCI*, and *FDI* scores were therefore used to estimate field vole abundance more generally in further analyses. The *FDI* correlated more strongly with *VTI* in August than April (Fig. 2) perhaps because fresh droppings were easier to distinguish from old ones in August, when higher temperatures may have caused faster decay rates.

Table 5: Relationships between various measures of vole abundance in 15 1x1km squares. (a). Spearman rank correlation coefficients for 5 vole sign indices (data from each census period and study site pooled). (b). Spearman rank correlation coefficients for relationships between each sign index and a vole trapping index (*VTI*). April, August and combined assessments are shown for each study site. *N* = number of assessments, *FCI* = fresh clippings index, *FDI* = fresh droppings index, *OCI* = old clippings index, *ODI* = old droppings index, *RNI* = runways in the grass. * = $P<0.05$, ** = $P<0.01$.

(a).

FDI	.84 **			
OCI	.51 *	.52 *		
ODI	.54 *	.63 **	.93 **	
RNI	.50 *	.49 *	.96 **	.90 **
	FCI	***FDI***	***OCI***	***ODI***

(b).

Study site	**Vole sign index**	**April**	**August**	**Combined**
Kintyre		*N = 7*	*N = 7*	*N = 14*
	FCI	0.843 *	0.944 **	0.875 **
	FDI	0.867 *	0.944 **	0.904 **
	OCI	0.774 *	0.787 *	0.542 *
	ODI	0.844 *	0.687	0.681 *
	RNI	0.746	0.674	0.480
Lorn		*N = 8*	*N = 8*	*N = 16*
	FCI	0.672	0.796 *	0.864 **
	FDI	0.960 **	0.857 **	0.864 **
	OCI	0.453	0.340	0.402
	ODI	0.692	0.714 *	0.544 *
	RNI	0.526	0.295	0.408

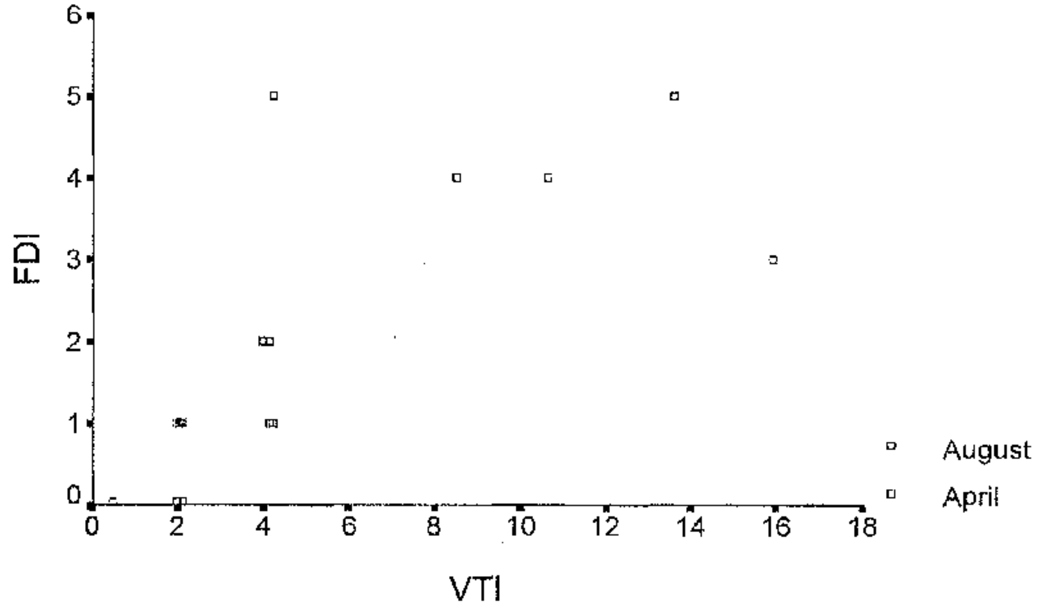

Figure 2: Relationship between the fresh dropping index (FDI) and vole trapping index (VTI). Kintyre and Lorn assessments have been combined. Spearman rank correlations, April: R_S = 0.90; August: R_S = 0.93.

Lagomorphs

A total of 14 lagomorphs (6 rabbit, 5 brown hare, and 3 mountain hare) were recorded from 160km of line transect walked in April and August. Brown hare were recorded only in Islay and mountain hare only in Kintyre. Rabbit were recorded in all 4 study sites, although they occurred in only one of the 3 years of study in Lorn. Overall, 86% of lagomorphs were recorded in neutral grassland and 14% in acid grassland. In view of the small number of sightings, records from both recording bands were used to calculate numbers recorded per km (Appendix 4). These data ranked lagomorph abundance as follows: Islay (0.94 km^{-1}) > Cowal (0.40 km^{-1}) > Kintyre (0.37 km^{-1}) > Lorn 1992-4 (0.08 km^{-1}).

Variation in harrier prey abundance

Meadow pipit

The composite density estimate scores for meadow pipit varied significantly between habitats (*Kruskal-Wallis one-way anova* $\chi^2_6 = 13.14$, $P = 0.04$). Meadow pipit were relatively abundant in all habitats except post-thicket forest and restock (Fig. 3). Scores for the remaining habitats did not vary significantly between sites/years ($\chi^2_3 = 6.73$, $P = 0.081$), nor between years within Lorn ($\chi^2_2 = 0.70$, $P = 0.704$).

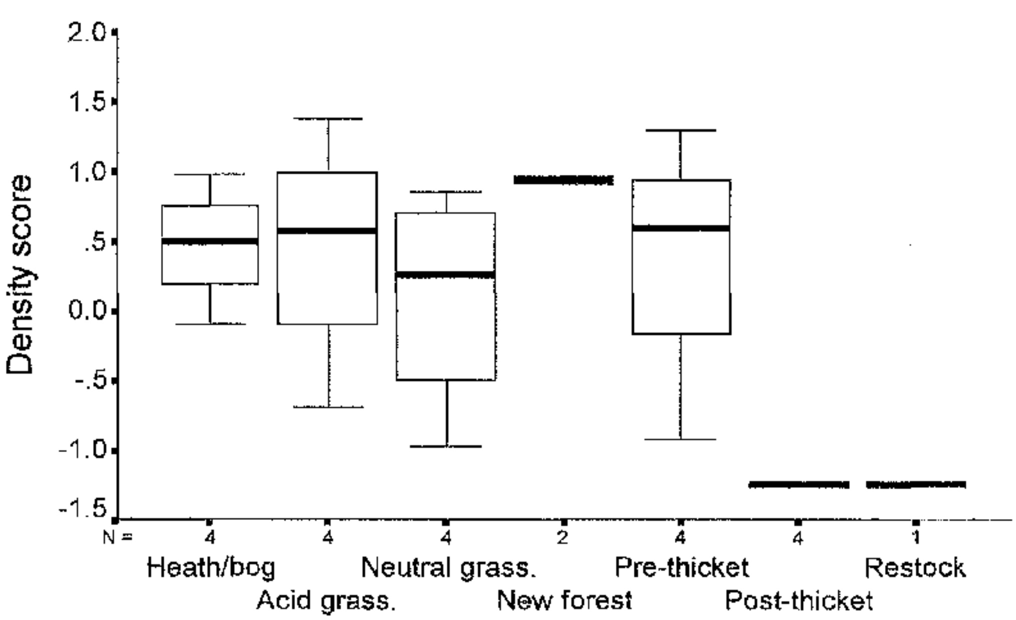

Figure 3: Variation in composite density estimate scores (standardised for site/year) for meadow pipit. Median values are shown by the solid bar. The boxes show inter-quartile values and the "whiskers" the highest and lowest values. N = sample size of study sites. Lorn data for 1993-94 excluded.

Passerines

Variation in passerine abundance between habitats was investigated after first controlling for differences between study sites/years by dividing the habitat-specific passerine totals in each site/year by the relevant site/year mean. Passerines km^{-1} did not vary significantly between the habitats tested (*Kruskal-Wallis* $\chi^2_6 = 3.80$, $P = 0.70$). Furthermore, there was no significant difference in passerines km^{-1} (standardised to control for habitat effects) between study sites/years ($\chi^2_3 = 3.53$, $P = 0.32$), nor between years within the Lorn study site ($\chi^2_2 = 1.63$, $P = 0.44$).

Field voles

Within each study site/year, a habitat-specific *FDI* was determined by summing the April and August assessment scores for each observation square (Appendix 4). In 3 cases where 2 squares of identical dominant habitat were selected in the same site/year, mean *FDI* scores were calculated. Variation in the *FDI* between habitats was investigated after first controlling for differences between sites/years by dividing each habitat-specific score by the relevant site/year mean. There was a significant difference in these standardised scores between habitats (*Kruskal-Wallis* $\chi^2_6 = 15.09$, $P = 0.02$). Field voles were more abundant in new forest, pre-thicket and restock than other habitats (Fig. 4).

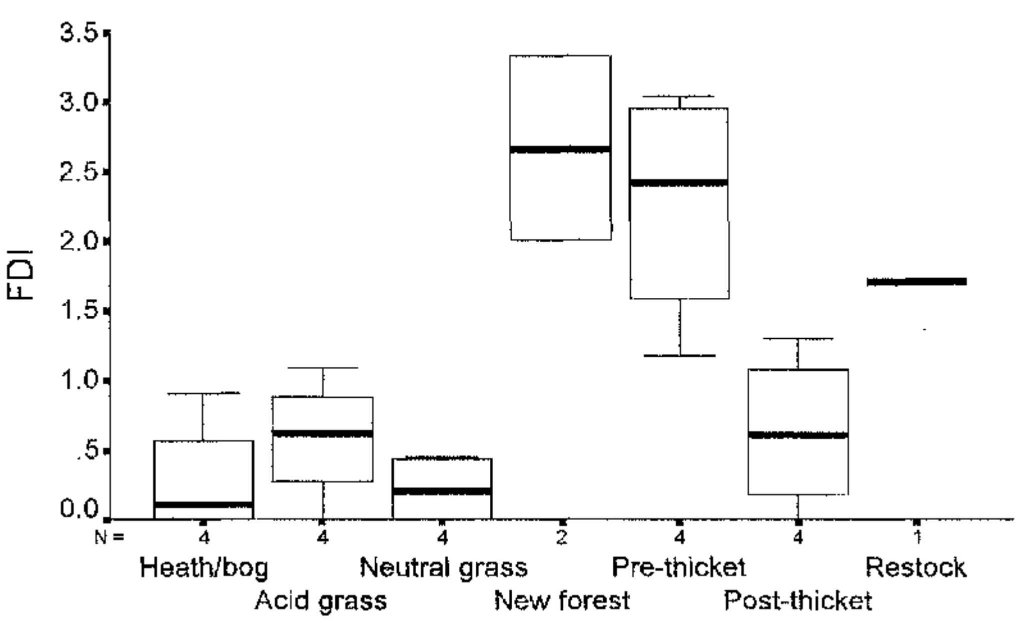

Figure 4: Variation in FDI scores (standardised for site/year). Data are represented as per Fig. 3. N = sample size of study sites. Lorn data for 1993-94 excluded.

FDI scores (standardised for habitat effects) also varied significantly between study sites/years (*Kruskal-Wallis* $\chi^2_3 = 12.49$, $P = 0.006$), and between years within Lorn (*Kruskal-Wallis* $\chi^2_3 = 7.85$, $P = 0.02$). Overall, scores were low in sites studied in 1992 and moderate or high in sites studied in 1993-94 (Fig. 5).

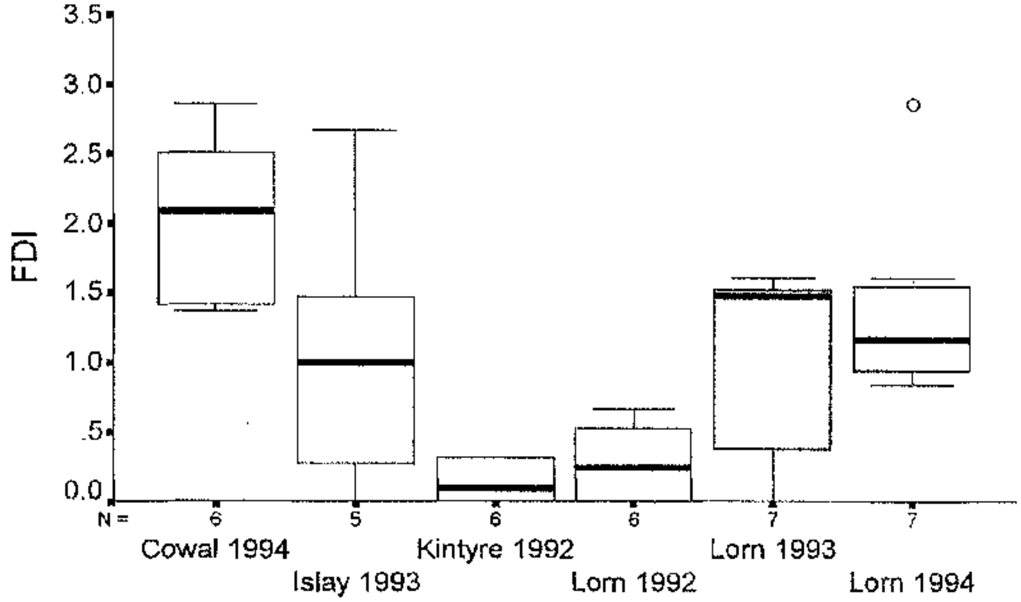

Figure 5: Variation in FDI scores for 6 study sites/years (standardised for habitat). Data are represented as per Fig. 3, except the open circle which represents an outlying data point. N = sample size of habitats.

