THE EFFECT OF HEN HARRIERS AND OTHER PREDATORS ON RED GROUSE POPULATIONS IN SCOTLAND.

BY

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ABSTRACT

Red grouse populations were monitored for three years on study areas in Speyside and Perthshire (Scotland), where numbers have generally been declining since the mid 1970's. These low density populations are thought to be especially vulnerable to extrinsic factors, such as predation. The aim of this research was to discover what effect predators were having on grouse populations throughout the year.

Adult grouse mortality, examined by searching for corpses on six $1km^2$ study sites, was concentrated in the winter months. Birds killed were in good condition and a greater proportion were found dead than in any other similar study. Peregrine falcons and red foxes were the main predators involved. Initial evidence suggested that the grouse killed were, at least partly, territorial birds and not surplus individuals. Both the number of raptors and the percentage of grouse killed was inversely related to density. Low density populations were maintained by net immigration.

In the summer, the behaviour of the hen harrier, both at the nest, and whilst hunting was examined. Harriers exhibited a type II functional response to grouse chicks, which appeared to be their preferred prey. Moors with breeding harriers produced fewer young grouse, and on those moors where harrier predation was examined, it could account for the bulk of the losses. On the study areas, it was estimated that harriers took up to 32% of the grouse chicks in 8 weeks.

A simulation model was produced which suggested that harriers can reduce the numbers of grouse shot, although there was a high degree of variation in shooting levels. The impact of harriers on subsequent grouse spring numbers was dependent on the level of overwinter losses, variation in harriers and possibly alternative prey densities.

Further research is necessary to clarify some issues, but it was apparent that the effects of predators would be greatest on low density grouse populations. At these low densities, their impact will depend upon grouse breeding success and the degree of overwinter mortality relative to movement between estates. The importance of conserving heather moorland, to protect both raptors and grouse, was stressed.

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This thesis is dedicated to my parents for their unremitting support.

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CHAPTER 1

RED GROUSE POPULATION DYNAMICS AND PREDATION

1.1 Introduction

Within the Tetraonidae or grouse family, the genus Lagopus contains the ptarmigan and grouse species which generally occur in moorland and open montane or arctic habitats (Cramp & Simmons 1980). This genus is represented by two species in Britain: the ptarmigan (Lagopus mutus Montin) which inhabits montane habitats over 1000 metres, and the red grouse (Lagopus lagopus scoticus Lath.) which is dependent on heather (Calluna vulgaris L.) dominated moorland. In the United Kingdom there are approximately three million acres of moorland (Hudson 1986a) and much of this habitat is managed for red grouse. Populations of this species can increase to high density and the harvesting of grouse, through shooting in the autumn, can provide an important source of income for land-owners.

Increasing economic pressures have meant that many upland estates now rely on sporting income for their maintenance (Rands et al. 1988). In several areas, estates which have not produced sufficient grouse to shoot have been forced to sell their land to forestry companies and this afforestation is causing increasing concern amongst conservationists (N.C.C. 1986; Thompson et al. 1988). There is therefore a strong need to pinpoint the factors which affect grouse population levels and in particular the numbers of grouse available for harvesting.

Estates involved in gamebird management employ gamekeepers to maintain populations at levels high enough to shoot. Traditionally, the primary job of the keeper has been the removal of predator species (Lovat 1911). However, after the work of Errington (1946), who suggested that predators may have little, or no, effect on their prey, the value of this aspect of their work has come into question (Curry-Lindahl 1961; Jenkins et al. 1964), although Hudson (1986a) has claimed that predator control is a vital job in maintaining high density grouse populations. In this chapter the role of predation is re-examined and discussed with respect to red grouse population dynamics. This leads on to an evaluation of some conservation issues raised by red grouse management. Firstly, however, population regulation is examined to see when major changes in density occur, and the impact of these changes on population dynamics.

1.2 Population Regulation

The issue of population regulation in *Lagopus* spp. is a contentious one. Opinions have generally become polarised into two schools of thought, one supporting regulation via intrinsic mechanisms, involving territorial behaviour (Jenkins *et al.* 1963; Bergerud 1970; Watson & Moss 1979; Hannon 1983; Moss & Watson 1985), the other favouring extrinsic processes (Myrberget 1984; Hudson *et al.* 1985, Hudson 1986a + b; Angelstam 1986). However, before discussing population regulation, it is helpful to examine the mechanics of annual change, to see what features are associated with changes in abundance from one year to the next.

Key factor analyses have been carried out on three red grouse populations (Watson 1971 reanalysed in Dempster 1979; Watson *et al.* 1984; Hudson 1986a). These studies have shown that there are two critical periods when losses are largely responsible for annual changes. These occur during the summer (chick losses) and winter (overwinter losses) and include losses through mortality and dispersal. Two main hypotheses have been put forward to explain annual changes, one emphasising the importance of overwinter losses, the other chick losses (see Bergerud, Mossop & Myrberget 1985, Watson & Moss 1987, Bergerud 1987).

The first hypothesis concerns spacing behaviour (Watson & Moss 1979). Briefly, this idea, known henceforth as H1, postulates that spacing behaviour in early winter dictates the number of breeding birds in the following spring and any mortality that occurs overwinter is concentrated on surplus birds and is compensatory in nature. Alternatively, the breeding success hypothesis, H2, proposes that changes in breeding success can account for the population size in the following spring. Any mortality that occurs overwinter is additive and reduces the potential breeding stock (see Fig.1.1).

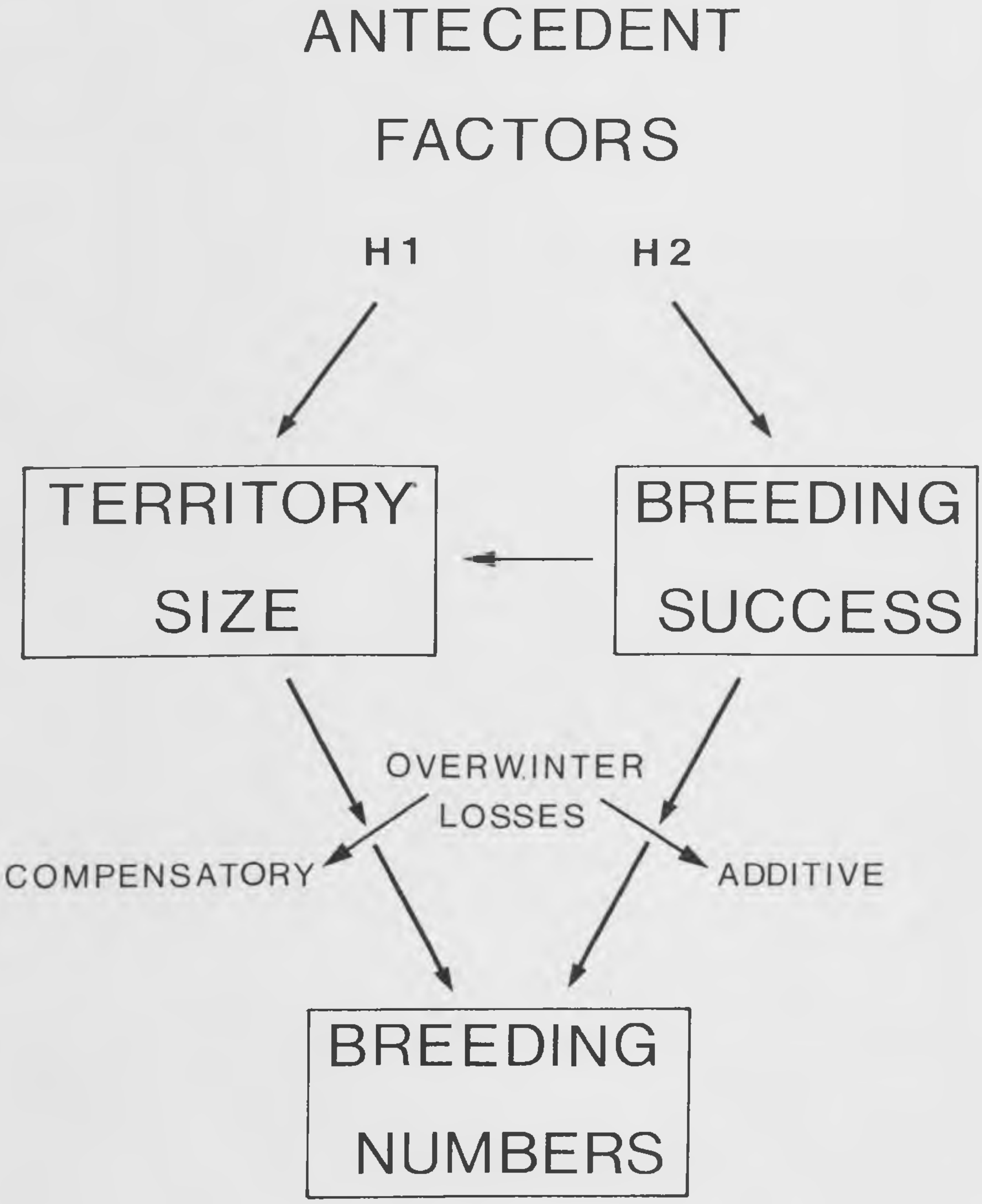

ANTECEDENT
FACTORS
H1
H2
TERRITORY SIZE
BREEDING SUCCESS
OVERWINTER LOSSES
COMPENSATORY
ADDITIVE
BREEDING NUMBERS

FIGURE 1.1. Diagrammatic representation of the two hypotheses developed to explain annual variation in grouse populations. H1 - Spacing behaviour hypothesis; H2 - Breeding success hypothesis. (After Bergerud, Mossop & Myrberget 1985).

There have been strong arguments put forward as to how these two mechanisms operate and these have hinged around correlations observed in natural systems. The main thrust of H2 is that breeding numbers are strongly correlated with breeding success in the previous year. However, Watson & Moss (1987) claim that compensatory overwinter mortality may still be determining losses. Although they agree that breeding success is correlated with breeding numbers in the following year, they show that it is also correlated with winter losses (Watson et al. 1984) and it is this relationship, acting through territorial behaviour, which is important in determining numbers.

The major difference between the two hypotheses lies in the pattern of overwinter losses. If losses are additive then H2 will be operating, but if losses are compensatory then spacing behaviour will be more important. However, there is no a priori reason why both pathways should not be operating, though their importance may vary within and between areas. To determine which of these mechanisms is operating at any one time and place, it is obviously important to examine overwinter losses to see whether they are compensatory. One method used for examining this question is to see whether or not the losses are density dependent. If losses are dependent on density then compensation is shown. However, if there is no such relationship then losses will be additive to other forms of mortality. It is also important to examine the strength of the dependence (Watson & Moss 1987) as this can greatly influence its effects and the resulting dynamics of a population (see May 1981).

1.2.1 **Factors influencing losses.**

Once the key periods of loss are known, it is then necessary to recognise the potential antecedent factors and understand how they can influence a population. Both hypotheses agree that chick losses can be important, although H1 indicates that this will only be important at low density.

The main factors which can influence red grouse chick survival are: hen condition, in turn influenced by food quality (Watson, Moss & Parr 1984), parasites (Trichostrongylus tenuis - Hudson 1986b); insect abundance (Hudson 1986a); predation (Picozzi 1978) and disease (Louping ill - Hudson 1986a). Various authors have stressed different factors though the importance of each and other possible factors, such as weather conditions, will vary between moors and between years.