Hen harrier foraging activity in relation to prey abundance

Five types of independent variable were used in a regression model relating harrier foraging activity to prey abundance in the observation squares. These were: (1). composite density estimates for the 12 most abundant bird species, (2). total individuals within 25m of transects for 3 bird groups (passerines, waders and gamebirds, and other birds), (3). field vole *FDI* scores, (4). total lagomorphs recorded from transects, and (5). measures of hen harrier nest proximity (Table 6). The values of individual IVs were calculated by using a planimeter to measure the habitat areas in each observation square, then multiplying these areas by the appropriate habitat-specific prey abundance scores for all squares in the relevant study site/year. The total time spent by foraging harriers, area of each habitat, and proximity to harrier nests, is shown for each observation square in Appendix 1.

Several candidate variables were strongly correlated (Table 7), in particular those representing the abundance of prey species associated mainly with moorland habitats (e.g. skylark and wheatear) or woodland habitats (e.g. song thrush, siskin, coal tit and goldcrest).

Table 6: Candidate variables used in a multiple regression model relating prey abundance to foraging activity by hen harriers in 1x1km observation squares.

Variable		Description	Code
DEPENDENT	Observed hen harrier foraging time in 1x1km square		**HH**
INDEPENDENT			
Birds	Meadow pipit	Composite transect and point count density estimate scores	**MP**
	Song thrush		**ST**
	Skylark		**S.**
	Wren		**WR**
	Wheatear		**W.**
	Siskin		**SK**
	Whinchat		**WC**
	Robin		**R.**
	Chaffinch		**CH**
	Willow warbler		**WW**
	Coal tit		**CT**
	Goldcrest		**GC**
	All passerines	Number recorded within inner recording band of transects	**PA**
	Waders & gamebirds		**WG**
	Other birds		**OB**
Mammals	Field vole	*FDI* scores	**FV**
	Lagomorphs	Number recorded from transects	**LG**
Other	Harrier nest proximity	$\sum {}^{1}/_{D^2}$, where D = the distance between the centre of each observation square and each harrier nest within 5 km.	**NP**

Table 7: Matrix of Pearson correlation coefficients for independent variables. Correlations significant at the 1% level are shown in **bold**. Variable transformations: † = inverse, ‡ = logarithm

ST †	+.19																
S. †	+.26	+.03															
WR †	-.36	+.08	-.09														
W. †	+.01	+.06	**+.41**	-.09													
SK †	-.11	+.02	**-.51**	+.04	-.35												
WC ‡	+.06	+.01	-.12	+.08	-.05	+.35											
R. ‡	**-.45**	+.18	-.31	+.25	-.17	-.04	-.21										
CH †	-.35	+.02	-.15	**+.76**	-.17	+.14	+.20	+.23									
WW †	+.17	-.12	+.31	-.10	-.03	-.02	+.10	-.09	-.01								
CT †	+.15	**+.94**	+.08	+.07	+.07	+.05	+.03	+.05	-.08	+.01							
GC †	-.03	+.02	**-.47**	+.05	-.39	**+.40**	-.10	+.29	+.21	+.04	+.04						
PA ‡	+.17	+.33	-.06	0.00	-.10	+.06	+.04	+.15	+.09	**+.43**	+.37	**+.46**					
WG ‡	+.35	+.13	+.23	-.20	-.06	-.11	-.18	+.07	-.11	**+.42**	+.07	+.08	+.20				
OB †	-.08	+.01	+.22	-.07	+.03	-.23	-.12	+.04	-.06	+.26	+.05	-.05	+.11	-.10			
FV	**+.41**	+.20	-.18	-.04	-.14	-.12	.03	-.05	-.17	-.14	+.10	+.18	.01	+.09	-.27		
LG	+.17	+.10	+.02	-.04	-.04	-.08	-.08	-.11	-.07	+.07	+.05	+.04	+.28	+.01	+.16	-.17	
NP	+.13	+.08	+.01	-.19	-.04	+.11	+.32	-.10	-.04	-.17	+.08	+.14	-.04	-.20	-.25	+.24	-.07
	MP	**ST †**	**S. †**	**WR†**	**W. †**	**SK †**	**WC‡**	**R. ‡**	**CH †**	**WW†**	**CT †**	**GC †**	**PA ‡**	**WG‡**	**OB †**	**FV**	**LG**

With the variable for harrier nest proximity in the regression equation, the model selected 2 further variables, representing the abundance of meadow pipits and field voles. This model explained 40% of the variance in harrier use of observation squares. The addition of field vole abundance made a greater contribution to change in R^2 than the subsequent addition of meadow pipit (Table 8). With all 3 IVs in the equation, $R = 0.67$, $F_{3,36} = 9.86$, $P = 0.0001$. The frequency distribution of the residuals for the selected model did not depart significantly from zero (Kolmogorov - Smirnov goodness of fit test: $z = 0.863$, $P = 0.45$). Using Mahalanobis distance with $P < 0.001$, a single multivariate outlier (observation square NR 17/52) was detected. Examination of the data revealed that harrier foraging time in this square was 3 times greater than that predicted by the model.

When the model was re-selected with the variables representing study site (X1-3) forced into the equation, only the variable representing field vole abundance was selected. After entry of all IVs, $R = .70$, $F_{5,34} = 6.57$, $P = 0.0002$.

Table 8: Statistical regression of prey abundance and nest proximity variables on use of observation squares by foraging hen harriers. The table shows the unstandardised regression coefficients (β) and intercept, standardised regression coefficients (*Beta*), semi-partial correlations (sr^2), squared multiple correlations (R^2), incremental *F* ratio, and *R*, R^2 and adjusted R^2 after entry of all IVs. NP = harrier nest proximity, MP = composite density estimate scores for meadow pipit, FV = *FDI* scores for field voles.

	β	***Beta***	***T***	***P***	***sr²*** **(a)**	***R²*** **(b)**	***F**inc* **(df 1,36)**	
NP	1.73	.214	1.68	.102	.12	.12	5.24	*
FV	10.01	.391	2.83	.008	.25	.37	14.71	***
MP	7.71	.310	2.29	.028	.08	.45	5.25	*
Intercept	3.76							
				R	.67	$P = 0.0001$		
				R²	.45			
				Adj. *R²*	.40			

(a). = incremental. **(b).**= cumulative. * $P < 0.05$ *** $P < 0.001$

This analysis shows that, for a given nest proximity, harriers preferred to forage in areas with relatively high densities of field vole and meadow pipit. Vole abundance was the most influential variable overall, and the only one to have a significant effect after adjustment for differences in study site. When the relationship between harrier foraging activity (controlled for the effects of nest proximity) and the abundance of pipits and voles was examined with respect to the dominant habitat in each observation square, it was found that foraging activity tended to increase with prey abundance mainly in those squares that had much young forestry (Fig. 6). The greatest abundances of voles, but not pipits, occurred in these squares.

It was hypothesised that the strength of the effects of vole and pipit abundance on harrier foraging activity might be dependent upon the structure of the vegetation in which these species occurred. Thus the most profitable areas for harriers to forage may have been those where the vegetation was dense enough to allow harriers to surprise prey, but not so dense that prey were difficult to detect or capture. This dependence was tested using measurements of foliage volume within 0-0.5m and 0.6-2m height (i.e. corresponding to the ground and shrub vegetation layers, respectively) made at ≥30 points in each observation square (see Chapter 3). Within each square, the mean foliage volume in each height class was calculated, to give the variables VS1 (representing the mean density of ground vegetation) and VS2 (representing the mean density of shrub vegetation). These values were then used in conjunction with the square-specific values for field vole and meadow pipit abundance in order to create interaction terms that represented the combined effects of prey and vegetation density. Vole and pipit abundance were each positively related to ground vegetation density, and the combined effects of these variables were therefore represented by the interaction terms FV*VS1 and MP*VS1. However, vole and pipit abundance were negatively related to shrub vegetation density, and these effects were therefore represented by the interaction terms FV*(1/VS2) and MP*(1/VS2).

The 4 interaction terms were included among the candidate variables in a regression model that related harrier foraging activity to pipit and vole abundance in each square. With nest proximity again forced into the equation the model selected one further variable, representing the interaction between ground vegetation density and vole abundance (FV*VS1). This model explained 44% of the variance in harrier use of observation squares (Table 9). With both IVs in the equation, $R = 0.69$, $F_{2,37} = 16.42$, $P = 0.0001$. When the variables representing study site were forced into the equation, FV*VS1 remained significant and no further variables were selected. After entry of all IVs, $R = 0.77$, $F_{5,34} = 9.81$, $P < 0.0001$.

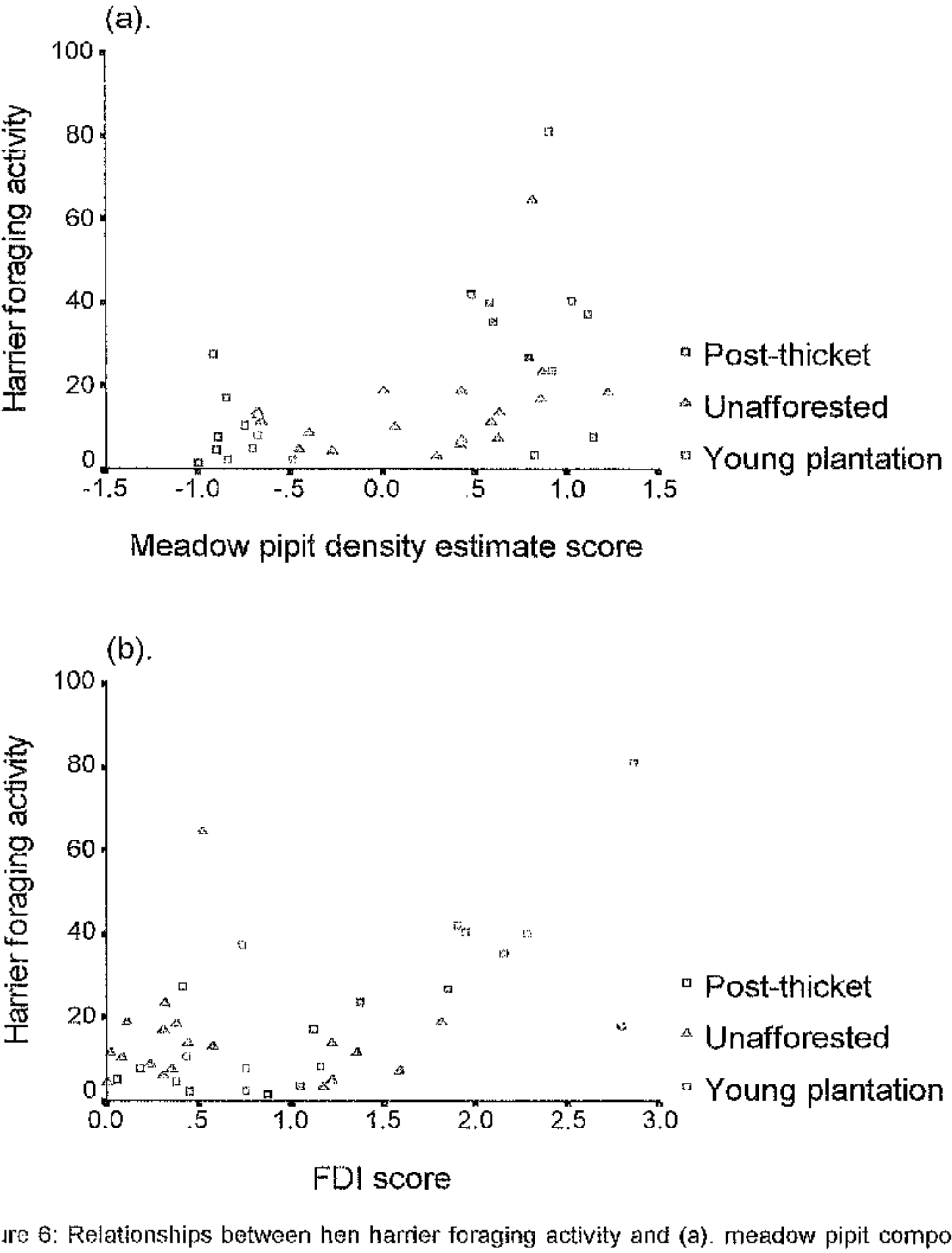

Figure 6: Relationships between hen harrier foraging activity and (a). meadow pipit composite density estimates, and (b). field vole FDI scores, after first controlling for nest proximity. Data are for 1x1km observation squares. Foraging activity data are the residuals between the foraging time observed in each square and that expected given the squares' proximity to harrier nests (as calculated from the regression equation Y = 1.73 [NP] + 3.76). A value of 7.89 was added to the resultant scores in order to bring the minimum score to zero. Symbols indicate the dominant habitat groups in each square.

This analysis suggests that foraging activity was influenced more by the interaction between vole abundance and vegetation density (i.e. vole availability) than by vole abundance alone. Thus harriers' preference for areas where voles were abundant increased if these areas had dense ground vegetation. One explanation for this might be that voles in dense ground vegetation could not easily detect (and therefore flee) approaching harriers. Why did the model not also select one of the variables representing pipits? FV*VS1 was strongly correlated with pipit abundance and the interaction term MP*VS1. It is therefore possible that FV*VS1 masked the effects of both pipit abundance and availability. This was tested by repeating the analysis after first removing FV*VS1 from the variables available for selection. The variable representing vole abundance and the interaction term MP*VS1 were subsequently selected. The addition of vole abundance resulted in a highly significant increase in R^2 (F_{inc} = 14.70, P = 0.0005). The addition of MP*VS1 resulted in a further significant increase in R^2 (F_{inc} = 6.72, P = 0.014). With all IVs in the equation, R = 0.68, $F_{3,36}$ = 10.65, P = 0.0001. Although this result suggests that harriers foraged according to the availability of pipits, rather than their abundance, it also shows that foraging activity continued to be determined mainly by voles.

Table 9: Statistical regression of variables representing (1). meadow pipit and field vole abundance, (2). interactions between these prey and vegetation density, and (3). nest proximity, on the use of observation squares by foraging hen harriers. Details as per Table 8 except VS1 = foliage volume within 0-0.5m height, VS2 = foliage volume within 0.6-2m height.

(a). Matrix of Pearson correlation coefficients for independent variables. Correlations significant at the 0.1% level are shown in **bold**.

	MP	**MP*VS1**	**MP*(1/VS2)**	**FV**	**FV*VS1**
MP*VS1	**.95**				
MP*(1/VS2)	**.68**	**.56**			
FV	.41	.43	.23		
FV*VS1	**.51**	**.55**	.24	**.95**	
FV*(1/VS2)	.33	.23	.47	.45	.33

(b). Summary statistics for selected model.

	β	*Beta*	*T*	*P*	*sr^2* (a)	*R^2* (b)	*F_{inc}* (df 1,36)	
NP	1.25	.154	1.22	.230	.12	.12	5.24	*
FV*VS1	0.27	.622	4.94	.000	.35	.47	24.38	***
Intercept	3.70							
					R	.69	*P* = 0.0001	
					R^2	.47		
					Adj. *R^2*	.44		

(a). = incremental. **(b).**= cumulative. * *P* <0.05 *** *P* <0.001

DISCUSSION

Evaluation of analysis

Several problems confound accurate quantification of prey abundance. Hutto (1990) concluded that the usefulness of sampling the food resources available to a bird was limited because (1). researchers lack the bird's perception, (2). food is not uniformly distributed, and (3). the effect of depletion is usually ignored.

An unknown amount of prey actually present is unavailable to predators because of it's crypticity (Janzen 1980), inaccessibility (Kantak 1979, Moermond and Denslow 1983, Avery and Krebs 1984) and difficulty of capture (Hespenheide 1973). I attempted to correct for these biases using the cross products of prey abundance and vegetation density variables. In reality, the availability of prey to harriers is likely be far more complex.

Bias due to spatial variation in the distribution of food was reduced by sampling potential prey within relatively large units (1km^2), stratified across several habitat-types and study sites. Bias due to temporal variation was minimised by sampling prey in more than one year, and on more than one occasion within years. Food depletion by harriers is unlikely to have had serious impact on any but the scarcest of prey species, since harriers breeding in Argyll occupy very large foraging ranges (males ca. 80km^{-2}, females ca. 12km^{-2}; *pers. obs.*) and predation per unit area was therefore extremely low. However, it is acknowledged that prey depletion by other predators, for example fox *Vulpes vulpes*, buzzard *Buteo buteo* and short-eared owl *Asio flammeus*, is unknown and may have been sufficient to reduce the abundance of some species, especially field voles and lagomorphs.

Foraging activity in relation to prey abundance

This study shows that hen harrier foraging activity was associated with the distribution of the 2 most-frequently captured prey species (meadow pipit and field vole). Meadow pipits were abundant and occurred in all open-structured habitats, where they and their young are likely to have been readily accessible to harriers. Numbers in the present study varied little from year to year and this might lead us to conclude that pipits represent a relatively stable food resource. However, meadow pipits are partial migrants in upland Britain and the timing of the spring influx varies between years (Thirgood *et al.* 1995). As a result, pipits may not always be widely available to harriers during the period in which females require dependable food resources in order to attain breeding condition (Simmons *et al.* 1986). Furthermore, young pipits (i.e. näive birds which are likely to be most easily caught) are generally available only during the latter part of the harrier breeding period.

Field vole abundance varied considerably between study sites and years. Thus voles were scarce in sites assessed in 1992 relative to those studied in 1993-94. Comparison of vole abundance estimates with data on harrier diet composition (as determined by pellet analysis; Chapter 6) in each site/year shows that the proportion of small mammals taken by harriers tended to increase with vole abundance (Fig. 7). Thus harriers ate relatively few small mammals in 1992, when voles were scarce, and relatively large numbers in 1994, when voles were more abundant. This relationship did not apply in 1993, however, when fewer than expected small mammals were taken in both Lorn and Islay. Examination of the raw scores for the *FDI* in Lorn 1993 reveals that voles were 5 times more abundant in August than April, indicating that the population was building during the period that harriers provisioned their nests. Young harriers normally fledge in early July, and it is therefore possible that the main increase in vole numbers came too late for breeding harriers to fully exploit. April and August *FDI* scores were similar in Islay 1993, however, and indicated that voles were moderately abundant throughout the breeding season. Why were more voles not taken by harriers therefore? One possibility is that vole-rich habitats were available to a relatively small proportion of the harriers on Islay, since the study site was less afforested than those elsewhere.

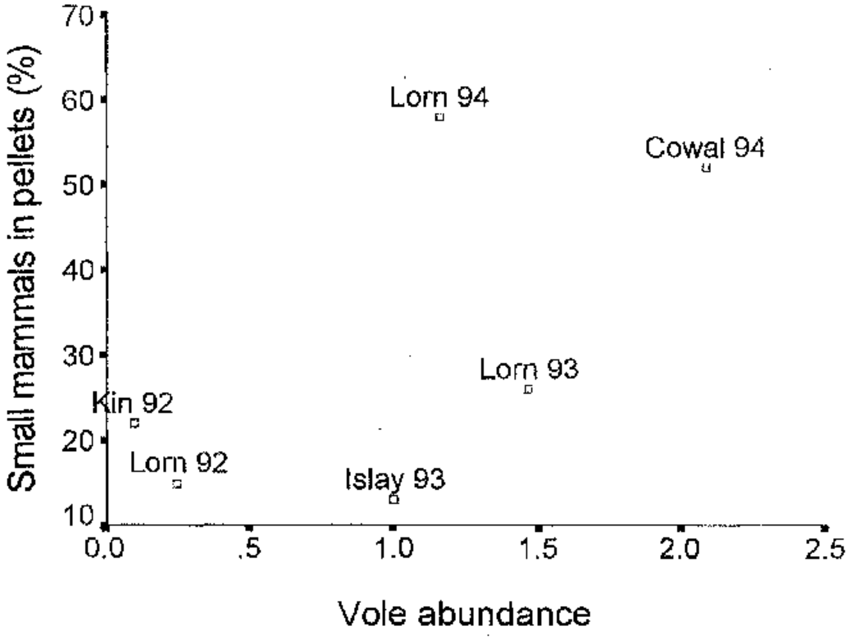

Figure 7: Relationship between the occurrence of small mammals in hen harrier pellets (adjusted for detection bias) and estimates of field vole abundance, grouped by study site/year. Vole abundance data are median *FDI* scores.

Fluctuations in vole populations between years presumably explain why the influence of voles on harrier foraging activity increased when the effects of the different study sites were taken into account.

The density of vegetation <0.5m tall had an important positive effect on the relationships between vole and pipit abundance and harrier foraging activity. Overall, harriers foraged in accordance with the distribution of vole-rich dense ground vegetation. This is consistent with their preference for pre-thicket forests (Chapter 3) since both vole and ground vegetation densities were greater in this habitat than unafforested habitats (which were grazed by livestock and sometimes burnt) and post-thicket forests (which were subject to the shading effects of trees). Although pipits were abundant in pre-thicket forests, they were not especially so. However, their scarcity in post-thicket forests is likely to have been a further factor in the avoidance of this habitat by harriers. Harriers tended to exhibit a stronger preference towards young forests when voles were most abundant. However, voles were more numerous in young plantations than other habitats regardless of their absolute abundance, and we would therefore expect harriers to forage preferentially in these habitats even in years that the vole population was low.

Several previous studies have shown that vegetation cover and structure have important effects on raptor foraging (Southern and Lowe 1968; Wakeley 1978; Baker and Brooks 1981; Bechard 1982; Janes 1985), presumably because prey are more easily detected and caught in some habitats than others. Thus Simmons (*in prep.*) found that African marsh harriers were most successful at catching small mammals (their preferred prey) in less dense habitats, despite small mammals being twice as abundant in denser habitat.

Dense ground vegetation may allow harriers to approach prey stealthily, thereby increasing the chances of capture success. If so, we might expect that the proportion of prey strike attempts that were successful would be higher in young forests than other habitats, whereas they were not (Chapter 5). However, capture success is also likely to be dependent on the type of prey hunted. Thus, of the 2 main prey-types taken by harriers, passerines were presumably easier to capture (once detected) than small mammals, since most were taken as nestlings unable to flee. Passerines occurred in all of the habitats studied, whereas small mammals were available mostly in young forestry, and these differences in distribution may have obscured trends in prey strike success.

Large prey, such as waders, gamebirds and lagomorphs, were rarely observed. West Scotland holds relatively low densities of red grouse (Hudson 1993) and mountain hare (Watson and Hewson 1973), 2 important harrier prey species elsewhere in Scotland (Watson 1977; Picozzi 1978; Redpath 1991). Brown hare and rabbit occur mainly in agricultural and coastal grassland habitats which (except on Islay) were seldom frequented by harriers during the breeding season. Although brown hare are scarce in mainland west Scotland, they were widely introduced to many islands, including Islay (Millais 1904-1906, Barrett-Hamilton and Hinton 1910-1921), where a strong population persists (M.A. Ogilvie, *pers. comm.*). Given this distribution, it is perhaps unsurprising that large prey were taken only occasionally by harriers and mainly on Islay (Chapter 6), or that they appeared to have little influence on harrier foraging effort. This is in contrast to north-east Scotland, where harriers occupying moorland managed for red grouse foraged mainly in accordance with the density of large prey, and selected alternative species (passerines) only where large prey were scarce (Redpath 1992).

Conclusions

Harriers in Argyll foraged preferentially in areas where they appeared to have the greatest chance of surprising field voles, an important prey species. Thus, they selected areas where voles were most abundant and the ground vegetation was relatively dense. This is consistent with the finding elsewhere that harriers preferred foraging in pre-thicket forests to other habitats. Foraging activity was also influenced by the abundance of meadow pipits, which were widely distributed across all habitats except post-thicket and restock forests. Unlike voles, pipits varied little in abundance from year to year, and therefore represented a more stable, if less energetically efficient, food resource.

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CHAPTER 8

NEST SITE SELECTION AND BREEDING PERFORMANCE IN RELATION TO FORAGING HABITAT AVAILABILITY

Contents:

"That's the whole problem with science. You've got a bunch of empiracists trying to describe things of unimaginable wonder."

Bill Watterson (1991). Scientific progress goes "Boink."

INTRODUCTION

The distribution of nesting raptors is normally determined by the availability of nest-sites and food (Newton 1979). Thus, provided suitable nesting sites exist, raptors can be expected to settle according to the proximity of food resources (Andrew & Mosher 1982; Rich 1986). Many studies (e.g. Dijkstra *et al.* 1982; Newton 1986; Daan *et al.* 1989) have shown that food availability also influences raptor breeding performance.