Overwinter losses can also be influenced by most of the above factors, but the key to their importance lies in whether these losses are compensatory or additive. Studies in North East Scotland were unusual in that they suggested that territorial behaviour excluded birds in winter at all observed densities and these were then doomed to die. Although there was space for individuals to breed, some were too subordinate to have done so (Watson & Moss 1987). Approximately 40% of these "surplus" or non-territorial birds were killed by predators, whilst the rest disappeared (Watson 1985). In other bird species, where winter territorial behaviour is important, the birds do not necessarily die, but move into secondary habitats, when available, to breed (eg. Perrins 1979).

An alternative explanation of grouse behaviour overwinter is that during the winter, birds without territories are not surplus, but stay in optimal habitats in the hope of a territory appearing (Jenkins *et al.* 1963) and during this stage they are more vulnerable to predation. Mossop (1985) has described such birds as being in a 'waiting flock' where they assess when and where to compete for territories. In other words there are two strategies for birds during the winter months; either they can become territorial immediately, or they can remain in packs, as seen in the pied wagtail (Davies 1977) and rock ptarmigan (Watson 1965) and disperse to find territories later. As the breeding season approaches, birds are faced with a decision as to when to move into a secondary habitat. Lack (1954) and other authors have argued that this problem should only occur at high density when optimal habitats are filled. However, the spacing behaviour hypothesis states that, in the absence of secondary habitats, there will be surplus grouse in all years, as indicated by Jenkins *et al.* (1963) and Watson (1985). In reviewing grouse removal experiments aimed at testing for the existence of surplus birds, Hannon (1986) showed that they were not always present and may only be present at high density after good breeding. As Bergerud *et al.* (1985) concluded: "..the thrust in research should be to document that there is a non-breeding surplus,.".

1.2.2 **Grouse population dynamics**

Grouse populations exhibit a variety of states (Hudson, Dobson & Newborn 1985), though most cycle, with periods ranging from 4 to 10 years. Any hypothesis of grouse population regulation must therefore explain these differences. To understand the variation in the dynamics of the populations, it is helpful to examine the strength (i.e. slope) and time delays of the density dependent factors which operate on them. These two variables are important in determining whether populations are stable, cyclic or indeed chaotic (May 1981).

In Britain, the main proponent of the breeding success hypothesis is Hudson (1986a, 1986b; Potts _et al._ 1984; Hudson _et al._ 1985). He showed, for an area in northern England that breeding success was influenced by the parasite _Trichostrongylus tenuis_. A model was produced (Potts _et al._ 1984) which showed that these effects, acting in a delayed density dependent fashion, could account for observed cycles in the number of grouse shot, although only when stochastic elements were introduced. Interestingly, a further model (developed by Hudson, Dobson & Newborn 1985) could explain why some populations did not cycle, due to differences in rainfall affecting parasite burdens, in effect preventing the action of the time delay.

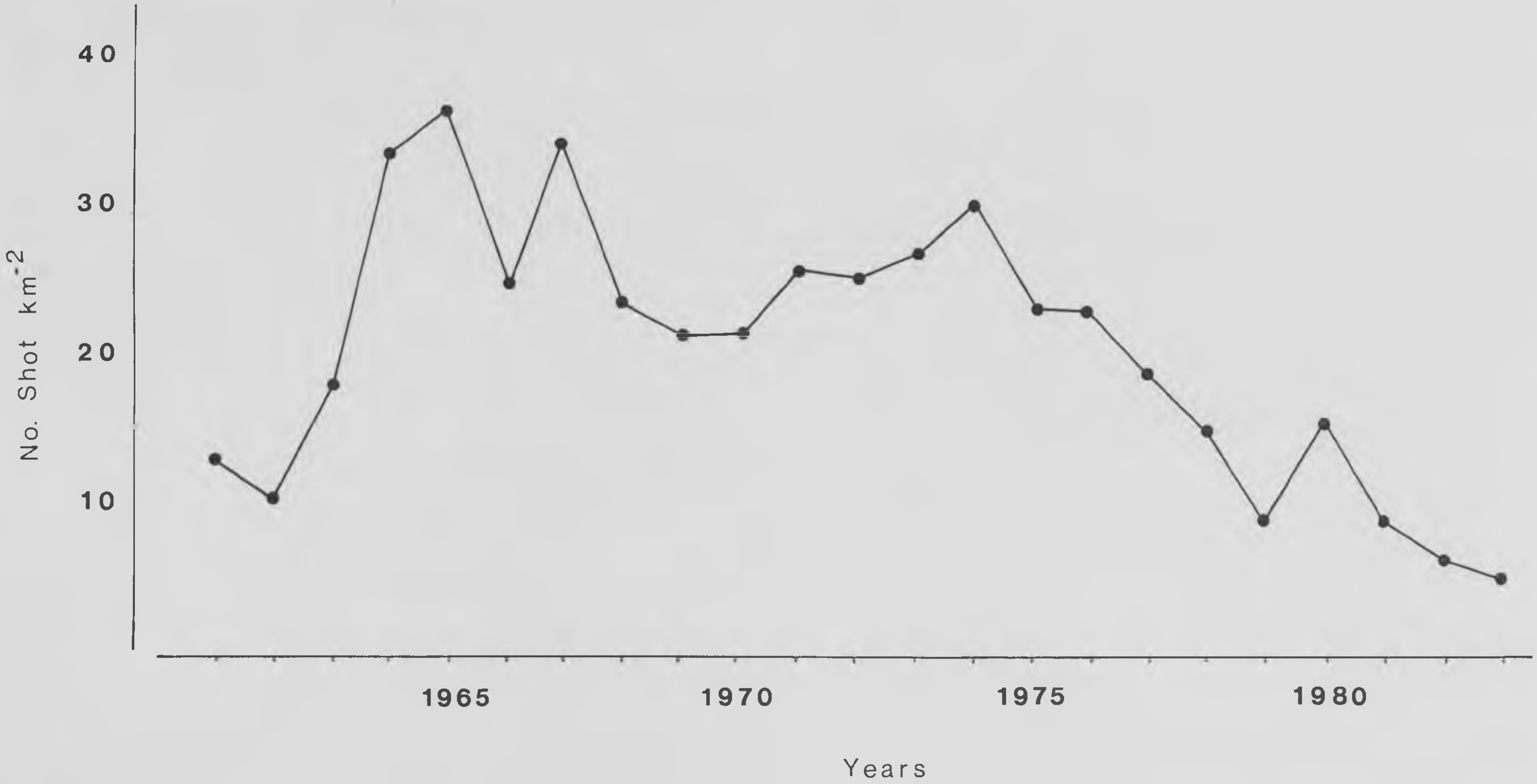
The general spacing behaviour hypothesis proposed by Watson & Moss (1979), based on Chitty (1967), is that cycles are caused by delayed density dependent changes in spacing behaviour. This hypothesis has been developed and refined over several years. Initially, it was proposed that changes in food quality affected aggression through breeding success (Watson & Moss 1972). At high density, food quality was poor and hens were thought to produce small broods containing aggressive cocks which took large territories in the following year causing a decline. This idea was later refuted (Moss, Watson & Rothery 1984). It was also shown that aggression increased after numbers had peaked, indicating that it did not initiate the decline (Moss & Watson 1980), although it could push the population down further. The current idea is that changes in behaviour are adaptive (Moss & Watson 1985). At low density and during the increase phase of the cycle, birds are tolerant of their neighbours, but as numbers peak, birds become more aggressive and rates of dispersal increase. These workers argue that cycles have arisen to avoid the effects of parasites and predators.

How then, can these two hypotheses (H1 and H2) be reconciled? One point made by Hudson, Dobson & Newborn (1985) is that they themselves were looking at changes in the number of grouse shot and therefore tended to stress the importance of breeding success. Studies examining the changes in breeding numbers would tend to stress overwinter losses. However, whilst this can explain differences in emphasis, it cannot explain the separation between the intrinsic and extrinsic hypotheses. Such differences could be a reflection of the populations studied, with intrinsic factors becoming important when the effects of extrinsic factors are low (Hudson, Dobson & Newborn 1985; Moss & Watson 1985; Watson 1985). Therefore for any population we can expect the equilibrium position (in effect the average level) to depend upon the strength of extrinsic factors relative to the intrinsic ones. As an example, Picozzi (1968) showed that density was related to moorland management. Where management of heather was good, with many small burns, bird densities were high, but poorly managed heather moorland produced fewer grouse, probably through decreased chick production. Here the equilibrium density for the grouse populations had been reduced by poor management or, in other words, the carrying capacity of the habitat was lowered. Similarly, Hudson (1986b) found that fewer grouse were shot on moors in areas with fewer keepers. He found that this relationship was not associated with heather management or soil type, but was associated with the density of keepers and hence foxes.

An increase in the importance of extrinsic factors, over a number of years, provides a possible explanation for the decline of grouse populations in some areas of Scotland in the 1970's (eg Speyside, Fig 1.2), which was associated with a series of poor breeding years (Barnes 1984, 1987). The exact reason for the poor breeding could not be determined, but was thought to be due to a variety of extrinsic factors. Populations are only now starting to recover in some areas.

To summarise, the studies of *Lagopus* spp. populations have indicated that chick losses and overwinter losses act in a density dependent fashion and together can regulate grouse abundance. There is disagreement over the relative importance of each of these and in particular over how winter losses act at low density. More work needs to be done to see whether a non-breeding surplus of birds is

FIGURE 1.2 Variation in the number of grouse shot (km^{-2}) from 1960 to 1983 in Speyside. Graph shows the decline in numbers from 1974 (Hudson 1988).


40
30
20
10
No. Shot km^{-2}
1965
1970
1975
1980
Years

widespread and exists throughout the winter and how any intrinsic mechanisms operate. The position of population equilibria will depend upon an array of extrinsic factors, which in turn will largely depend on moorland management. The extent to which populations cycle around their equilibria and with what periodicity, will depend upon the strength and time delays of the density dependent factors.

1.3 Predation and grouse populations.

Although there is controversy over the principal forces governing red grouse population dynamics, there is general agreement that populations at low density are most vulnerable to extrinsic factors, especially during the breeding season. In this section the importance of predation, with specific reference to its impact on breeding success and on changes in subsequent breeding density, is examined from previous studies.

Recent reviews of studies examining the effects of predators on gamebird populations (Angelstam 1986; Reynolds *et al.* 1988) have indicated that predators can have a great impact on breeding success, although the effect on breeding density is often less apparent. This is partly due to the difficulty of examining the role of predation overwinter when many other factors can influence survival. A possible approach to this problem is to experimentally remove the predators from isolated populations and examine the effect on grouse survival, though these populations may be different anyway due to lack of movement. Also, as Taylor (1985) points out, predator removal can have important consequences on the stability properties of the system and therefore research needs to be carried out over a long period. Such an experiment has recently been performed by Marcstrom *et al.* (1988). They removed mammalian predators from an island in the Baltic for five years and compared grouse densities with another similar island. The species studied were: capercaillie (*Tetrao urogallus* L.), black grouse (*Tetrao tetrix* L.), hazel grouse (*Bonasa bonasia* L.) and willow grouse (*Lagopus lagopus* L.) Treatment of the two islands was then reversed for the next four years. When predators were removed a 120% increase in productivity was observed, which they considered a minimum estimate. Increases in the adult populations of capercaillie and black grouse also occurred with spring numbers at leks increasing by up to 174% over the control area.