Hen harriers are ground nesting birds that hunt over open and semi-open habitats (Schipper 1977; Martin 1987; Redpath 1992). In Argyll, harriers forage preferentially over young first rotation coniferous forests, and select heathland and grassland habitats ahead of closed canopy woodland (Chapter 3). Foraging ranges are large (typically: males 80km^{-2}, females 10km^{-2}, *unpubl. data*) and overlap with those of neighbouring pairs. Redpath *et al.*, (*in prep.*) showed that harriers in west Scotland (including those in Argyll) select nest sites in heaths and young forests, but failed to find any relationship between nesting habitat and breeding performance. This may have been because habitat was measured for only a small area (0.25ha) around each nest, and variation in the quality of the wider foraging environment was not taken into account.

The aims of the present study were to investigate variation in (1). nesting density and (2). breeding success, in relation to the habitat available to foraging harriers. Specifically, I wanted to test whether harriers bred in greater number and more successfully in areas that had much young first rotation forest. Furthermore, since harriers' preference for hunting within forests declines as the trees mature (Chapter 3), it was predicted that breeding success in areas with much young forestry might decline over time.

METHODS

The study was conducted in Argyll during 1988-94. Land cover and terrain were measured in a sample of 30 10x10km squares searched comprehensively for breeding harriers in 1988-89 (Fig. 1). These squares included 17 surveyed as part of a national hen harrier census (Bibby and Etheridge 1993), and which represented a stratified random sample selected according to harriers' breeding status (confirmed or probable, possible, and absent) in 1968-72 (Sharrock 1976). The remaining squares were selected randomly from those considered to have suitable breeding habitat.

Habitat data were extracted from a Geographic Information System (GIS, ARC / INFO package, copyright 1987,1988, 1989 Environmental Systems Research Institute Inc., USA) containing information interpreted from 1:24,000 scale black and white aerial photographs taken in 1988. Land cover data were captured for tiles representing 50x50m on the ground. More than 1500 cover-types were initially discriminated, but unsuitable types such as water and human settlements were excluded and the remainder aggregated into 7 broad habitat classes, corresponding to those used for foraging observations (Chapter 3). Terrain data were measures of altitude made at intersections of a grid with cells representing 100x100m. These data were aggregated into 3 elevation classes: 1-50m, 51-250m, and >251m above mean sea level.

Occupancy

Broad-scale site selection

Each 10x10km square was surveyed in either 1988 or 1989. At least 2 visits were made during the breeding season, including one between mid-April and mid-May when courtship and display by territorial birds are most conspicuous. Variation in nesting density in relation to habitat was investigated by using the number of nests located in each square as the dependent variable in a least squares multiple regression analysis that had measures of the various habitat classes as the independent variables. Forward entry of variables was specified, with an F-to-enter value of $P = 0.05$

Fine-scale site selection

Within the searched 10x10km squares, the area of each habitat class was calculated for radii of 1km and 3km around (1). harrier nests occupied in 1988-9, and (2). random (non-nest) locations. In the few instances where male harriers were bigamous, the mid-point between nests provisioned by the same male was used. Random co-ordinates were generated using a computer; co-ordinates which lay within 1km of a nest site were re-selected. To control for gross differences in the distribution of habitat, random points were constrained such that (1). the number within each 10x10km square was equal to the number of harrier nests present, and (2). the number within each habitat was the same within each square as for harrier nests. The area within 1km of nests was considered to be the core foraging area used by both sexes, whilst the area within 3km represented the foraging hinterland, used mainly by males.

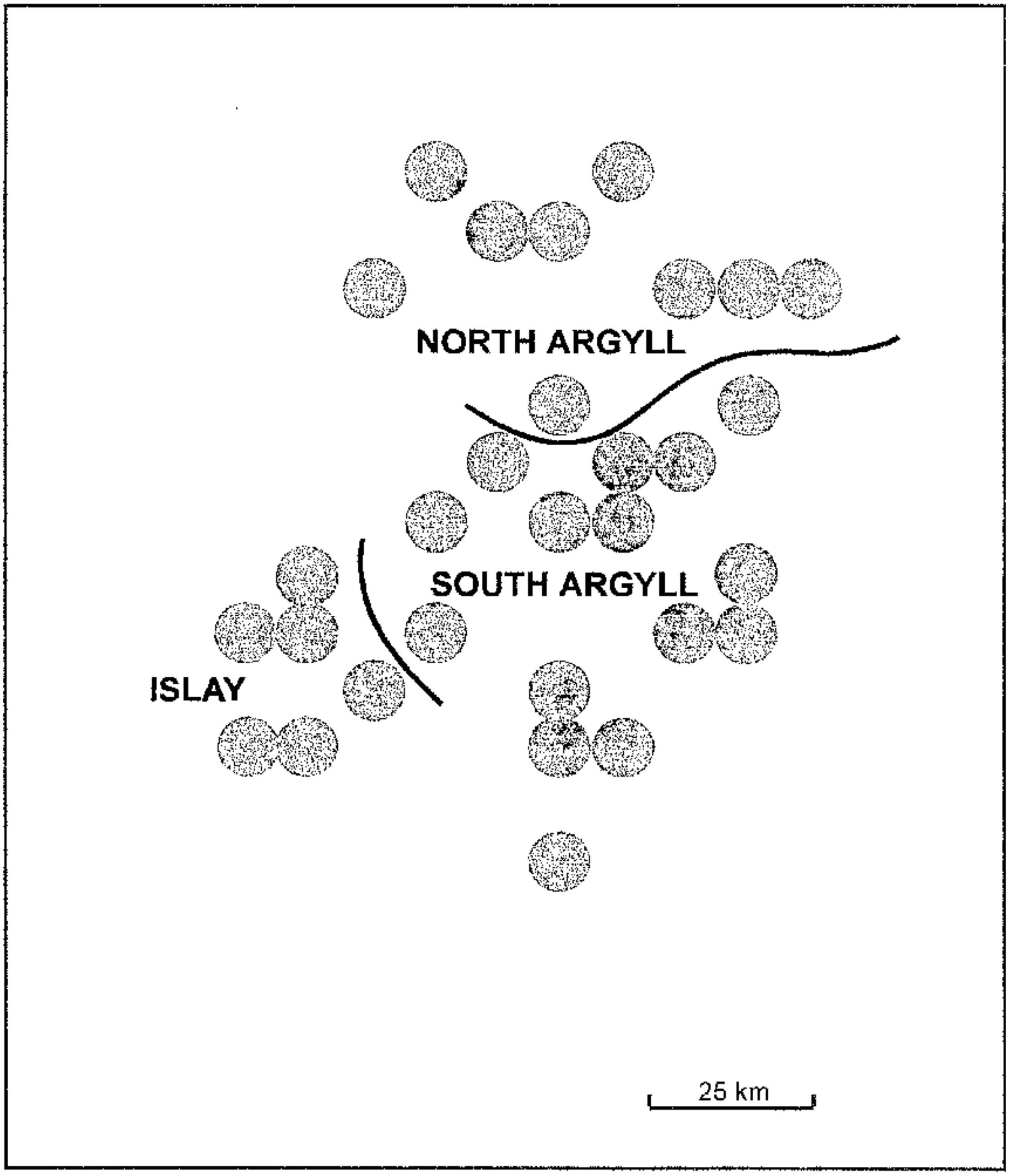

Figure 1: Location of 10x10km squares searched for breeding hen harriers in 1988-89. Fifteen squares were searched each year.

Logistic regression analysis was used to estimate the probability that a sample point was used by a nesting harrier. The dichotomous dependent variable was the point-type (i.e. nest or random) and the covariates were measures of habitat around each point. Data from all searched 10x10km squares were pooled. Two models were built, using the habitat variables for 1km and 3km radii, respectively. Backwards elimination of variables was specified, and a likelihood ratio test used to select variables for removal.

Breeding performance

The precise locations of harrier nests vary from year to year, sometimes by >1km (*pers. obs.*). However the distribution of nests relative to one another generally remains constant and, over time, discrete clusters of nests ('nest ranges') are normally easy to identify. A sample of 30 nests occupied by harriers in 1989 were randomly selected. These included 10 nests in north Argyll, 8 in south Argyll, and 12 on Islay (these areas are indicated in Fig. 1). Nest locations were re-visited annually until 1994 and an area of ca. 7km^{-2} searched for evidence of breeding during early May. Located nests were visited on 2 occasions, at least 10 days apart, during the laying and incubation period. Clutch size was recorded on each visit and the greater figure taken as the number of eggs laid. Further visits were made during the period that young were present, including one when the chicks were approximately 25 days old. The number of young present on this visit was taken as the brood size at fledging.

Estimated laying dates for first eggs were calculated following guidelines given in Etheridge *et al.* (*in prep*). These assume (1). a 2-day interval between the laying of each egg, and (2). that incubation commences when the 3rd egg is laid and lasts for 30 days. The timing of breeding was determined largely from incomplete and part-hatched clutches found during the laying and hatching periods, respectively. Where nest visits did not coincide with either of these periods, first egg dates were calculated from estimates of chick age based on measurements of the maximum closed-wing length (Scharf & Balfour 1971). Wing length increases at a constant rate from day 8 after hatch up to at least day 28, and both growth rates and actual measurements are similar for each sex during this time (Etheridge 1993).

The central point of each nest range was determined by calculating the mean northing and easting of grid references used for nesting, 1989-94, counting each nest once every time it was used. The areas of each habitat class were then measured for radii of 1km and 3km around each range centroid. Linear regression analysis with forward selection of variables was used to investigate the effects of habitat on 3 range-specific measures of breeding performance. These were: (1). median laying date, (2). mean clutch size, and

(3), mean brood size at fledging. Nests occupied by beta females[1] in bigamous matings were excluded, since the broods of these birds tend to be less well provisioned by males than those of alpha females (Simmons 1988) and we might therefore expect them to be smaller. Habitat data for 1km and 3km around each range centroid were pooled in these analyses, since the distinction between the 2 radii had less meaning than in the case of measurements around actual nests sites. In order to reduce the number of variables used in each analysis, univariate correlations were examined between the range-specific values for each breeding parameter and those for each habitat variable. Variables that correlated using a significance level of $\propto = 0.5$ were chosen for further consideration. In cases where the variables representing a habitat class at different radii each correlated with one of the breeding parameters, only the more strongly correlated variable was retained.

Statistical analyses were carried out using SPSS ver. 6 (Norusis/SPSS Inc. 1993). Prior to each analysis, frequency distributions of the habitat and elevation variables were examined to check that the data met the assumptions of multivariate analysis. Where necessary, variables were transformed to improve normality. *Ad hoc* evaluations of assumptions regarding the distribution of data were carried out by examining residuals scatter plots. Plots of independent variables against residuals were inspected for systematic differences in residual variance. A summary of the variables used in each analysis is shown in Table 1.

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[1] Beta females were defined as those that commenced laying eggs last within bigamous matings.

Table 1: Variables used in analyses of hen harrier occupancy and breeding success.

DESCRIPTION	VARIABLE	ANALYSIS		
		Occupancy		Breeding performance
		Broad-scale	Fine-scale	Spatial variation
DEPENDENT				
No. nests in 10x10km sqs.	**NEST**	●		
Point-type (nest / random)	**TYPE**		●	
Breeding parameters:				
Median laying date	**LDAY**			●
Mean clutch size	**EGGS**			●
Mean brood size	**YNG**			●
INDEPENDENT				
Area (ha) of land cover and elevation classes[1] within:				
10x10km sqs.		●		
1km and 3km of nest and random points[2]			●	
1km and 3km around centroids of nest ranges[2]				●

[1] Land cover and elevation classes: Heath/bog (HB), Acidic grassland (AG), Neutral grassland (NG), New forest (NF), Pre-thicket forest (PR), Post-thicket forest (PO), Restock (RS). Elevation classes: 1-50m (AL), 51-250m (AM), >250m (AH).

[2] Variables measured within 1km and 3km radii of points and range centroids were given the suffixes '_1' and '_3', respectively.

RESULTS

Occupancy

A total of 54 harrier nests were located in the 30 10x10km squares searched in 1988-9. Each square held 0-7 harrier nests (mean = 1.8 ±1.94 *S.D.*). The number of nests and areas of each habitat class are shown for each square in Appendix 5. When the number of nests was regressed on the habitat variables for each square (model I), no variables were selected. This analysis suggests that, at a landscape scale, variation in hen harrier nesting density cannot be explained by differences in land cover and elevation.

Five variables, representing the amounts of heath/bog, new forest, pre-thicket forest, post-thicket forest and terrain >250m around each point, were retained by a logistic regression model that related point-type to habitat within 1km (model II). The model fitted the data well (X_{1}^{2} = 25.85, P = 0.0001), and correctly classified 81% of nest and 67% of random locations. The likelihood of a point being occupied by a harrier nest was most influenced by the amount of heath/bog and pre-thicket forest, followed by the extent of terrain >250m and other forest habitats (Table 2). Each of the habitat variables had a positive effect on harrier occupation, whereas that representing ground >250m had a negative effect.