Whilst changes in chick survival were quickly apparent on the removal of predators, increases in breeding density were slower and masked by factors such as dispersal. In this case at least, predators were influencing spring density. As stated in the previous section, the impact of predation during the winter, and therefore on spring density, will depend upon whether losses are compensatory or additive. There is little doubt that at high density losses will be mainly compensatory, but at low density the issue is less clear.

This experiment by Marcstrom _et al._ also highlighted another important aspect of predation studies. They found that the number of breeding females and brood sizes were correlated to vole abundance, but only on the island where predators were not removed. The authors concluded that high vole densities reduced predation on grouse broods although they may have increased overwinter predation. In any study of predation it is clearly necessary to study the whole range of prey species.

A similar study was performed over four years on the ruffed grouse (_Bonasa umbellus_) in north America (Darrow 1947). He examined populations on just over 1000hectares and killed predators on half the area for the first two years and on the other half for the next two. He found that, whilst the predators took many eggs, they had no effect on overall breeding success and adult densities.

A possible explanation for the differences between these two studies may lie in the length of the removal experiment. Marcstrom _et al._ (1988) found that the impact of predators became more apparent as the experiment progressed. If the experiment had been reversed after two years then the results would have appeared ambiguous. The ruffed grouse study may therefore simply not have been carried out long enough for differences to emerge.

1.3.1 Predation and red grouse.

The effects of predators on red grouse populations were examined in North East Scotland by Jenkins et al. (1964). They concentrated on the effects of predation overwinter, and considered that the impact on adult grouse during the summer months was negligible, partly due to increased predator control during that period. In the winter months, predators were wide-ranging and more difficult to kill. Their findings suggested that predation was unimportant in influencing spring numbers the following year; grouse mortality was compensatory and it was mainly the dispersing, non-territorial birds that were killed. However, this work was carried out at high grouse density when overwinter losses are most likely to be compensatory, the number of breeding birds being set by territorial behaviour. It is at lower densities, when this behaviour is likely to be less important and overwinter losses are likely to be additive, that predation could be deleterious to a grouse population.

The grouse population decline which has occurred over much of Scotland (see Fig. 1.2) indicates that the populations are no longer regulated around their former levels, but appear to be limited at low density, although populations may now be starting to increase. These declines are based on the number of grouse shot, not on the number counted, though this is generally considered an acceptable index (Picozzi 1968; Hudson 1986a). Under these conditions, both of the main hypotheses of grouse population regulation would claim that there should be space for all the individuals to breed. The breeding success hypothesis states that there is always room to breed and the spacing behaviour hypothesis claims that birds should be more tolerant of their neighbours as numbers increase from low density. In other words we would expect overwinter losses to be additive and breeding success to be high. Under these circumstances losses to predators would be important in influencing breeding success and density. Such studies need to be undertaken on a scale large enough to account for dispersal, as local movement of birds will take place at all densities.

Since the studies of Jenkins et al. in the 1950's and 60's several predator species have increased in density. Peregrine numbers were low during that period, because of pesticides and were rarely seen in their study. However, numbers have since increased back to former levels (Ratcliffe 1980, Newton 1979). The fox also has rapidly increased in density, judging from records of numbers shot (Barnes 1984). This increase in important predators, together with the low grouse densities, means that predation could potentially be more important now.

The issue of whether predators should be controlled by gamekeepers is dependent on which of the two hypotheses is operating. Whilst both schools favour legal control of foxes and crows in spring (Moss & Watson 1985; Hudson 1986), to minimise chick losses, only the breeding success hypothesis would favour removal during the rest of the year. This reflects the theories on overwinter losses; if losses are compensatory, there is no need to control predators other than in the spring, but if losses are additive then predator control is necessary to reduce mortality and increase breeding density in the following year.

1.4 Red grouse management and conservation issues.

The red grouse has seven main predators: the red fox (_Vulpes vulpes_ L.); stoat (_Mustela ermina_ L.); carrion crow (_Corvus corone_); peregrine falcon (_Falco peregrinus_ Turnstall); hen harrier (_Circus cyaneus_ L.) and golden eagle (_Aquila chrysaetos_ L.). These and several other less important species, are listed in Table 1.1, alongside the vulnerable age groups of grouse.

As discussed in section 1.3, both hypotheses concerning grouse population dynamics agree that bags can be increased if certain predators are controlled during the breeding season. However, the hen harrier is one species of predator which can potentially remove large numbers of grouse chicks (Picozzi 1978), but which is legally protected under the Wildlife and Countryside Act (1981). This species is regarded by many gamekeepers as a threat, and consequently suffers illegal persecution.

The removal of predators can be highly efficient and may even greatly reduce their geographical distribution (Moore 1957; Langley & Yalden 1977; Newton 1979). As an example of this, the distribution of the hen

TABLE 1.1 A list of the potential predators of red grouse and the age classes of grouse which are vulnerable (+). ? - represents those classes which are suspected of being vulnerable, though evidence is poor. Young birds are those up to twelve weeks old. Crow includes carrion and hooded subspecies.

PREDATORS	GROUSE AGE CLASSES		
	EGGS	YOUNG	ADULTS
RED FOX (*Vulpes vulpes*)	+	+	+
BADGER (*Meles meles*)	+		
WILD CAT (*Felis sylvestris grampia*)	+	+	+
STOAT (*Mustela ermina*)	+	+	+
WEASEL (*Mustela nivalis*)	+	+	
CROW (*Corvus corone*)	+	+	
RAVEN (*Corvus corax*)	+	+	
MERLIN (*Falco columbarius*)		+	
KESTREL (*Falco tinnunculus*)		+	
SPARROWHAWK (*Accipiter nisus*)		+?	+
PEREGRINE (*Falco peregrinus*)		+?	+
HEN HARRIER (*Circus cyaneus*)		+	+
GOLDEN EAGLE (*Aquila chrysaetos*)		+	+
SHORT EARED OWL (*Asio flammeus*)		+	+
COMMON BUZZARD (*Buteo buteo*)		+	+?

harrier in Scotland has often been quoted (see Watson 1977). Harriers generally breed on open moorland or within young forestry plantations (Sharrock 1976) and in the nineteenth century were common in the uplands but became virtually extinct from the mainland by the beginning of this century, only returning during the 1930's and 40's when the first forestry plantations appeared and keeper densities were reduced because of World War II (Fig. 1.3). Upto the mid 1970's, numbers increased steadily, but in recent years they are thought to be declining (Bibby 1988). Changes in gamekeeper numbers and by implication, persecution, have been cited as the reason for these fluctuations in density, especially with regard to World War II when keeper numbers dropped dramatically (Fig.1.4). However, persecution is not the only factor influencing distribution, as habitat changes can also have an effect. O'Flynn (1983) attributed a rapid decline of harriers in Ireland to changes in habitat, in particular to the growth of forestry plantations. It is likely that some of the changes in Scotland have also been due to forestry, where habitat is initially good through providing nesting cover and food densities but later too dense (Thompson, Stroud & Pienkowski 1988; Sykes, Lowe & Briggs 1989).

If harrier breeding densities are compared between North England and Scotland, there is a notable difference (Fig. 1.5). This is possibly because England has almost four times the density of gamekeepers than Scotland (Hudson pers. comm.). However, whether the proximate reason lies in habitat differences (poorer nesting cover or food in England) or because of persecution (less in Scotland) remains to be seen, though the two are not mutually exclusive.

In an attempt to determine the present scale of persecution in Speyside, questionnaires were sent to 17 gamekeepers in the area, of which 16 replied anonymously. All keepers killed birds of prey on their land, though some species suffered more than others (Table 1.2). In 1988 ten pairs of harriers were known to have attempted breeding on these moors and of these, seven were killed by the keepers. Of the three which were not killed, two survived on unkeepered ground and one pair remained unfound on an estate where three other pairs were killed. Peregrines suffered less persecution (one of eleven pairs killed) and the reason for this difference appeared to be that peregrines were less accessible (nesting on cliffs) and also they were more frequently watched by birdwatchers. The fox was considered the

FIGURE 1.3 Changes in the distribution of the hen harrier in Scotland from 1865 to 1975, where only areas of definite breeding are shown. (Watson 1977).

1865

1900

1945

1975

FIGURE 1.4 Changes in the number of game keepers in the United Kingdom as recorded by the National Census. Keeper numbers dropped after the two world wars (Hudson 1986a).


NUMBER OF GAME-KEEPERS
25,000
20,000
15,000
10,000
5,000
0
1871
1881
1891
1901
1911
1921
1931
1941
1951
1961
1971
YEAR OF CENSUS

FIGURE 1.5 Distribution of breeding hen harriers in Britain in 1976. Note differences in density betwen Scotland and England. The three grades of dots represent breeding sites ranging from possible (smallest) to confirmed (largest). (Sharrock 1976).

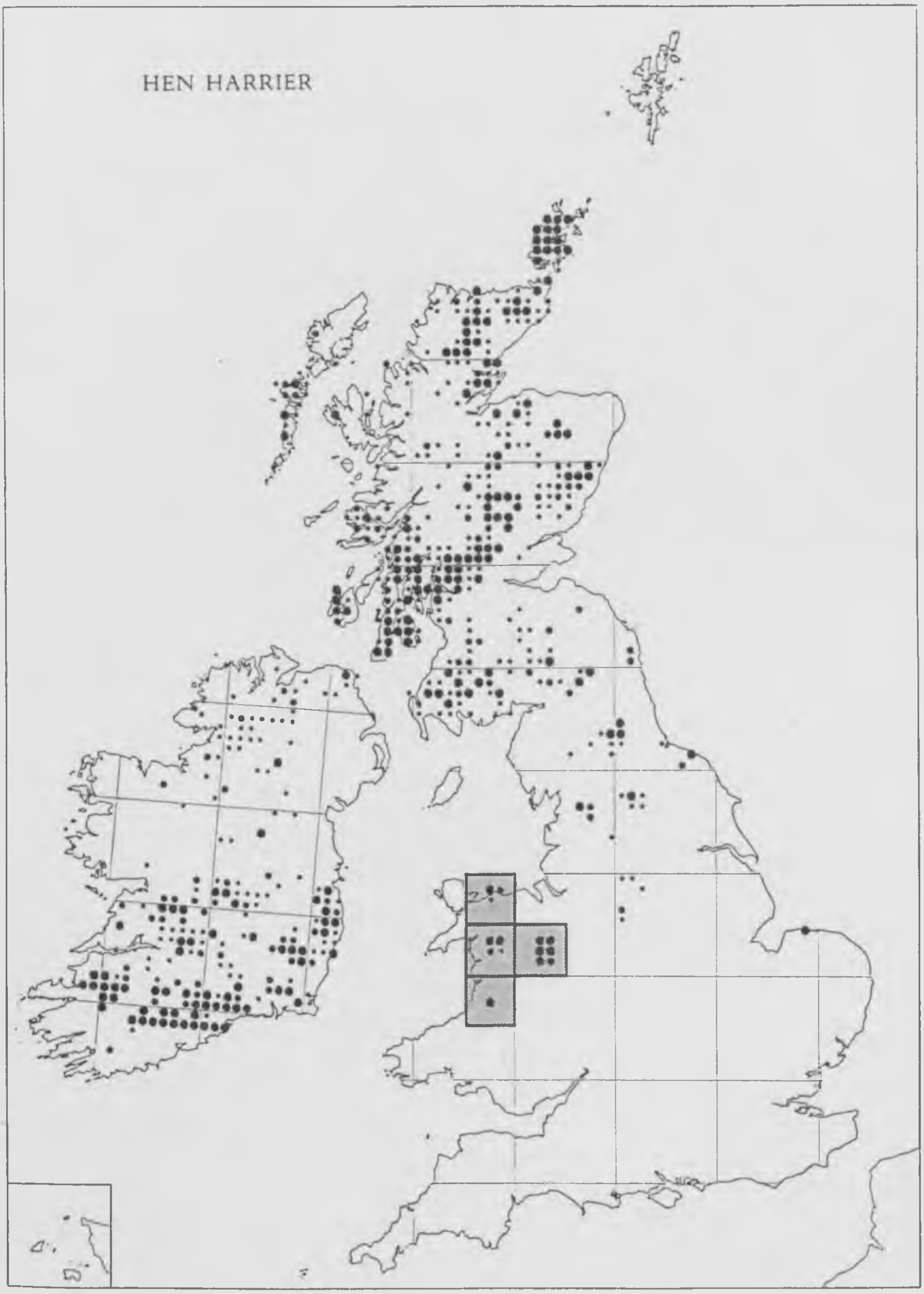

HEN HARRIER

TABLE 1.2 Findings of questionnaire sent to grouse keepers in Speyside 1988, showing proportion of keepers time spent managing grouse, what they considered the main predators, the numbers of predators breeding and the number killed (both the average per year and the number in 1988). Fox dens and crow nests just show numbers killed.

SUMMARY OF QUESTIONNAIRE.

ESTATE	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
% Grouse Man.	30	75	50	25	0	70	40	100	70	100	10	75	90	0	50	5
Main Predator	F	H	H+C	F	F	F	H	F	F+C	F	F	H	F+C	P	F+H	F+H
Main Raptor	P	H	H	P	P	H	H	E	P	P	P	H	E+P	P	P	P
Peregrines 1988	1	1	2	1	2	0	1	0	0	0	0	0	0	2	1	1
P's.killed 1988	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Av. no. Pegs.	2	1	2	1	1	0	1	0	0	0	1	0	1	2	1	1.5
Harriers 1988	0	1	4	0	0	0	2	0	0	0	0	1	0	0	0	2
H's.killed 1988	0	1	3	0	0	0	2	0	0	0	0	1	0	0	0	0
Av. no. Harriers	0	2	3	0	0	0	2	1	1.5	1.5	0	2	0	0	0	2
Fox dens 1988	2	1	3	1	1	2	2	0	1	0	0	0	1	6	2	9
Crow nests 1988	0	3	1	0	0	6	9	2	4	0	1	7	1	0	5	6

F = FOX
H = HEN HARRIER
C = CROW
P = PEREGRINE
E = EAGLE

major predator on estates and the peregrine and harrier equally important raptors. This was reflected by the finding that foxes were still killed on areas where little or no grouse management was undertaken, whereas raptors were left.

These data give some idea of persecution levels in Speyside and there is no reason to suppose that levels are much different on grouse moors elsewhere. If this is the case, then the scarcity of harriers in England could well be due to persecution. It is surprising that harrier populations can suffer such persecution levels and still maintain reasonable breeding densities in Scotland. Perhaps the birds breeding on unkeepered, recently afforested, areas provide a continual supply of recruits. However, as the size and age of plantations increases, individuals are forced from the forests (Watson 1977) and grouse moorland may soon become a vital habitat for breeding harriers. If so, their numbers can be expected to decline further through continued persecution, although harriers will also breed in restocked forests (Petty & Anderson 1986).

The British population of hen harriers, peregrines and golden eagles are of international significance (Ratcliffe & Thompson 1988) and they are listed on Annex 1 of the EEC Directive on the Conservation of Wild Birds, which requires that active conservation measures be taken to protect them (Bibby 1988). Their persecution has therefore created a conflict between the gamekeepers and conservationists, who, whilst seeing the value of moorland managed for red grouse, wish to protect these raptor species. As Cadbury (1987) stated: "Conflicting views on the predatory role of the hen harrier provide an unfortunate obstruction to the RSPB's wish to improve relationships with owners of grouse moors and their keepers, whose management of heather is in many ways beneficial to a number of breeding birds characteristic of the open uplands".

There is therefore an obvious need to discover what effect, if any, these species have on red grouse populations. If their effects are unimportant, then active measures to prevent the persecution of these important predators must be supported. However, if they are proved to have a detrimental impact, then their total protection could lead to a loss in income for grouse moor owners and, in the present financial climate, a loss of environmentally important moorland to forestry, ironically resulting in a decline of both harrier and grouse densities.

1.5 Aims of study.

The aim of this research was to discover what effect predators and in particular the hen harrier, were having on red grouse populations. As the effects of predation are potentially most important at low densities, research concentrated on low densities. The work was divided into two parts: firstly, an examination of annual variation in predation on adult grouse, and secondly a study of the impact of hen harriers on grouse breeding success.

In Chapter 2, the study areas and basic methodology are described, along with a discussion of annual variation in densities of various moorland species. Changes in adult grouse mortality are examined in chapter 3, with reference to selection by various predators and the findings are compared with other similar studies. Chapters 4 to 6 deal with the effect of the hen harrier on grouse chick production, including an examination of the behaviour of harriers in relation to their prey (chapter 4) and the number of chicks they take at various densities (chapter 5). The findings from these two chapters are then brought together in a computer simulation model (chapter 6) to determine the potential effect of harriers on harvesting levels and breeding numbers. All the elements are discussed in chapter 7 and the importance of predation in red grouse population dynamics is re-examined.

CHAPTER 2

STUDY AREAS, METHODOLOGY AND SPECIES ABUNDANCE

The aim of this chapter is to provide a general introduction to the main study sites, examined throughout the three years, and methodology involved. The detailed methods used for each of the two parts of this study are discussed in relevant chapters.

2.1 **Study Areas**

Red grouse populations were monitored on 40 study areas, as part of a long term programme with the Game Conservancy's Scottish (S.G.R.P) and North of England Grouse Research Projects (N.E.G.R.P). Nineteen of these sites were located in Scotland and 21 in England and each covered one square kilometre (247 acres). Sites were chosen as being representative of the estate on which they were positioned and where possible they were within easy access of roads or tracks.

Six of these study areas were monitored in detail throughout the three years. All were located within ten miles (15 kilometers) of each other, on three separate estates in Speyside (Fig. 2.1), where grouse densities have been low since the population decline in the 1970's (see chapter 1). All sites occurred on relatively base poor substrate (quartz-feldspar-granulate) and heather was the dominant vegetation. Grouse shooting and red deer stalking were the main sporting interests for the estates.

2.2 **Methodology**

On all study areas, grouse densities were recorded in April (spring count) and July (autumn count) during six evenly spaced transect / walks with a trained pointing dog. During each transect the dog quartered the ground up to 100 metres on both sides of the observer and different counts on the same area were within 10% (Hudson unpub.). For all areas covered by the Game Conservancy, spring counts varied from 6 to 192 (mean 50) grouse km^{-2} and autumn counts from 4 to 761 km^{-2} (mean 131). Grouse counts over the three years in the Speyside areas are displayed in Table 2.1. and show that grouse were at low density on these sites, though numbers increased over the three years.

FIGURE 2.1 Map showing position of estates (R, C and D) and main study sites of 1 km^2 in Speyside.

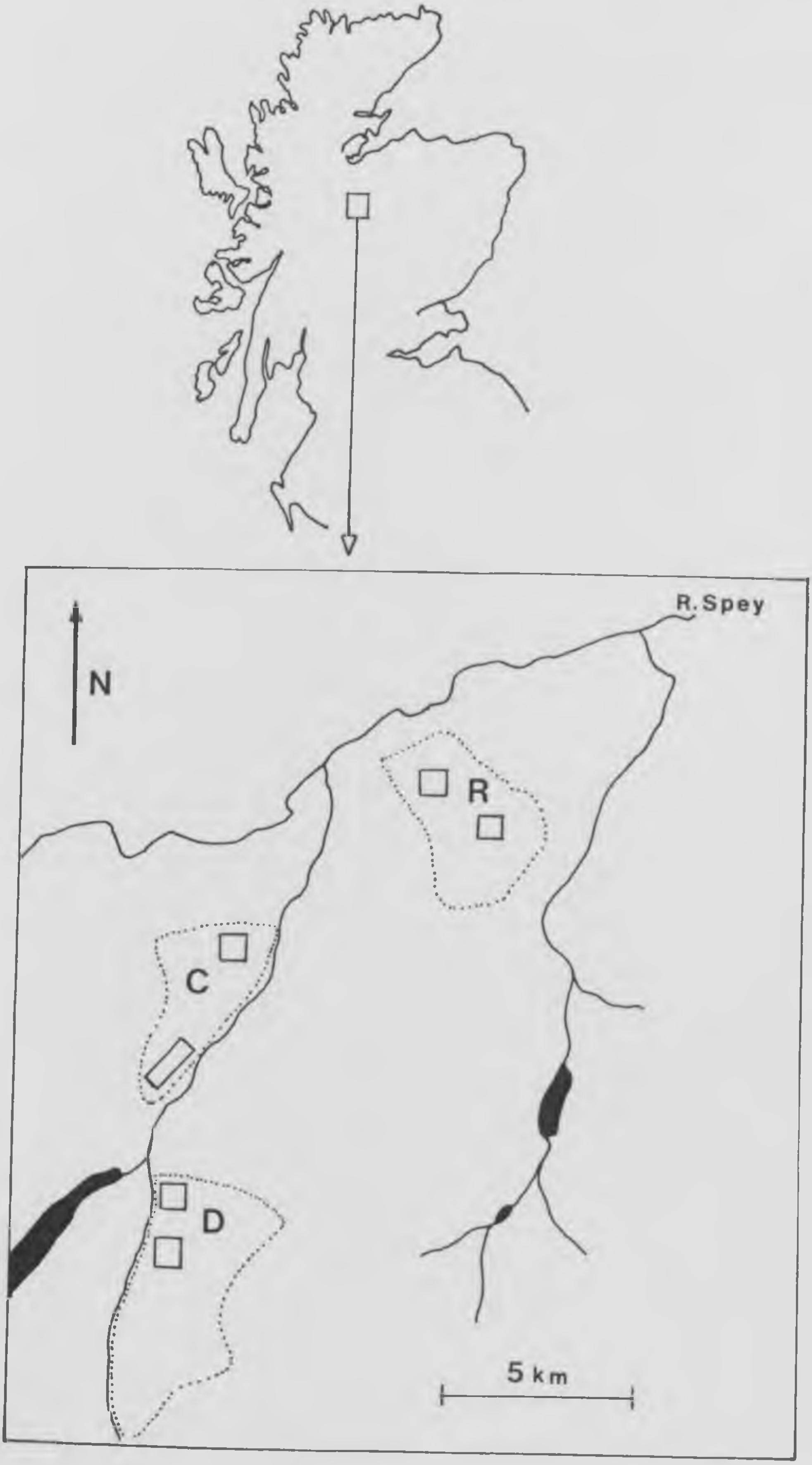

N
R. Spey
R
C
D
5 km

TABLE 2.1 Number of grouse counted (km^{-2}) on the six study sites in spring (S) and autumn (A) 1985 to 1988.