Table 2: Summary statistics for a logistic regression model to estimate the probability of a point being occupied by a hen harrier nest using characteristics of land cover and elevation within 1km (model II). All variables except HB_1 and AM_1 were log (n+1) transformed.

(a). Matrix of Pearson correlation coefficients between candidate variables.

	HB_1	**AG_1**	**NG_1**	**NF_1**	**PR_1**	**PO_1**	**RS_1**	**AL_1**	**AM_1**
AG_1	**-.37**								
NG_1	-.04	+.06							
NF_1	**-.36**	-.13	**-.21**						
PR_1	**-.34**	-.14	-.16	-.18					
PO_1	**-.35**	-.05	-.11	**-.20**	+.01				
RS_1	-.02	+.05	-.07	-.09	+.06	+.06			
AL_1	**+.20**	-.06	**+.54**	**-.29**	**-.19**	-.06	-.06		
AM_1	-.12	+.08	**-.34**	**+.30**	+.05	+.11	+.08	**-.77**	
AH_1	+.03	-.11	**-.21**	-.02	**+.27**	-.12	-.01	-.24	**-.34**

Correlations significant at P<0.05 shown in **bold**.

(b). Regression coefficients, Wald statistics (and associated significance *P*), partial correlations (*R*) and changes in likelihood (Exp [B]) for the variables selected. † = log (n+1) transformed.

Variable	**B**	**S.E.**	**Wald**	**df**	***P***	***R***	**Exp[B]**
HB_1	.013	.004	11.68	1	.001	.254	.987
PR_1†	.017	.005	10.41	1	.001	.237	.983
AH_1†	-.018	.006	8.73	1	.003	-.212	1.019
NF_1†	.010	.004	6.41	1	.011	.172	.990
PO_1†	.011	.005	5.22	1	.022	.147	.989
Constant	-2.611	.862	9.17	1	.002		

Therefore $Prob(y) = a / 1 + a$,

where $a = e^{-2.611 + 0.013 HB\_1 - 0.017 \log PR\_1 - 0.018 \log AH\_1 + 0.01 \log NF\_1 + 0.011 \log PO\_1}$

The robustness of this analysis was tested by introducing a geographic factor into the model. This was achieved by creating dummy variables X1 and X2, representing the 3 areas north Argyll, south Argyll, and Islay. These were then forced into the logistic equation as a single group. When the model was re-selected, all but one of the variables previously selected (representing post-thicket forestry) were retained. Inclusion of area made little difference to the fit of the model ($X_L^2 = 24.98$, $P = 0.0001$), but led to a decline in the accuracy with which points were classified (nest 74% and random 63%).

When the areas of habitat within 3km were used in the analysis (model III), variables representing the amount of heath/bog, acid grassland, pre-thicket forest, post-thicket forest and terrain >250m were selected. This model fitted the data less well than model II ($X_L^2 = 134.04$, $P = 0.008$), and correctly classified fewer points (nest 76% and random 59%). The likelihood of a point being occupied by a harrier nest was most influenced by the amount of terrain >250m, followed by the extent of heath/bog and post-thicket forest (Table 3). Pre-thicket forest and acid grassland had relatively small effects. Once again, the effects of the habitat variables were positive whilst that of altitude >250m was negative. With area variables X1 and X2 in the equation, model III retained only 2 of the previously selected variables. These represented terrain >250m and heath/bog. Inclusion of area resulted in considerably improved goodness-of-fit ($X_L^2 = 15.54$, $P = 0.0004$), but made little difference to the accuracy with which nest and random points were classified (68% and 59%, respectively).

Table 3: Summary of a logistic regression model to estimate the probability of a point being occupied by a hen harrier nest using characteristics of land cover and elevation within 3km (model III). All variables except HB_3, AG_3, NG_3 and AM_3 were log (n+1) transformed.

(a). Matrix of Pearson correlation coefficients between candidate variables.

AG_3	**-.50**								
NG_3	+.02	0							
NF_3	**-.24**	-.03	**-.23**						
PR_3	**-.31**	-.02	**-.29**	+.05					
PO_3	**-.62**	+.19	**-.20**	+.03	+.18				
RS_3	**-.24**	-.11	-.10	+.03	+.17	**+.39**			
AL_3	**+.29**	**-.29**	**+.55**	**-.42**	**-.31**	-.19	-.04		
AM_3	**-.22**	**.36**	-.16	**+.51**	+.15	+.18	+.10	**-.74**	
AH_3	+.02	+.04	**-.49**	+.07	**+.36**	+.02	-.05	**-.40**	-.12
	HB_3	**AG_3**	**NG_3**	**NF_3**	**PR_3**	**PO_3**	**RS_3**	**AL_3**	**AM_3**

Correlations significant at $P<0.05$ shown in **bold**.

(b). Regression coefficients, Wald statistics (and associated significance *P*), partial correlations (*R*) and changes in likelihood (Exp [B]) for the variables selected. † = log (n+1) transformed.

Variable	**B**	**S.E.**	**Wald**	**df**	***P***	***R***	**Exp[B]**
AH_3†	-.002	.001	8.05	1	.004	-.201	1.002
HB_3	.002	.001	7.15	1	.007	.185	.998
PO_3†	.002	.001	5.06	1	.024	.143	.998
PR_3†	.002	.001	3.33	1	.068	.094	.998
AG_3	.001	.001	2.63	1	.105	.065	.999
Constant	- 2.817	1.191	5.59	1	.018		

Therefore *Prob(y)* = *a* / 1 + *a*,

where $a = e^{-2.817 - 0.002 \log AH\_3 + 0.002 HB\_3 + 0.002 \log PO\_3 + 0.002 \log PR\_3 + 0.001 AG\_3}$

These analyses suggest that harriers preferred nest sites where both the local environment and wider hinterland included much heathland and forestry, and that they avoided terrain above 250m.

Breeding performance

Eggs were laid every year in 25 of the 30 monitored nest ranges, and in all but one year in the remaining 5 ranges. Of 175 clutches laid, 151 (86%) hatched at least one young that survived to fledging age. First egg dates ranged from April 9 to June 7 (median: May 7, inter-quartiles May 1-13), and clutch size from 2 to 7 eggs (mean 4.38 ±*SD* 0.85). The number of young that survived to fledging per nest where eggs were laid ranged from 0 to 5 (mean 2.57 ±*SD* 1.48).

Spatial variation

Between 5 and 8 habitat variables met the criteria for inclusion in regression models to investigate variation in breeding performance between ranges (Table 4). No variables were selected by the model to predict laying date (model IV). The model to predict clutch size (model V) selected a single variable, representing pre-thicket forestry within 1km of range centroids. However, this model did not fit the data particularly well ($R = .38$, $F_{1,28} = 4.82$, $P = 0.037$) and, based on adjusted R^2, explained only 12% of the variance in clutch size. The model to predict brood size at fledging (model VI) selected variables representing heath/bog within 1km and terrain >250m within 3km. With both variables in the equation this model gave a good fit to the data ($R = .61$, $F_{2,27} = 8.04$, $P = 0.002$) and explained 33% of the variance in brood size. Analysis of the frequency distribution of the residuals for this model showed that they did not depart significantly from zero ($Z = 0.517$, $P = 0.95$, *ns*).

Table 4: Candidate land cover and elevation variables available for inclusion in multiple regression models to predict breeding performance. The table shows the correlation coefficients between each variable and the range-specific values for median laying date, mean clutch size, and mean brood size at fledging.

Land cover and elevation variables	**Breeding performance**					
	Laying date (Model IV)		**Clutch size (Model V)**		**Brood size (Model VI)**	
	r	***P***	***r***	***P***	***r***	***P***
HB_1	-0.24	0.194	-	-	+0.42	**0.019**
HB_3			-0.25	0.176	-	-
AG_3			+0.22	0.249	-0.17	0.358
NG_3	-0.22	0.251	-	-	+0.17	0.382
NF_1†	+0.13	0.482				
PR_1†			+0.38	**0.037**	-	-
PR_3†	+0.24	0.199	-	-	+0.24	0.210
PO_1†	-0.14	0.470	-0.19	0.312	-	-
PO_3†			-	-	+0.14	0.475
AL_1†	-0.29	0.122	-	-	+0.20	0.296
AM_1	+0.26	0.169				
AM_3			-	-	-0.29	0.120
AH_3†	+0.23	0.228	+0.20	0.294	+0.33	0.071

† Log (n+1) transformed. Correlations significant at $P < 0.05$ are shown in **bold**.

Correlations among the candidate variables and summary statistics for model VI are shown in Table 5. Terrain >250m within 3km of the range centroids correlated strongly with the amount of pre-thicket forest within the same radius (Pearson r = 0.607, $P <$ 0.001) and it was hypothesised that this might largely explain why the terrain variable was significant in the model. In order to test this, model VI was re-run using all the candidate variables except AH_3. Heath/bog was again selected, followed by the variable representing pre-thicket forest. The re-selected model fitted the data well (R = .59, $F_{2,27}$ = 7.24, P = 0.003) and explained only slightly less of the variance in mean brood size (adjusted R^2 = .30) than previously.

Table 5: Statistical regression of land cover and elevation variables on mean brood size at fledging in each nest range (model VI).

(a). Pearson correlation coefficients between candidate variables.

AG_3	**-.56**						
NG_3	**.57**	-.37					
PR_3†	**-.35**	.08	**-.53**				
PO_3†	-.16	.07	**-.37**	**.53**			
AL_1†	**.38**	**-.48**	**.76**	**-.35**	-.27		
AM_3	**-.40**	**.52**	**-.62**	.14	.25	**-.88**	
AH_3†	-.22	.13	**-.54**	**.61**	.27	**-.36**	.08
	HB_1	**AG_3**	**NG_3**	**PR_3†**	**PO_3†**	**AL_1†**	**AM_3**

† Log (n+1) transformed. Correlations significant at $P<0.05$ shown in **bold**.

(b). Unstandardised regression coefficients (β) and intercept, standardised regression coefficients (*Beta*), departure of coefficients from zero (*T*) and significance, semi-partial correlations (sr^2), squared multiple correlations (R^2), *F* ratio for change in R^2 (F_i), and *R*, R^2 and adjusted R^2 after entry of both independent variables.

	β	***Beta***	***T***	***P***	sr^2	R^2	F_{i} **(1,28)**	
					(a)	**(b)**		
HB_1	0.004	0.52	3.36	0.002	0.18	.18	6.14	*
AH_3†	0.001	0.45	2.89	0.008	0.19	.37	8.33	**
Intercept	1.653							
					R	.61 **		
					R^2	.37		
					Adj. R^2	.33		

(a). = incremental. **(b).** = cumulative. † Log (n+1) transformed. * $P<.05$, ** $P<.01$.

When model VI was re-selected with the variables representing area (X1-2) forced into the equation, only the variable representing heath/bog was selected. After entry of all IVs, R = .53, $F_{3,26}$ = 3.43, P = 0.031. This analysis shows that the effects of altitude on brood size were not consistent across the 3 areas.

Temporal variation

Change in breeding performance over time was investigated by fitting regression lines to plots of each breeding parameter against year separately for each nest range. Since the hypothesis being tested was whether breeding performance declined in ranges with much young forestry relative to those elsewhere, ranges were grouped according to forest cover. The proportions of unafforested, young first rotation forest (new and pre-thicket), and established forest (post-thicket and restock) habitat within a radius 3km of each range centroid were determined. Ranges with >75% unafforested ground (n = 17) were classified as 'open', and the remainder as either 'young' or 'established' forest (n = 8 and 5, respectively) depending on which type was dominant.

When the mean values of each breeding parameter were plotted against year for each habitat group, no significant trends were found in either laying date (open: r = 0.24, P = 0.65; young forest: r = -0.30, P = 0.56; established forest: r = 0.62, P = 0.20) or clutch size (open: r = -0.66, P = 0.15; young forest: r = -0.70, P = 0.12; established forest: r = -0.78, P = 0.07). However, brood size declined significantly in all 3 groups (Fig. 2).

There were no significant differences in the means of the range-specific regression coefficients for plots of each breeding parameter against year between open and young forest populations (laying date: t = 1.29, P = 0.21; clutch size: t = -0.59, P = 0.56; brood size: t = 0.12, P = 0.91; df = 23 in all cases), or between young and established forest populations (laying date: t = -1.79, P = 0.10; clutch size: t = 0.90, P = 0.39; brood size: t = -0.72, P = 0.49; df = 11 in all cases).