MOOR	STUDY SITE	YEAR							
		1985		1986		1987		1988	
		S	A	S	A	S	A	S	A
R	I	---	---	6	4	9	17	11	33
	II	---	---	6	7	14	39	22	47
D	III	---	73	28	45	19	108	30	93
	IV	---	---	17	68	21	59	32	88
C	V	---	---	14	67	21	79	29	86
	VI	---	14	9	16	9	80	17	102
	MEAN	---	43.5	13.3	34.5	15.5	63.7	23.5	74.8

In the summer, nests and broods were also located using dogs, to give estimates of breeding success and each of the six areas was searched every month for grouse corpses (see Chapter 3).

In all, 1437 hours were spent on the study areas, of which 597 hours was observational work aimed at determining the behaviour of hunting hen harriers (chapter 4). The rest of the time was spent in general field work: grouse counts, corpse searching or looking for nests or young. The abundance of bird species was recorded during general work and was measured as an index from 1 (not seen) to 5 (very common), whilst hare densities were measured as the number seen during six transects. Small mammals were caught using break-back traps in spring and autumn. Traps were baited with peanut butter (Hamerstrom 1986) and placed 10 metres apart on a transect across the moor. In the first year, 50 traps were set for 10 nights on the three moors giving a total of 1500 trap nights, but in the final two years, 100 to 150 traps were set on only one of the moors (taken as representative of the other two), for 10 nights.

In accordance with other studies, raptor densities were recorded as the number seen per 100 hours. To see if predator species were more obvious during periods of intensive observation, field work on the study areas was divided into observational and general work. Of all the raptors seen, only the hen harrier showed a significant difference between the two methods of study (Table 2.2).

2.3 **Annual variations in species abundance**

During the summer, the most abundant bird species on the moor (apart from red grouse) were the meadow pipit (*Anthus pratensis* L.) and the skylark (*Alauda arvensis* L.). Other passerines seen included the wheatear (*Oenanthe oenanthe* L.) and whinchat (*Saxicola rubetra* L.). Breeding wader and duck species included the curlew (*Numenius arquata* L.), snipe (*Gallinago gallinago* L.),redshank (*Tringa totanus* Mathews), greenshank (*Tringa nebularia* Gunner.), mallard (*Anas platyrhynchos* L.), teal (*A. crecca* L.) and wigeon (*A. penelope* L.). Of the mammals, mountain hares (*Lepus timidus* L.), wood mice (*Apodemus sylvaticus* L.) and shrews (*Sorex* spp.) regularly occurred, whilst field voles (*Microtus agrestis* L.) were occasionally caught.

TABLE 2.2. Numbers of raptors seen per 100 hours on the six study sites from 1986 to 1988 during observational and general work. Numbers in brackets are totals seen. Numbers from observational and general work are compared to see if different from a 1:1 expected ratio.

SPECIES	OBSERVATIONAL WORK	GENERAL WORK	SIGNIFICANCE	
			χ^2	P
HEN HARRIER (Circus cyaneus)	20.4 (122)	6.1 (51)	55.9	***
PEREGRINE (Falco peregrinus)	3.3 (20)	4.3 (36)	0.85	NS
GOLDEN EAGLE (Aquila chrysaetos)	2.5 (15)	1.2 (10)	3.40	NS
BUZZARD (Buteo buteo)	9.9 (59)	7.9 (66)	1.70	NS
SHORT-EARED OWL (Asio flammeus)	1.5 (9)	1.1 (9)	0.50	NS
KESTREL (Falco tinnunculus)	5.4 (32)	3.9 (33)	1.60	NS
SPARROWHAWK (Accipiter nisus)	0.2 (1)	0.1 (1)	--	--

Annual variations in the main species, on the six study areas combined, are shown in Fig.2.2. Generally, bird species only remained on the study areas during the summer and left for the winter months. One exception to this was the snow bunting (Plectrophenax nivalis L.) which was not seen during the summer, but occurred in flocks in the winter. Hares stayed on site throughout the year, though their numbers were low. More small mammals were caught in autumn (Fig. 2.3), probably due to high density after breeding combined with dispersal, and overall numbers appeared to remain constant between years. Voles were uncommon on the sites and were only caught in the spring of 1987.

Numbers of raptors seen were measured as the number per 100 hours general work. For the harrier, numbers seen during observations were divided by three to make the results equivalent to those during general work. For all other species, data were combined. Overall raptor numbers increased in August (Fig. 2.4), probably associated with dispersal. This peak was mainly due to buzzards and kestrels and less so to the three main grouse predators. Numbers were low during the winter, when prey were scarce, but remained approximately constant through the spring and summer.

The association between prey species and raptor numbers was clearly shown for the hen harrier. As it was difficult to distinguish between juvenile males and females in the field (as both are brown with a white rump), harrier sightings were divided into mature males (grey in colour) and the brown 'ring-tails'. Females are roughly 10% larger than the males (Cramp & Simmons 1980) and can therefore take larger prey. Marquiss (1980) suggested that harriers move away from moorland when prey are scarce and this is supported here. Ring-tails were seen throughout the year (Fig. 2.5), though less frequently in May and June when females were incubating and brooding their young. The males were seen only between March and October, when passerines were on the moor. Although there were small mammals and snow buntings present, overall prey density was probably not enough to sustain males on the moor overwinter.

In summary, the sites examined in this study contained grouse at low density, relative to other sites. The majority of bird species moved away from the study areas for the winter, with only certain raptors, red grouse, mammals and flocks of snow buntings remaining. Those birds

FIGURE 2.2 Monthly variations in abundance of mountain hares, curlew, skylark and meadow pipits on the six study sites (three years combined). Abundance was measured on a scale of 1 to 5 (see text). Hares were measured as the number seen during six transects. Note that the three avian species left the sites for the winter.

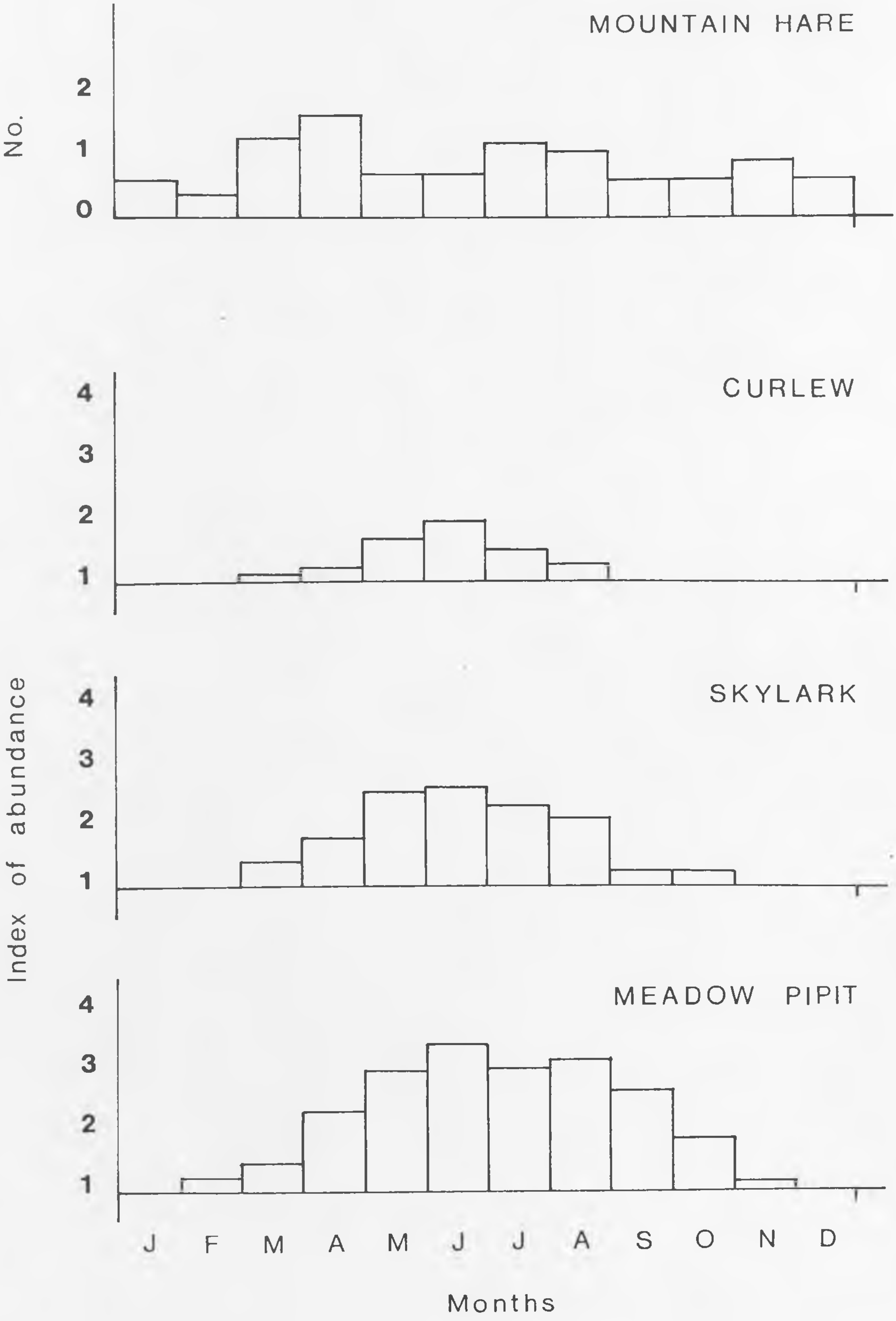

MOUNTAIN HARE
No.
0
1
2
CURLEW
1
2
3
4
SKYLARK
1
2
3
4
MEADOW PIPIT
1
2
3
4
Index of abundance
J
F
M
A
M
J
J
A
S
O
N
D
Months

FIGURE 2.3 Annual variations in the numbers of small mammals caught per 100 trap nights in spring and autumn from 1986 to 1988 in Speyside.

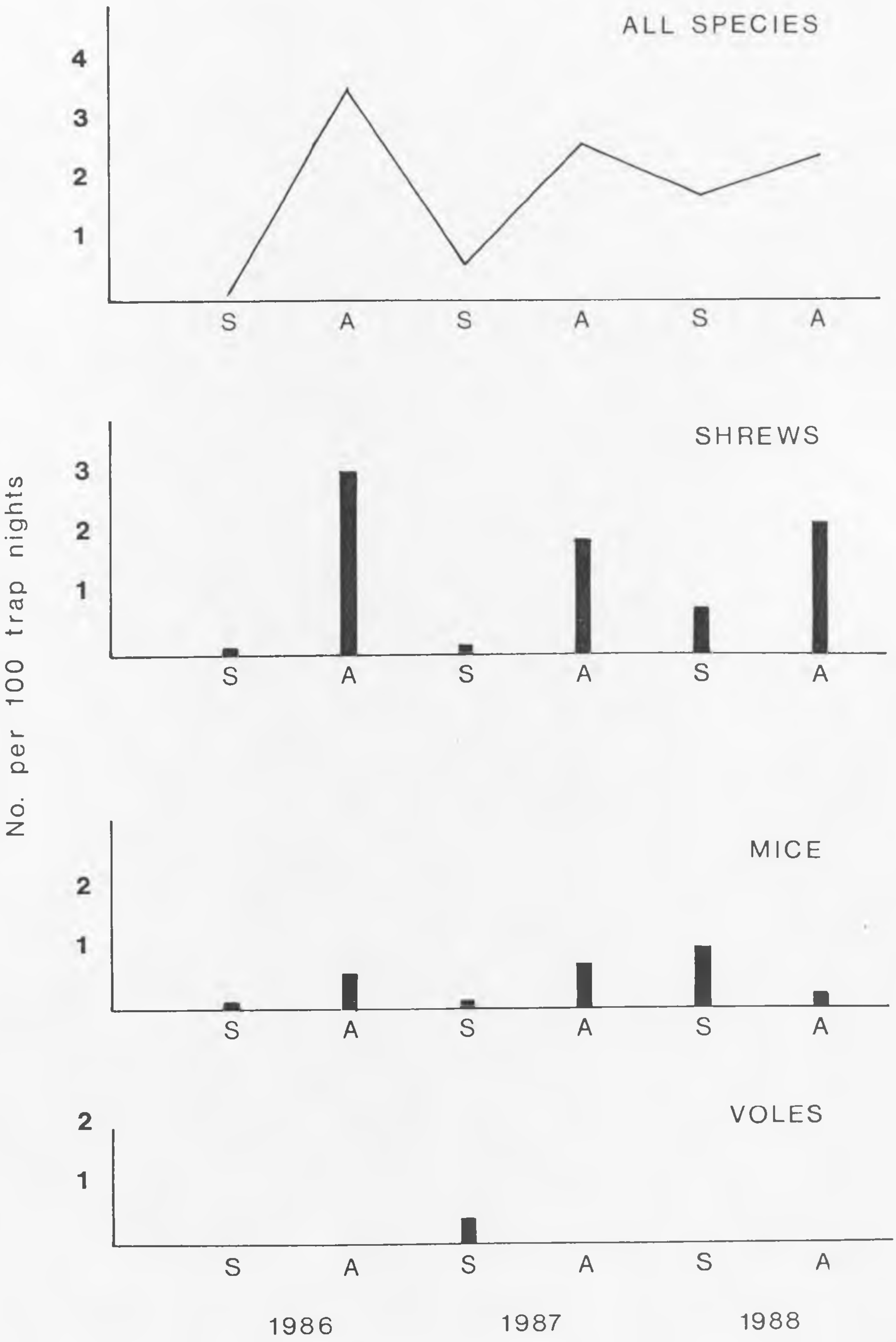
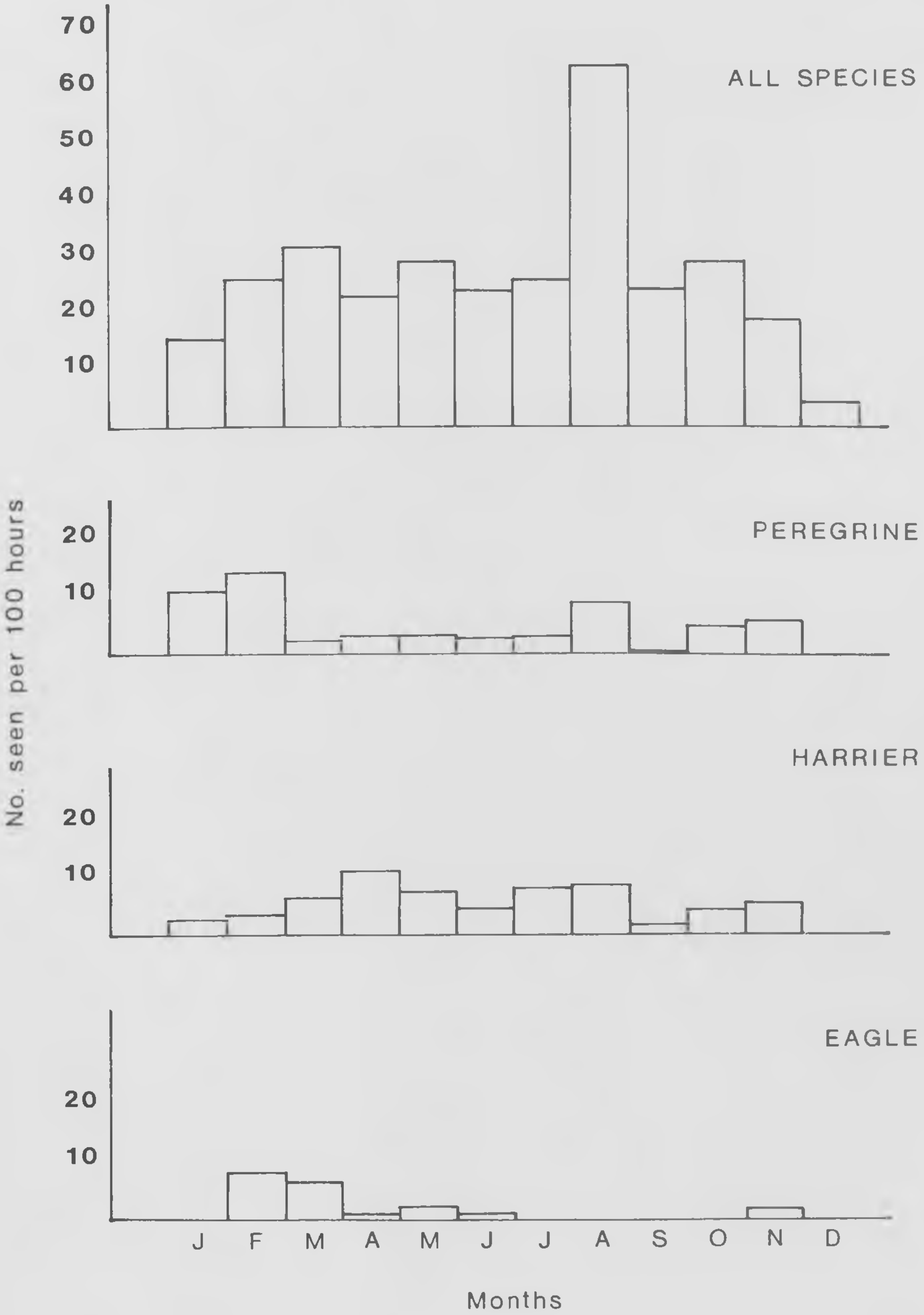
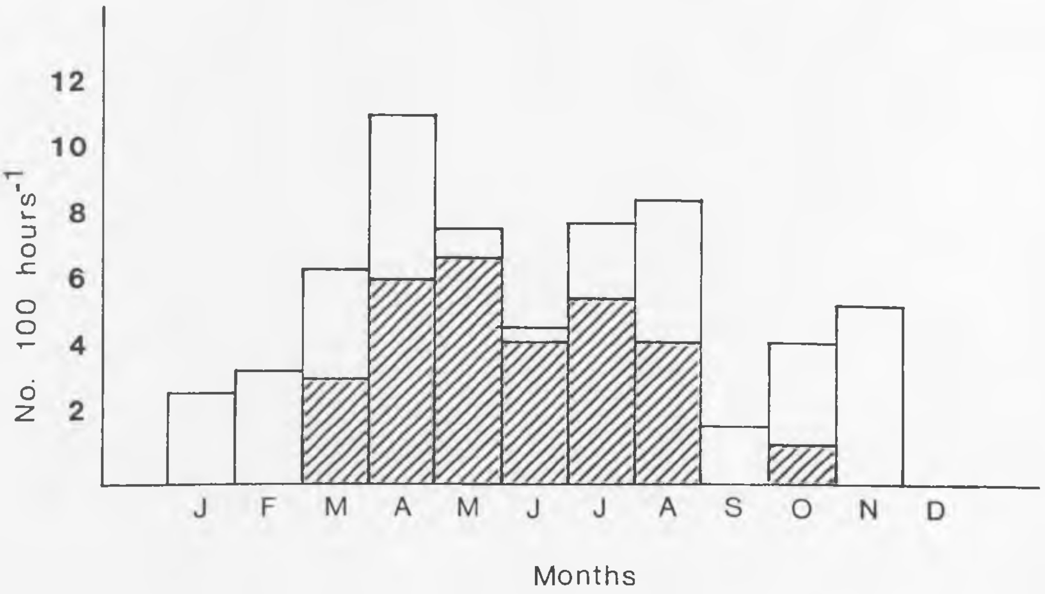

No. per 100 trap nights
ALL SPECIES
4
3
2
1
S A S A S A
SHREWS
3
2
1
S A S A S A
MICE
2
1
S A S A S A
VOLES
2
1
S A S A S A
1986
1987
1988

FIGURE 2.4 Annual variations in raptor sightings on the six study sites from 1986 to 1988. Based on 1437 hours of field work. (Species as for Table 2.2).



70
60
50
40
30
20
10
ALL SPECIES
20
10
PEREGRINE
HARRIER
20
10
EAGLE
20
10
No. seen per 100 hours
J
F
M
A
M
J
J
A
S
O
N
D
Months

FIGURE 2.5 Annual variations in mature male (shaded) and "ring-tail" harrier (open) sightings (100 hours $^{-1}$) on the six study sites from 1986 to 1988. Note that males were only seen from March to October.



12
10
8
6
4
2
No. 100 hours^{-1}
J
F
M
A
M
J
J
A
S
O
N
D
Months

of prey which were dependent on small prey were less frequently seen in winter, whilst the larger raptors stayed in the area. This was clearly seen in the hen harrier, with the males leaving and the larger females remaining.

CHAPTER 3

ANNUAL VARIATIONS IN ADULT GROUSE MORTALITY

3.1 Introduction

The impact of predation on a prey population depends not only on the number of individuals killed, but also on when this mortality occurs and whether it is selective. Red grouse are relatively sedentary for most of the year and their corpses are easily found (Jenkins et al. 1963). Regular searching of moorland for corpses can therefore reveal the pattern of predation on a grouse population.

This chapter examines annual variations and selectivity in predation, combined with population changes in grouse and variations in the number of raptors seen hunting. Similar investigations for grouse species have been performed by Jenkins et al. (1964), Hannon & Gruys (1988) and by the Game Conservancy in the North of England (Hudson & Newborn unpub.) and the findings are compared.

3.2 Methods

Six sites of 1km^2 in Speyside (see chapter 2) were systematically searched each month, during six transect-walks, from February 1986 to April 1988, and all corpses found were recorded. During each transect, binoculars were used to scan the heather for feathers. Each time feathers were seen, the surrounding area was searched for a corpse. After Jenkins et al. (1964), corpses were classified into violent, non-violent or unknown causes of death. Violent deaths were further classified into mammal, raptor or other (eg fence or car) kills and depending on the state of the corpse and other signs, the species of predator involved, using the criteria of Einarsen (1956), Jenkins et al. (1964), Watson & Miller (1970) and Whitfield (1985). The accuracy with which corpses were classified to predator species was scaled from 1 (uncertain which species was involved) to 5 (predator seen killing grouse). In analysing selection by predator

* Corpses may also be less apparent in snowy conditions and also decay at a slower rate.

species only those kills which had an accuracy level of 3 or more were used. Kills which ranked 5 were used to help identify other corpses where the same species of predator was involved. Corpses were also collected from other moors over Scotland during routine grouse work, but these moors were not systematically searched.

When grouse were killed, the predator generally removed many feathers but the presence of feathers in the heather was not taken as a definite sign of death, since feathers were also lost in territorial disputes and in 'fright moults' (when grasped by a predator, but not killed). Some flesh, bone or feathers which were obviously bitten or plucked, had to have been located before being classified as a kill. All remains, other than feathers, were removed and the larger feathers stuck in the ground to prevent recounting.