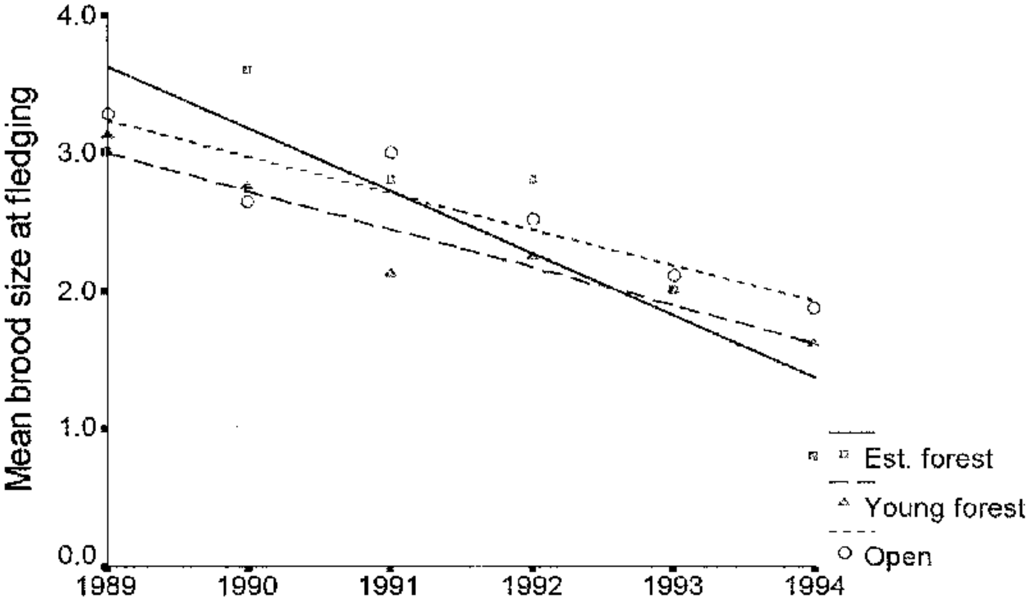

Figure 2: Trends in hen harrier nest productivity (as measured by the number of young fledged per nest where eggs were laid) for nest ranges grouped by forest cover. Relationships between mean brood size at fledging against year: open $r = -0.92$, $P = 0.008$, n = 17; young forest $r = -0.95$, $P = 0.003$, n = 8; established forest $r = -0.86$, $P = 0.03$, n = 5).

Summary

The measured variables did not influence the timing of breeding by harriers and had only a weak effect on clutch size. However, ranges whose cores contained much heathland in 1988 tended to fledge larger broods in subsequent years. Ranges with more elevated hinterlands also produced larger broods, although the strength of this effect varied between areas and may have been largely due to the strong positive relationship between altitude and pre-thicket forest cover. Nest productivity in both open and afforested habitats declined during the study. The amount of young first rotation forestry within the nest range hinterland did not significantly influence the magnitude of this decline.

DISCUSSION

An understanding of the relationships between the distribution of birds and their environment is important to decisions affecting land management (Haworth & Thompson 1990). This is particularly important in the case of hen harriers because of concern about the long-term effects of forestry. Although nest site selection by harriers has been described previously (e.g. Hamerstrom & Kopeny 1981; Simmons & Smith 1985; Redpath *et al. in press*) this is the first study to relate nesting preferences to the composition of the habitat available for hunting.

Variation in habitat composition within the 10x10km squares did not explain differences in nesting density. This may have been because there was not enough variability between squares in the amounts of those habitats that had an effect on nest site selection. Given the high degree of nest site fidelity exhibited by harriers (Watson 1977), it is also possible that nesting density was influenced by the past availability of habitat, rather than that present in 1988. Finally, habitat effects may have been masked by those of other factors, such as human disturbance. This could be investigated by mapping anthropogenic features such as buildings and roads.

Harriers chose low and medium elevation nest sites that maximised the amount of heathland and forestry within the surrounding environment. Heathland and forest cover-types were strongly negatively correlated yet both had positive effects on the likelihood of harrier occupation, suggesting that harriers found them to some extent interchangeable. We might expect the availability of habitats most suitable for nest concealment to have a greater influence on nest site selection at the local rather than landscape scale. Scottish hen harriers nest mainly in tall (ca. 0.5m) heather (Redpath *et al. in press*), and in the present study this vegetation occurred mainly in young conifer plantations. This may explain why the cover of new and pre-thicket forest had a stronger effect on selection within 1km of nests than it did within 3km.

The positive effect of post-thicket forest (a habitat largely avoided by foraging harriers) on nest selection is surprising. It is possible that closure of the tree canopy was incomplete in some of the forests classified as post-thicket, and that these therefore still provided suitable foraging for harriers. Using black and white aerial photographs, it was probably easier to mis-classify heather / conifer mixtures as post-thicket forest than it was closed canopy cover as pre-thicket forest. This may also have caused the importance of pre-thicket forest to be under-estimated. If genuine, harriers' preference for nesting in post-thicket forest may be cultural. Expansion of the harrier population in Scotland since 1945 coincided with the establishment of forestry in many areas of former moorland

(Blake 1976; Watson 1977). Harriers reared in forests may have an inherent preference for nesting in this habitat, resulting in the continued occupation of forests beyond the point at which the habitat provides suitable foraging. This might explain the location of several nests in heather rides and other unplanted areas deep within mature forests.

Despite the strong positive correlation between pre-thicket forestry and terrain >250m, these variables had opposite effects on nest site selection. Thus the likelihood of harrier occupation increased with the extent of pre-thicket forest, whereas it decreased with the extent of high altitude ground. This suggests that harriers liked to settle in areas with young trees, but only if these were located at low to moderate elevations. This may have been because prey in low-lying pre-thicket forests were more abundant, or available earlier in the season, or both. Paradoxically, over the 6 years that breeding performance was studied, brood sizes were greater in more elevated nest ranges. However, we would expect tree growth rates to decline with altitude, and any pre-thicket forest may therefore have remained a profitable foraging environment for longer in elevated ranges than in low ones.

Foraging harriers selected pre-thicket forests ahead of heathlands (Chapter 3), suggesting that heathlands were less profitable foraging environments. Why then did the availability of heathland have a more positive effect on the production of young? A possible explanation is that food availability in heathland areas remained more or less constant throughout the study, whereas in pre-thicket forests it declined rapidly as the trees matured. Thus many of the areas classified as pre-thicket forest in 1988 probably became unsuitable for foraging during the following 6 years, and this may have led to a reduction in nest provisioning and therefore breeding success. If so, we would expect the observed declines in productivity to have been greater in ranges with much young forest than in those with little or no forestry, whereas this was not the case. A more plausible explanation is that heathlands were superior in terms of available prey biomass. Thus, although harriers did not capture prey any more frequently in heathland than in pre-thicket forest (Chapter 5), they might have caught larger items such as gamebirds and lagomorphs. This hypothesis is consistent with the finding of Etheridge *et al.* (*in press*) that, after taking human interference into account, more young are fledged from nests located in moorland managed for red grouse *Lagopus lagopus scoticus* than other moorlands and forests. Although suitable large prey were scarce in Argyll (Chapter 7), their distribution was heavily biased toward unafforested habitats (Appendix 4). Furthermore, the biomass of these prey is often dramatically greater than that of small items (see Chapter 6) and harriers might therefore need to catch only a few individuals in order to make a large impact on nest provisioning. It is also possible that harriers nesting in heathland suffer fewer losses of eggs and young to predators such as fox *Vulpes vulpes*, stoat *Mustela erminea* and ferret *Mustela furo*, which are widespread in many forests. This is not supported by Etheridge's data, however, since predation normally involves the loss of entire clutches or broods and he compared only successful nests. In the present study, there was little evidence of egg predation, and complete brood loss was rare.

Productivity declined across all of the habitat-types tested. In view of the relatively short duration of the study, we might expect trends in breeding performance to be dramatically affected by stochastic events, such as poor weather during one or more breeding seasons. Both spring 1993 and 1994 were unusually cold and wet, and this may have resulted in reduced provisioning rates and lower clutch and brood survival. However, it is worth noting that habitat change, especially the loss of rank ground vegetation, may also have had an effect. Thus, in open habitats, heather and other dwarf shrubs suitable for nesting declined as a result of the cumulative effects of grazing and burning. Likewise, in afforested habitats, tall heather and prey-rich grassland were suppressed by developing tree foliage. With the exception of one area managed specifically for harriers, breeding numbers remained stable or declined slightly over the study period, and the decline in productivity cannot therefore have been a result of density dependent effects. Why did harrier productivity not decline more in nest ranges with much young forestry? One answer might be that foraging harriers were able to compensate for the reduction in the suitability of forests by making greater use of other habitats. In this context the selection of nest sites with relatively large amounts of heathland is interesting, since it suggests that heathland may act as a buffer against the loss of young forest habitats. Harriers may also have coped by foraging further afield. The extent to which it is possible for them to do this without compromising productivity is unknown. However, the wide variation in recorded foraging range size (see Chapter 1) suggests that harriers are extremely adaptable.

Summary

The results of this study indicate that harriers located their nests so as to maximise the amounts of surrounding heathland or forest, and avoid land >250m. Nest productivity (as measured by the number of young fledged per nest where eggs were laid) was highest in areas with much heathland, possibly because more large prey were available in this habitat than elsewhere. Productivity declined over the period of study, but did not decline faster in areas where developing trees caused preferred foraging habitats to become less suitable. I suggest that this is because harriers were able to exploit alternative habitats more, or extend their foraging range, or both.

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CONCLUSIONS

GENERAL DISCUSSION

The hen harriers observed in this study foraged preferentially in recently established first rotation forests, where the interaction of dense ground vegetation and strong populations of meadow pipit *Anthus pratensis* and field vole *Microtus agrestis* resulted in relatively profitable hunting conditions. Developing trees tended to be avoided, presumably because they hindered harrier manoeuvrability and prey accessibility. Thus harriers' use of forests declined as trees developed, and closed-canopy forest was the least preferred habitat studied. Despite this, harriers continued to use some older forests, probably because they were able to exploit unplanted habitat, or areas in which tree development was sparse.

Foraging habitat preferences appear to explain local population increases or range expansions apparent in some areas where young forests have replaced open ground (Bibby and Etheridge 1993). Forestry and heathland were found to have strong positive effects on harrier nest site location, and harriers are therefore likely to have benefited most where plantations have been established on grassland habitats. This is perhaps unsurprising, since intensive grazing and regular burning mean that most grasslands have little tall ground vegetation suitable for nesting. Habitat preferences also appear to explain population declines reported in some areas where forests have matured (O'Flynn 1983; Bibby and Etheridge 1993), although the discovery of some nests in post-thicket plantations during the current study suggests that harriers may continue to breed in forests long after they have ceased to be useful for foraging.

The study was inconclusive in respect of harriers' preference for young second rotation forestry. This habitat is still relatively scarce in Argyll at present and was available to foraging harriers in only one of the 4 sites studied, where selection varied between years. Despite this, there is some indication that restocks are less attractive to harriers than first rotation crops of similar age. For example, over the 3 years of study I did not locate any harrier nests during searches of Argyll restocks known to have held harriers when first afforested. This included ca. 500ha of recently re-planted forest near Carradale on the Kintyre peninsula which in 1958-9 held 9 breeding pairs (D. Watson, *pers. comm.*).

Unlike some raptors (e.g. buzzard *Buteo buteo* and kestrel *Falco tinnunculus*) harriers do not normally hunt from perches or by soaring or hovering. Instead they forage whilst on the move, either by methodically quartering the ground or by following continuous landscape features such as streams and tracks. Foraging efficiency is therefore likely to be adversely affected by habitat fragmentation. Young first rotation plantations generally comprise large and unbroken areas of prey-rich habitat. Furthermore, they are generally bordered by extensive moorlands which provide further hunting opportunities. These conditions are unlikely to be re-created in second rotation forests, since trees are generally felled in small coups and rapidly replaced. As a result, only about 25% of forests are predicted to remain open at any one time (Petty and Avery 1990), and this is unlikely to form contiguous habitat. Harriers will therefore face the problem of having to cross (often extensive) areas of mature forest, unsuitable for foraging, in order to exploit relatively small patches of productive habitat. Even within these patches hunting conditions may not match those of first rotations, since restocks are normally established on ground bereft of vegetation and prey populations may therefore respond more slowly. Although developing restocks appear to hold populations of voles that are comparable with those of first rotations, meadow pipit densities are much lower. Moreover, debris and brash from the felled crop may cause prey to be less accessible to harriers.

The study considered the effects to harriers of afforestation as practised in west Scotland, where coniferous trees (mainly Sitka spruce *Picea sitchensis*) have been established on relatively unproductive moorlands hitherto grazed by large numbers of sheep *Oves aries* and red deer *Cervus elaphus*. The extent to which these effects might apply in other situations is unknown, but it seems reasonable to suppose that differences in vegetation and prey between moorland and forest habitats in Argyll and those elsewhere in Britain are likely to have a strong influence on harrier behaviour. For example, harriers' habitat preferences might be very different in areas where they have access to native broad-leaved woodland and heather moorland managed for red grouse *Lagopus lagopus scotticus*.

Harriers caught fewer prey per hour of foraging in Argyll than in north-east Scotland. This difference is likely to have been even greater in biomass terms due to greater availability of large prey, such as red grouse and lagomorphs, in the north-east. Further work is required to determine the reasons for harriers' relatively poor foraging success in Argyll, and establish whether they are able to compensate for lower capture rates by foraging over longer periods. Comparison of harrier diet and foraging behaviour in a number of upland areas in Britain, each having differing habitat characteristics, might enable differences in breeding performance to be explained.

IMPLICATIONS FOR FOREST MANAGEMENT

Economic enterprise in the British uplands often operates on the margins of financial viability and land use is therefore heavily dependent on public subsidy (Mowle & Bell 1988). Fiscal incentives to encourage forest establishment by private companies and individuals ceased in 1988, leading to a dramatic decline in new planting. However, shifts in public policy toward other land uses may result in renewed forest expansion. For example, reductions in hill farming subsidy might make alternative land uses more financially attractive, whilst incentives to take agricultural land out of production might make hitherto more expensive land affordable for forestry. Whatever strategic changes occur, afforestation is already a major upland habitat and expansion is likely to continue until at least the year 2000.

How can the use of commercial forests by harriers be made more sustainable? Based on the results of the current study, an obvious approach would be to increase the area occupied by open and semi-open ground, and design forests such that this area formed part of an integrated foraging environment. Integration might be achieved in one of 2 ways:

1. By creating large blocks of even-aged forest, each bordered by moorland or other suitable open habitat, such that at least one block is occupied by young trees at any one time. However, this approach requires that forests are more or less completely surrounded by suitable open habitat, which is rarely the case. Furthermore, it contradicts current forest restructuring objectives which aim to increase wildlife and landscape diversity.
2. By inter-linking relatively small areas of suitable habitat within the forest with one another and the adjacent moorland. This would enable harriers to forage through the forest at all stages of its development. Tree development is likely to disrupt habitat continuity and, in many cases, it may not be possible to design forests to take account of this problem. It is probably better, therefore, to create a more or less permanent matrix of open and semi-open habitat throughout the forest. For example, areas of unplanted ground and growth-checked trees could be linked by removing trees to create foraging corridors. Planting breaks and buffers alongside streams and tracks could also be assimilated into the design for this purpose.

The primary aim of upland forests is timber production, and this is likely to limit the scope for harrier management. Thus, it is unrealistic to expect foresters to maintain large areas of potentially productive land solely for the benefit of harriers. However, the Forest Authority allocate funds through annual management grants specifically to offset costs incurred in conserving or enhancing forest wildlife. Furthermore, passive management of areas of poor tree growth (i.e. withholding remedial treatment such as drainage and the application of fertilisers) reduces input costs. The financial return on growing timber in the upland of Britain is often marginal. This is particularly true of forests located on islands and the western Scottish seaboard, where exposed and remote terrain tends to result in relatively poor growth rates, greater windthrow hazard, and higher management and extraction costs. In many of these forests, grant-assisted operations to improve habitat for harriers may therefore represent a valuable supplement to the revenue from conventional management. Experimental work is required to assess the importance of scale and design in forest restructuring as a tool for harrier management. This should be given high priority in view of the declining amount of young first rotation forestry in Britain, which is likely to lead to an increasing proportion of the harrier population occupying moorland managed for red grouse, where raptors are percieved to conflict with shooting interests.

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Study site/year	Nests	Grid reference	NP	Foraging bouts	Foraging time (mins.)	Habitat	Area (km²)
Cowal 1994	8	NR 93/71	1.37	0	0.00	**Post-thicket**	0.81
		NR 94/82	5.94	4	25.00	Heath/bog	0.06
						Acid grass	0.77
		NR 94/84	4.17	8	43.12	Heath/bog	0.04
						New forest	0.63
						Post-thicket	0.04
		NR 95/71	0.47	0	0.00	Acid grass	0.24
						Neutral grass	0.39
						Post-thicket	0.04
		NR 96/86	2.81	5	42.81	**Pre-thicket**	0.82
		NS 03/78	0.69	1	4.37	**Heath/bog**	0.77
						Pre-thicket	0.02
Islay 1993	14	NR 17/52	2.44	13	64.50	Heath/bog	0.31
						Neutral grass	0.59
						Pre-thicket	0.01
		NR 19/54	4.55	6	22.25	Heath/bog	0.05
						Acid grass	0.80
						Neutral grass	0.04
						Pre-thicket	0.07
		NR 21/56	8.55	10	46.25	Heath/bog	0.04
						Pre-thicket	0.93
		NR 34/52	1.82	5	15.84	**Heath/bog**	0.86
						Acid grass	0.01
		NR 35/56	2.20	5	16.75	Acid grass	0.03
						Neutral grass	0.06
						Post-thicket	0.76
		NR 36/54	1.45	3	21.94	**Heath/bog**	0.89

Study site/year	Nests	Grid reference	NP	Foraging bouts	Foraging time (mins.)	Habitat	Area (km²)
Kintyre 1992	3	NR 69/41	0.82	1	7.50	**Neutral grass** Pre-thicket	0.75 0.07
		NR 70/42	1.49	2	6.14	**Heath/bog** Pre-thicket	0.41 0.34
		NR 71/40	0.91	1	1.07	**New forest** Pre-thicket	0.81 0.06
		NR 72/44	3.11	2	9.37	**Pre-thicket**	0.88
		NR 76/50	0.83	1	2.59	Pre-thicket **Post-thicket**	0.05 0.62
		NR 76/52	0.67	6	5.62	Heath/bog **Acid grass**	0.08 0.62
		NR 78/52	0.61	8	34.50	**Pre-thicket**	0.86
Lorn 1992	5	NN 00/26	1.83	5	5.00	**Acid grass** Post-thicket	0.78 0.05
		NN 01/22	2.12	7	27.09	Acid grass **Post-thicket**	0.06 0.77
		NN 03/23	3.02	7	20.00	**Heath/bog** Acid grass Post-thicket	0.56 0.20 0.05
		NN 05/22	1.60	5	10.01	**Neutral grass** Post-thicket	0.62 0.04
		NN 05/23	10.85	6	25.42	Neutral grass Pre-thicket Post-thicket **Restock**	0.10 0.03 0.24 0.26
		NN 05/24	1.84	1	4.03	**Post-thicket**	0.73
		NN 06/24	0.94	0	0.00	**Pre-thicket**	0.53

Study site/year	Nests	Grid reference	NP	Foraging bouts	Foraging time (mins.)	Habitat	Area (km^2)
Lorn 1993	3	NM 98/24	0.47	6	37.00	**Pre-thicket**	0.79
		NN 01/22	1.09	3	5.63	Acid grass	0.06
						Post-thicket	0.77
		NN 02/24	1.27	4	11.88	**Acid grass**	0.66
		NN 02/27	1.52	5	25.62	**New forest**	0.72
						Pre-thicket	0.11
		NN 04/23	0.49	1	1.25	**Heath/bog**	0.60
						Post-thicket	0.09
		NN 05/22	0.47	3	9.50	**Neutral grass**	0.62
						Post-thicket	0.04
		NN 05/23	0.47	1	5.00	Neutral grass	0.10
						Pre-thicket	0.03
						Post-thicket	0.24
						Restock	0.26
Lorn 1994	6	NM 98/24	5.52	9	29.38	**Pre-thicket**	0.79
		NN 00/28	0.97	0	0.00	**Post-thicket**	0.68
		NN 02/24	2.53	3	5.00	**Acid grass**	0.66
		NN 02/28	1.46	10	79.69	**New forest**	0.93
						Pre-thicket	0.01
		NN 04/23	5.85	4	17.50	**Heath/bog**	0.60
						Post-thicket	0.09
		NN 05/22	1.55	5	12.50	**Neutral grass**	0.62
						Post-thicket	0.04
		NN 05/23	2.39	0	0.00	Neutral grass	0.10
						Pre-thicket	0.03
						Post-thicket	0.24
						Restock	0.26

Appendix 2: : Estimation of selection indices for each habitat in the 6 study site/years.

Study site/year	**Habitat**	***Ai***	***A+***	***Ai/A+***	***ui***	***u+***	***ui/u+***	w_i	B_i
COWAL 1994	HB	0.87	4.63	0.188	10.94	115.31	0.095	0.505	0.086
COWAL 1994	AG	1.01	4.63	0.218	24.06	115.31	0.209	0.956	0.162
COWAL 1994	NG	0.39	4.63	0.084	0.00	115.31	0.00	0.00	0.00
COWAL 1994	NF	0.63	4.63	0.136	37.19	115.31	0.322	2.370	0.402
COWAL 1994	PR	0.84	4.63	0.181	42.81	115.31	0.371	2.046	0.347
COWAL 1994	PO	0.89	4.63	0.192	0.31	115.31	0.002	0.013	0.002
COWAL 1994	RS	0	0	-	0	0	-	-	-
ISLAY 1993	HB	2.15	5.45	0.394	66.53	187.53	0.355	0.899	0.175
ISLAY 1993	AG	0.84	5.45	0.154	22.26	187.53	0.119	0.770	0.150
ISLAY 1993	NG	0.69	5.45	0.127	36.00	187.53	0.192	1.516	0.295
ISLAY 1993	NF	0	0	-	0	0	-	-	-
ISLAY 1993	PR	1.01	5.45	0.185	46.75	187.53	0.249	1.345	0.262
ISLAY 1993	PO	0.76	5.45	0.139	16.00	187.53	0.085	0.612	0.119
ISLAY 1993	RS	0	0	-	0	0	-	-	-
KINTYRE 1992	HB	0.49	5.55	0.088	2.05	66.79	0.031	0.348	0.086
KINTYRE 1992	AG	0.62	5.55	0.112	5.63	66.79	0.084	0.754	0.186
KINTYRE 1992	NG	0.75	5.55	0.135	7.50	66.79	0.112	0.831	0.205
KINTYRE 1992	NF	0.81	5.55	0.146	1.07	66.79	0.016	0.110	0.027
KINTYRE 1992	PR	2.26	5.55	0.407	49.00	66.79	0.734	1.802	0.445
KINTYRE 1992	PO	0.62	5.55	0.112	1.55	66.79	0.023	0.208	0.051
KINTYRE 1992	RS	0	0	-	0	0	-	-	-
LORN 1992	HB	0.56	5.02	0.111	20.00	91.55	0.218	1.958	0.270
LORN 1992	AG	1.04	5.02	0.207	6.67	91.55	0.073	0.352	0.048
LORN 1992	NG	0.72	5.02	0.143	9.80	91.55	0.107	0.746	0.103
LORN 1992	PR	0.56	5.02	0.111	1.25	91.55	0.014	0.122	0.017
LORN 1992	PO	1.88	5.02	0.374	40.08	91.55	0.438	1.169	0.161
LORN 1992	RS	0.26	5.02	0.052	13.75	91.55	0.150	2.900	0.400
LORN 1993	HB	0.60	5.09	0.118	1.25	86.39	0.014	0.123	0.016
LORN 1993	AG	0.72	5.09	0.141	11.88	86.39	0.137	0.972	0.126
LORN 1993	NG	0.72	5.09	0.141	9.50	86.39	0.110	0.777	0.101
LORN 1993	NF	0.72	5.09	0.141	24.38	86.39	0.282	1.995	0.259
LORN 1993	PR	0.93	5.09	0.183	38.25	86.39	0.443	2.423	0.314
LORN 1993	PO	1.14	5.09	0.224	5.63	86.39	0.065	0.291	0.038
LORN 1993	RS	0.26	5.09	0.051	5.00	86.39	0.058	1.133	0.147

Study site/year	**Habitat**	Ai	$A+$	$Ai/A+$	ui	$u+$	$ui/u+$	w_I	B_I
LORN 1994	HB	0.60	5.05	0.119	17.19	144.07	0.119	1.004	0.163
LORN 1994	AG	0.66	5.05	0.131	5.00	144.07	0.035	0.265	0.043
LORN 1994	NG	0.72	5.05	0.142	12.50	144.07	0.087	0.608	0.099
LORN 1994	NF	0.93	5.05	0.184	78.75	144.07	0.547	2.968	0.483
LORN 1994	PR	0.83	5.05	0.164	30.32	144.07	0.210	1.280	0.208
LORN 1994	PO	1.05	5.05	0.208	0.31	144.07	0.002	1.035	0.002
LORN 1994	RS	0.26	5.05	0.051	0.00	144.07	0.00	0.00	0.00

Habitats: HB = heath/bog, AG = acid grassland, NG = neutral grassland, NF = recently afforested, PR = pre-thicket forest, PO = post-thicket forest, RS = restock forest.