3.2.1 Potential sources of error

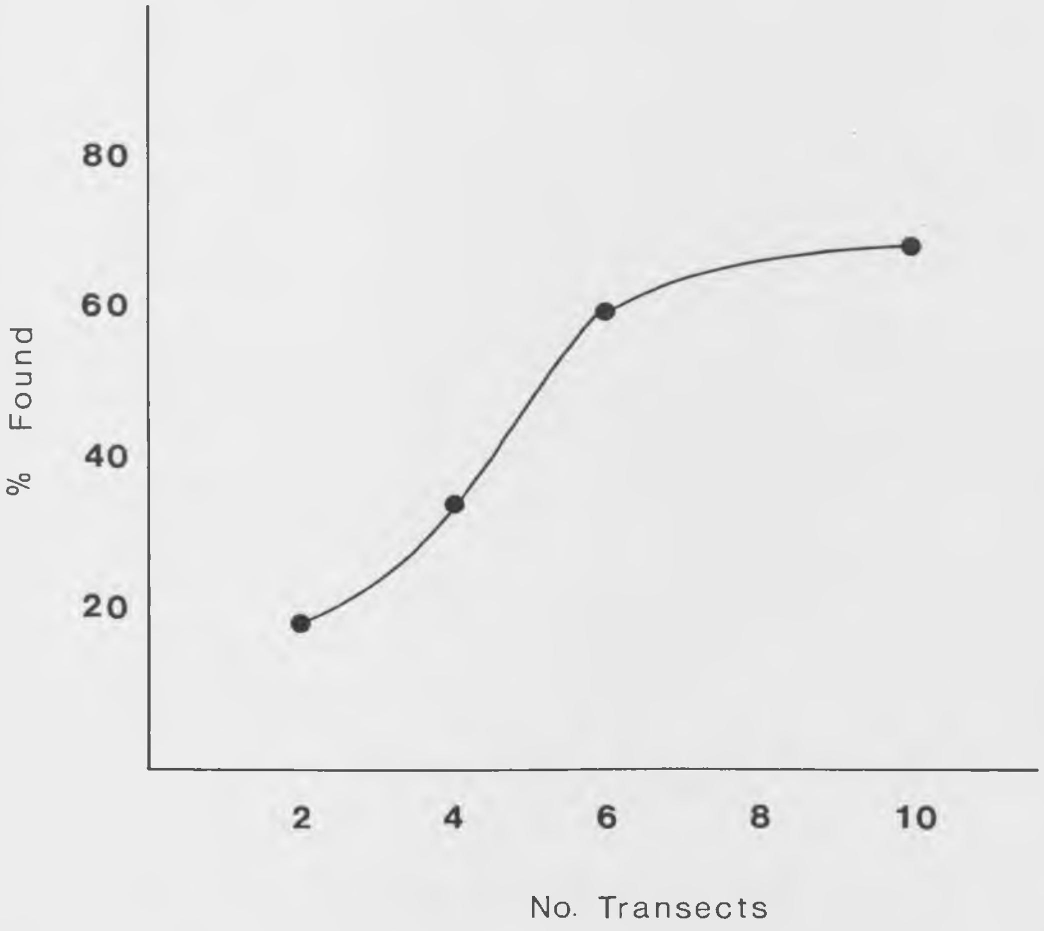
1. Not all kills were found. To test the efficiency of carcass finding a total of 28 corpses were placed at random onto two 0.5 km^2 areas with feathers plucked out and scattered in the heather to resemble kills. These areas were then covered during 2, 4, 6 and 10 even transects and the number of corpses found recorded (Fig.3.1). 61% of the carcasses were located after six transects and 69% after ten. As each transect took approximately half an hour six transects was regarded as the most efficient number.

The proportion of corpses found was thought to be dependent on weather conditions, with fewer found in snowy or wet weather (when feathers stuck to heather and were less easily seen) and also on the predator involved.* Raptors pluck large quantities of feathers from kills which are obvious, whereas mammal kills tend to be less spread out. In the above test corpses resembled raptor kills and when 13 'mammal kills' were distributed on one study area, only three (23%) were located after six transects.

When the month of death of corpses was examined, 59% of kills found were less than one month old.

This was lower for mammals (48%), but higher than the rest, indicating that either more mammal kills were found than the test suggested in the first month, or many corpses were never recovered. The main study areas were intensively covered by the S.G.R.P. using

FIGURE 3.1 The percentage of grouse corpses found on 0.50km^2 (50 ha.), during 2, 4, 6 and 10 even transects.


80
60
40
20
% Found
2
4
6
8
10
No. Transects

pointing dogs which showed an interest in the carcasses and in cached remains. However, it is unlikely that all mammal kills were recovered. The figure for raptors is probably more accurate.

Another source of error may occur in spring and summer when predators remove corpses to feed their mates or young. This was recorded in 1987 when a peregrine captured and flew from one study area with a female grouse. The extent of this loss was unknown, but by comparing the number of live grouse counted in early spring to the number in autumn, overall losses could be estimated. However, this did not take into account any dispersal from the areas in this period.

2. Scavenging by mammals. Mammals, and in particular foxes, will feed on the remains of kills, thereby increasing the proportion of kills attributed to mammals. Scavenging rates were examined by placing corpses on trays covered in a thin layer of clay (for footprints). These (N=24) were placed on the moor approximately 100m. apart and after three months five (21%) had been scavenged by foxes and two by raptors (probably buzzard). Foxes usually left very little meat (or cached the remains) and it is unlikely that many fox kills were attributed to raptors.

In consideration of these two sources of error the data should be regarded as minimum estimates of mortality, especially in the spring and summer and are likely to be biased in favour of raptors, although this may have been partially offset by mammals scavenging raptor kills.

3.2.2 **Determining time of death, sex and age of corpses**

The scavenging experiment indicated the rate of decomposition in the field, so that the month of death (up to the first three months) could be determined. Older than this, corpses were classified into seasonal kills (ie. winter, spring or summer) and these were later divided up into months depending on the proportion of kills already found in each. Seasonal kills were excluded from the analysis of monthly variations in raptor, mammal and fence kills. Numbers of birds found killed by fences on the boundaries of study sites were halved since birds were equally likely to have come from moorland on the other side.

In accordance with the behaviour of grouse: winter was defined as

September to March inclusive (when grouse were in packs or setting up territories); spring as April and May (grouse laying and incubating eggs) and summer as June, July and August (grouse with young).

Corpses were aged by studying the pigmentation on the 8th and 9th primaries (Bergerud et al. 1963) and examining whether the toe nails had been shed (Watson & Miller 1970). In this way birds were classified as yearlings (less than one year old) or adults (over one year old). The mortality of chicks (birds less than twelve weeks old) was not included in this analysis (see chapters 4 and 5). Birds were sexed by examining plumage, the size of wattles and where possible, the reproductive organs. Various body measurements were then taken and compared between birds of known sex. A discriminant function analysis was carried out using five of these measurements (length of: humerus, femur, sternum, tarsus and wing) and correctly classified 91% (N=37) of corpses where sex was known (reproductive organs examined). Birds of unknown sex were then identified if the probability of being correct was greater than 80%.

When fresh kills were found, their intestines were examined for parasites (in particular Trichostrongylus tenuis) using standard techniques (Hudson 1986b), to see whether there was any evidence of predators killing diseased grouse. These worms are associated with low body mass when the intensity of infection exceeds 3500 worms per bird. A second index of condition was taken from the chest (the size of the pectoralis muscle. These were graded from one to five, where one was very poor and five was in excellent condition (Hudson pers. comm.). The chest index of corpses was compared to that of live birds, caught at night by the Game Conservancy. These birds were caught at random and considered a random sample.

3.2.3 Raptor numbers on moors

Peregrine falcons, female hen harriers and golden eagles were the main raptor species present which could kill adult grouse. On the study sites their numbers were recorded during routine work as the number seen per 100 hours. To examine the relationship between raptors and grouse density, analysis was confined to the winter period, when raptors were not restricted to their nesting area, were not heavily persecuted and when grouse were the main prey species in the area.

To compare findings between the three moors in Speyside, data from the two sites on each estate were combined to allow for statistical testing. Within each estate the sites covered up to 17% of the area.

3.3 Results

3.3.1 Losses from study sites

On the six study areas in Speyside (totalling 1500 ha) from October 1985 to August 1988, 245 corpses were found. In addition to these, 54 dead birds were picked up on fences adjacent to the sites. Assuming that half of these were from the study areas, this gives a total of 272 dead grouse in 33 months (Appendix 1). These birds did not die equally throughout the year (Fig.3.2), but peaks in mortality occurred in the winter. As a proportion of those present at the start of winter and spring/summer, predation levels for these two periods were similar. For the three years combined, 28% of the population counted in autumn (minus the number shot) was found dead overwinter and 20% of the spring population found dead before autumn. However, this does not take into account any dispersal that takes place in early winter, after the counts (Jenkins et al. 1963; Hudson unpub), so the proportion killed during winter will generally be higher, unless there is net immigration, which can occur at low density (Watson et al 1984, chapter 6).

Counts of live grouse showed that over 50% of the grouse were lost, through dispersal and mortality, from the study sites during the winter months. These figures were compared with the number of birds found dead in each period (Table 3.1) and show that 35% - 89% of the birds lost over winter were found in different years. When the data from the three moors were considered separately, the number of grouse killed from one autumn to the next increased with density (Fig. 3.3a), but the proportion of the autumn population killed was inversely related to density (Fig. 3.3b) and at low density more birds died than were actually counted on the area. From spring to autumn, losses could largely be accounted for by kills found.

FIGURE 3.2 Monthly variations in adult grouse mortality on the six study sites, based on corpses found from February 1986 to August 1988. Data include fence kills, but exclude shooting mortality.