Ai = area of habitat i observed (km^2).

$A+$ = total area of all habitats observed (km^2).

$Ai / A+$ = habitat i as a proportion of total habitat.

ui = time hen harriers observed foraging in habitat i (mins.).

$u+$ = total time hen harriers observed foraging in all habitats (mins.).

$ui / u+$ = time hen harriers observed foraging in habitat i as a proportion of total observed foraging time.

w_i = selection ratio.

B_i = standardised selection ratio.

Appendix 3: Habitat-specific density estimates for the 12 most abundant bird species, grouped by study site/year. Data were derived from transect and point count density estimates, each standardised to have zero means and unit standard deviations, then meaned within each habitat/study site/year.

	Meadow pipit	Song thrush	Skylark	Wren	Wheatear	Siskin
Cowal 1994						
Heath/bog	.54	-.23	-.52	-.32	-.26	-.23
Acid grassland	.52	-.23	.20	-.32	-.26	-.23
Neutral grassland	.56	-.23	-.52	.77	-.26	-.23
New forest	.97	-.23	-.52	-.32	-.26	-.23
Pre-thicket	.59	-.23	-.52	-.32	-.26	-.23
Post-thicket	-1.23	4.67	-.52	.26	-.26	-.23
Restock	-	-	-	-	-	-
Islay 1993						
Heath/bog	.98	-.23	.98	-.32	-.26	-.23
Acid grassland	1.38	-.23	3.38	-.32	5.00	-.23
Neutral grassland	.86	-.23	.48	-.32	-.26	-.23
New forest	-	-	-	-	-	-
Pre-thicket	.60	-.23	-.52	1.5	-.26	-.23
Post-thicket	-1.23	-.23	-.52	-.13	-.26	-.23
Restock	-	-	-	-	-	-
Kintyre 1992						
Heath/bog	.46	-.23	.59	-.32	-.26	-.23
Acid grassland	-.70	-.23	.28	-.32	.11	-.23
Neutral grassland	-.03	-.23	2.00	-.12	-.26	-.23
New forest	.92	-.23	.30	-.32	-.26	-.23
Pre-thicket	1.30	-.23	-.52	-.06	-.26	-.23
Post-thicket	-1.23	-.23	-.52	5.16	-.26	-.23
Restock	-	-	-	-	-	-

	Meadow pipit	Song thrush	Skylark	Wren	Wheatear	Siskin
Lorn 1992						
Heath/bog	-.09	-.23	-.52	-.32	-.26	-.23
Acid grassland	.62	-.23	-.52	-.32	-.26	-.23
Neutral grassland	-.97	-.23	-.52	-.32	-.26	-.23
New forest	-	-	-	-	-	-
Pre-thicket	-.91	-.23	-.52	-.32	-.26	1.41
Post-thicket	-1.23	-.23	-.52	.06	-.26	5.05
Restock	-1.23	-.23	-.52	-.07	-.26	-.23
Lorn 1993						
Heath/bog	-.26	-.23	.20	-.32	.14	-.23
Acid grassland	.96	-.23	2.48	-.32	-.26	-.23
Neutral grassland	-1.00	-.23	1.78	-.32	2.87	-.23
New forest	.91	-.23	-.52	-.32	-.26	-.23
Pre-thicket	1.30	-.23	-.52	-.32	-.26	-.23
Post-thicket	-1.23	-.23	-.52	-.32	-.26	1.22
Restock	-1.23	-.23	-.52	-.01	-.26	-.23
Lorn 1994						
Heath/bog	1.17	-.23	.43	-.32	.14	-.23
Acid grassland	-.68	-.23	-.52	-.32	-.26	-.23
Neutral grassland	-1.01	-.23	-.52	-.32	-.26	-.23
New forest	.96	-.23	-.52	-.32	-.26	-.23
Pre-thicket	1.17	-.23	-.52	-.32	-.26	-.23
Post-thicket	-1.23	3.38	-.52	1.03	-.26	-.23
Restock	-1.23	-.23	-.52	-.32	-.26	-.23

	Whinchat	Robin	Chaffinch	Willow warbler	Coal tit	Goldcrest
Cowal 1994						
Heath/bog	-.26	-.47	-.38	-.40	-.29	-.41
Acid grassland	-.26	-.47	-.38	-.40	-.29	-.41
Neutral grassland	-.26	2.46	-.38	-.40	-.29	-.41
New forest	-.26	1.87	-.38	-.06	-.29	-.41
Pre-thicket	-.26	.90	-.38	.34	-.29	1.09
Post-thicket	-.26	-.47	.34	-.11	.45	-.41
Restock	-		-	-	-	-
Islay 1993						
Heath/bog	-.26	-.47	-.38	-.40	-.29	-.41
Acid grassland	-.26	-.47	-.38	-.40	-.29	-.41
Neutral grassland	-.26	-.47	-.38	-.40	-.29	-.41
New forest	-		-	-	-	-
Pre-thicket	4.06	-.47	-.38	1.27	-.29	-.41
Post-thicket	-.26	1.18	4.5	-.40	3.29	1.96
Restock	-		-	-	-	-
Kintyre 1992						
Heath/bog	-.26	-.47	-.38	-.40	-.29	-.41
Acid grassland	-.26	-.47	-.38	-.40	-.29	-.41
Neutral grassland	-.26	-.47	-.38	1.30	-.29	-.41
New forest	-.26	-.47	-.38	1.25	-.29	-.41
Pre-thicket	-.26	.02	-.38	.88	-.29	-.41
Post-thicket	-.26	1.71	1.2	4.96	-.29	2.48
Restock	-		-	-	-	-

	Whinchat	Robin	Chaffinch	Willow warbler	Coal tit	Goldcrest
Lorn 1992						
Heath/bog	-.26	-.47	-.38	-.40	-.29	-.41
Acid grassland	3.88	-.47	-.38	-.40	-.29	-.41
Neutral grassland	-.26	-.47	-.38	-.40	-.29	-.41
New forest	-		-	-	-	-
Pre-thicket	.89	-.47	-.38	-.40	-.29	-.41
Post-thicket	-.26	.64	.04	-.40	1.42	3.64
Restock	-.26	-.47	.62	-.40	-.29	-.41
Lorn 1993						
Heath/bog	-.26	-.47	-.38	-.40	-.29	-.41
Acid grassland	-.26	-.47	-.38	-.40	-.29	-.41
Neutral grassland	-.26	-.47	-.38	-.40	-.29	-.41
New forest	-.26	-.47	-.38	-.40	-.29	-.41
Pre-thicket	-.26	-.47	-.38	.67	-.29	-.41
Post-thicket	-.26	1.10	.20	-.11	-.29	2.31
Restock	-.26	-.47	2.19	-.40	-.29	-.41
Lorn 1994						
Heath/bog	-.26	-.47	-.38	-.40	-.29	-.41
Acid grassland	-.26	-.47	-.38	-.40	-.29	-.41
Neutral grassland	-.26	-.47	-.38	-.40	-.29	-.41
New forest	-.26	-.47	-.38	-.40	-.29	-.41
Pre-thicket	-.26	-.47	-.38	-.06	-.29	-.41
Post-thicket	-.26	3.36	2.19	-.40	4.40	.34
Restock	-.26	-.47	-.38	-.40	-.29	-.41

Appendix 4: Habitat-specific density estimates for 3 bird categories, field vole and lagomorph spp., grouped by study site/year. The table shows numbers of birds km^{-1} recorded within 25m of line transects, FDI scores for field voles, and total lagomorphs km^{-1} recorded from line transects.

	Passerines	Waders & gamebirds	Other birds	Field vole	Lagomorphs
Cowal 1994					
Heath/bog	6.00	1.33	0	10.0	0
Acid grassland	1.58	0	0	12.0	0
Neutral grassland	7.78	2.22	0	5.0	1.25
New forest	4.67	0	0	22.0	0
Pre-thicket	6.00	0.67	0	13.0	0
Post-thicket	3.53	0	0	4.0	0
Restock	-	-	-	-	-
Islay 1993					
Heath/bog	5.00	0	0	1.0	0
Acid grassland	11.33	0	0	0	0.50
Neutral grassland	11.11	0	7.78	2.0	1.67
New forest	-	-	-	-	-
Pre-thicket	6.00	0	0.67	14.0	0
Post-thicket	9.33	0	0	6.0	0
Restock	-	-	-	-	-
Kintyre 1992					
Heath/bog	7.78	2.22	0	0	0
Acid grassland	6.67	0	0	1.0	0
Neutral grassland	9.33	0	0	0	0.75
New forest	5.33	0.67	0	5.0	0
Pre-thicket	6.11	0.83	0.28	3.0	0
Post-thicket	11.33	0	0	0	0
Restock	-	-	-	-	-

	Passerines	Waders & gamebirds	Other birds	Field vole	Lagomorphs
Lorn 1992					
Heath/bog	7.33	0	0	0	0
Acid grassland	1.33	0	0	1.0	0
Neutral grassland	0	0	0	0	0
New forest	-	-	-	-	-
Pre-thicket	18.00	0	0	5.0	0
Post-thicket	6.36	0	0	1.5	0
Restock	4.17	0	0	3.0	0
Lorn 1993					
Heath/bog	0	0	0	0	0
Acid grassland	3.33	0	0	8.0	0
Neutral grassland	1.05	0	0	3.0	0.4
New forest	2.00	0	0	12.0	0
Pre-thicket	8.82	0	0	14.0	0
Post-thicket	7.06	0	0.59	0	0
Restock	4.00	0	2.00	16.0	0
Lorn 1994					
Heath/bog	8.00	0	0	10.0	0
Acid grassland	3.33	0	0	8.0	0
Neutral grassland	0	0	0	2.0	0
New forest	3.33	0	0	23.0	0
Pre-thicket	0	0	0	8.0	0
Post-thicket	6.00	0	0	2.0	0
Restock	.67	0	0	12.0	0

Appendix 5: Number of nests and amounts of 7 land cover and 3 elevation classes in 10x10km squares searched for hen harriers, 1988-9.

10km sq	**No. of nests**	**Land cover (ha.)**							**Terrain elevation (ha.)**		
		Heath /bog	Acid grass.	Neutral grass.	New forest	Pre-thicket	Post-thicket	Re-stock	1-50m	51-250m	>250m
NM 42	2	2965	1559	214	66	1375	640	0	1083	4306	1829
NM 54	2	2072	1247	616	1537	1045	773	6	1607	4964	797
NM 63	1	6661	464	54	924	1	599	0	844	4130	4691
NM 70	0	679	1679	432	129	0	449	0	1853	927	27
NM 73	2	1040	933	341	0	177	655	0	1691	973	100
NM 84	0	1530	381	1100	14	0	97	0	1300	858	695
NM 92	4	5941	1371	291	406	939	770	50	256	5019	4724
NN 00	0	1552	323	456	233	2258	3207	24	1087	3733	3382
NN 02	5	1188	3546	602	584	473	1800	15	1746	6568	1454
NN 12	0	3413	2603	332	685	625	1366	0	1457	4333	4209
NR 24	0	1275	44	154	0	0	0	0	272	1446	0
NR 26	7	4905	511	2019	22	0	52	0	5818	2317	0
NR 34	3	3507	806	1086	370	0	61	0	2467	3543	118
NR 36	7	3978	1386	2761	296	0	479	0	3578	5670	0

10km	No. of	Land cover (ha.)							Terrain elevation (ha.)		
sq	nests	Heath /bog	Acid grass.	Neutral grass.	New forest	Pre-thicket	Post-thicket	Re-stock	1-50m	51-250m	>250m
NR 37	4	4018	551	118	457	0	6	0	1178	3694	137
NR 45	1	4885	207	145	0	4	132	0	1145	3114	2002
NR 56	1	1002	436	82	0	0	468	0	710	1025	236
NR 58	1	6809	164	0	0	6	10	0	1884	3962	1225
NR 69	0	5800	569	0	0	0	26	0	707	5087	517
NR 72	1	523	1570	1808	500	11	1765	0	1249	4404	859
NR 74	3	2938	349	565	2520	1322	2206	53	702	7454	1832
NR 75	2	745	1704	879	956	175	1222	5	1296	4701	0
NR 77	0	4595	1454	387	113	159	1167	3	1369	5027	1429
NR 84	1	1619	560	227	325	323	845	3	696	2286	1084
NR 88	1	608	414	563	1156	1593	2406	98	1400	5020	1003
NR 89	2	1246	2394	1657	1310	369	2535	215	3502	6073	287
NR 97	2	1821	1290	955	320	1399	2042	100	1564	4670	1896
NR 99	1	1906	359	410	729	48	4283	120	806	6087	1118
NS 06	0	1211	713	3384	0	131	407	8	2764	3512	35
NS 07	1	2294	2547	422	929	239	798	2	1098	3928	2264