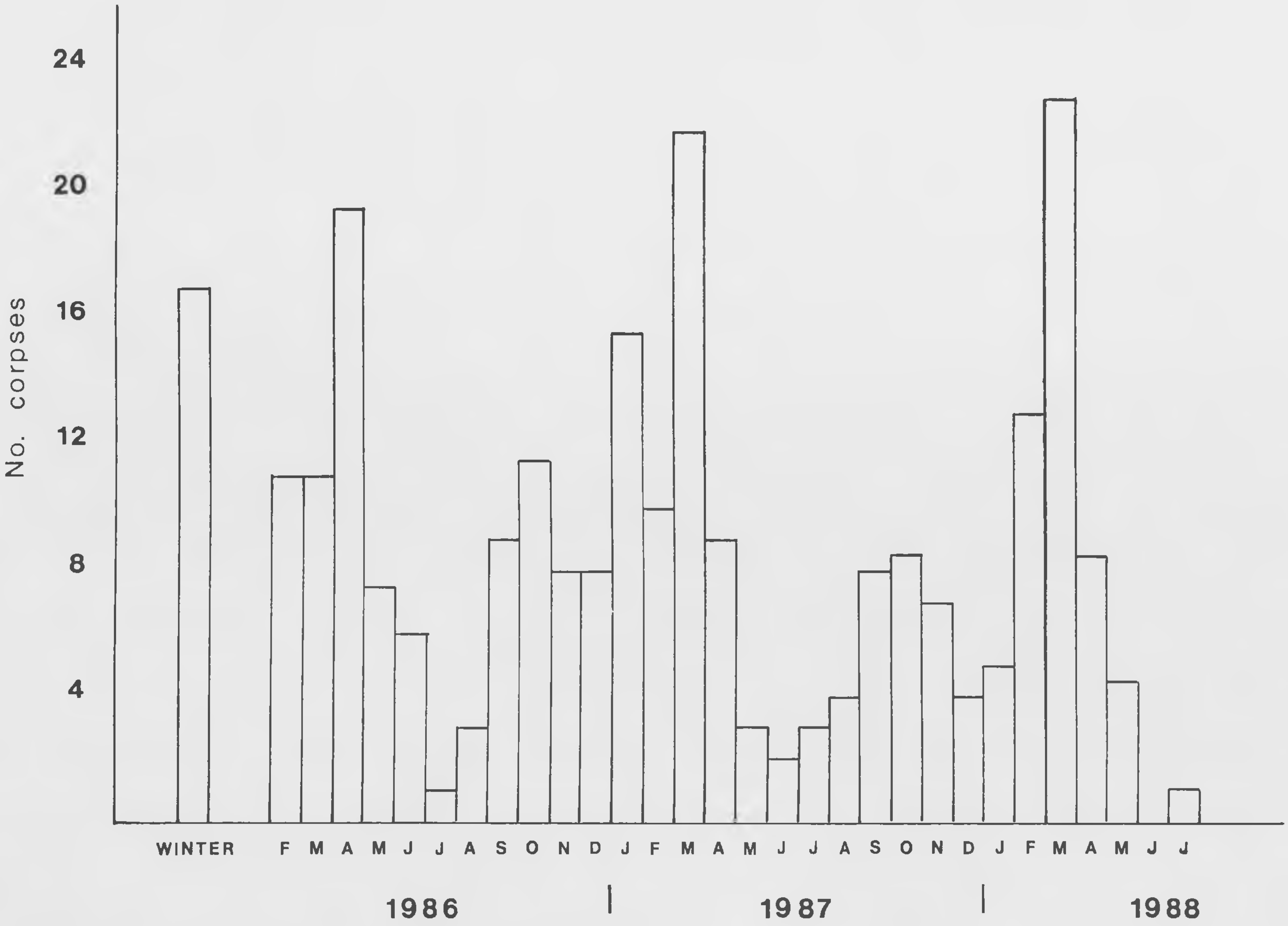
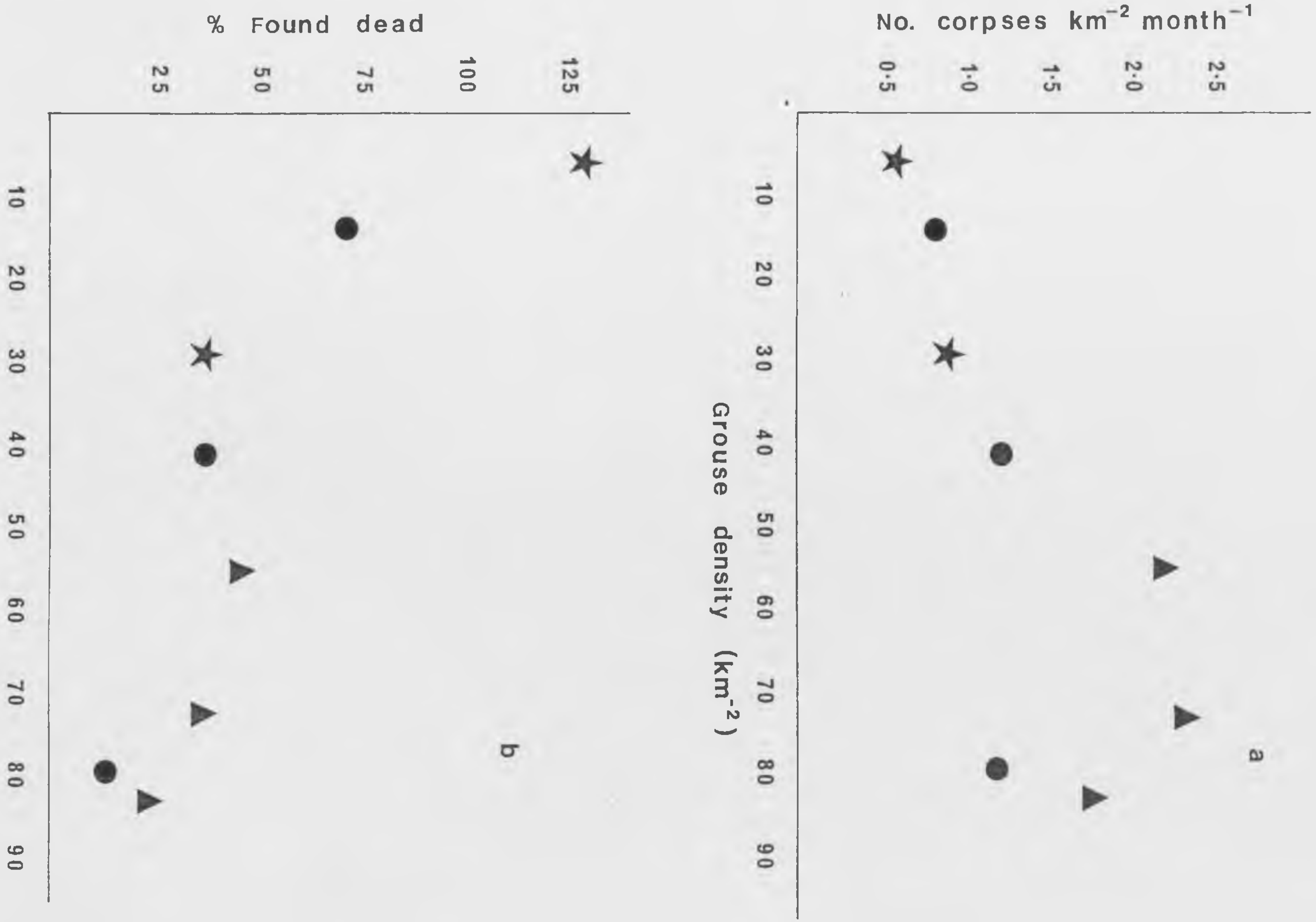

24
20
16
12
8
4
No. corpses
WINTER
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
1986
1987
1988

TABLE 3.1 Relationship between the number of grouse counted in autumn (AUT) and spring (SPR), the total number lost between counts and the number of kills found (to predators and fences) on the six study sites. Data presented as mean no. km^{-2}. (Autumn 1985 data for two study sites).

				BETWEEN COUNTS			
		COUNT	NO. SHOT	NO. LOST	% LOST	NO. FOUND	% LOST BIRDS FOUND
1985/86	AUT	43.5	0	26	60%	9	35%
	SPR	13.3	0	3.5	26%	5.6	+100%
1986/87	AUT	34.5	2	17	52%	15.2	89%
	SPR	15.5	0	0	0%	2.8	+100%
1987/88	AUT	63.7	8	32.2	58%	12.5	39%
	SPR	23.5	0	3.3	14%	2.3	70%

FIGURE 3.3 Relationship between autumn density and (a) the number of kills found km^{-2} month^{-1}, (b) the proportion of grouse found dead, up to the next autumn in four years. Data for the three estates: ★ - moor R; ● - moor C; ▲ - moor D.

Regressions: a) $Y = 0.65 + 0.015\,X$, $r=0.66$, $p=0.07$
b) $Y = 175 - 80.4\,\mathrm{LOG}(X)$, $r=0.93$, $p=0.001$.


No. corpses km^{-2} month^{-1}
0·5
1·0
1·5
2·0
2·5
a
% Found dead
25
50
75
100
125
b
Grouse density (km^{-2})
10
20
30
40
50
60
70
80
90

3.3.2 Causes of Mortality

The percentage of corpses found which could be attributed to various causes is displayed in Fig 3.4a, and shows that raptors killed more grouse (51%) than all the other causes, though the species involved was often difficult to ascertain. In 40% of raptor kills, the species of predator could not be determined above an accuracy level of two. When the results from the six study areas were compared with data collected from other Scottish moors (Fig. 3.4b), the proportions classified to predator types were not different (χ^2=0.72, $p>0.1$), indicating that the results were representative for other Scottish areas. Overall peregrines killed similar numbers of grouse to foxes and together these two accounted for at least 44% of all kills found.

Raptors killed most grouse from February to May and from September to December, whereas mammals tended to kill grouse in late winter (Fig. 3.5). Fences and wires killed most birds in midwinter and very few in summer and early winter. Within Speyside there were significant differences in the causes of mortality, both between moors (χ^2=20.2, $p<0.001$) and between years (1988 data excluded χ^2=7.3, $p<0.05$). Estates R and C had a higher proportion of raptor kills and estate D more mammal and fence kills (Fig. 3.6). In 1986, raptors killed 70% of all grouse kills as opposed to 51% in 1987. No birds were found killed by parasites on the six main areas in the three years of this study.

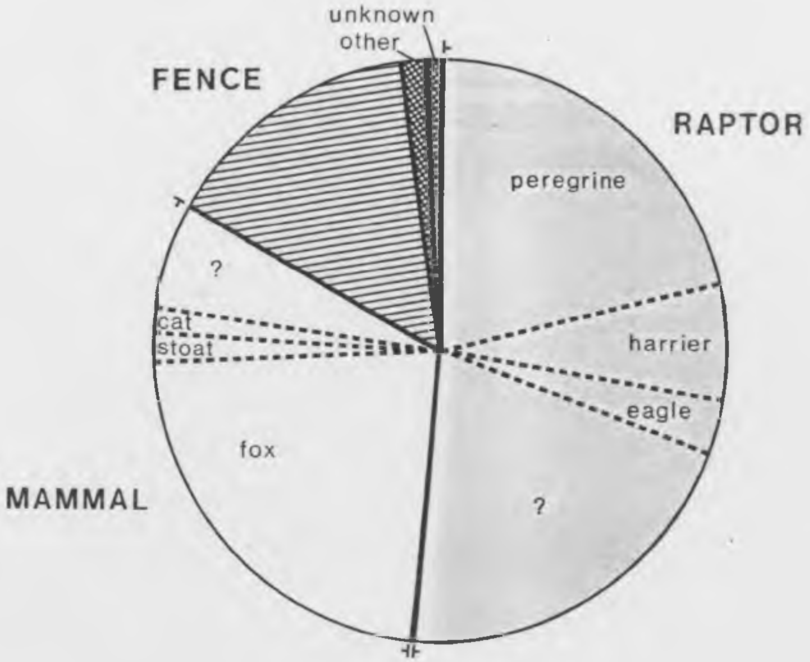
3.3.3 Age and Sex of Corpses

From one spring count to the next on the study sites, there was no significant difference between the ratios of males : females counted and the ratio found dead (Table 3.2 χ^2=2.4, $p>0.1$) and there was no significant heterogeneity between years. Overall, although more young than old were killed in each season, the differences were not significant (Fig. 3.7). However, when compared to the ratio of young to old counted in autumn the differences were significant (χ^2=19.2, $p<0.001$), with fewer young than expected being killed overwinter (Table 3.3). This applied in the winters of 1985/86 and 1987/88, but there was significant heterogeneity between years (χ^2=60.6, $p<0.001$), with a similar number of young killed to the expected in 1986/87.

The age and sex of birds killed by various predators on all moors was compared (Table 3.4) and showed that foxes killed significantly more male than female birds (χ^2=4.10, $p<0.05$), whilst harriers (χ^2=5.33,

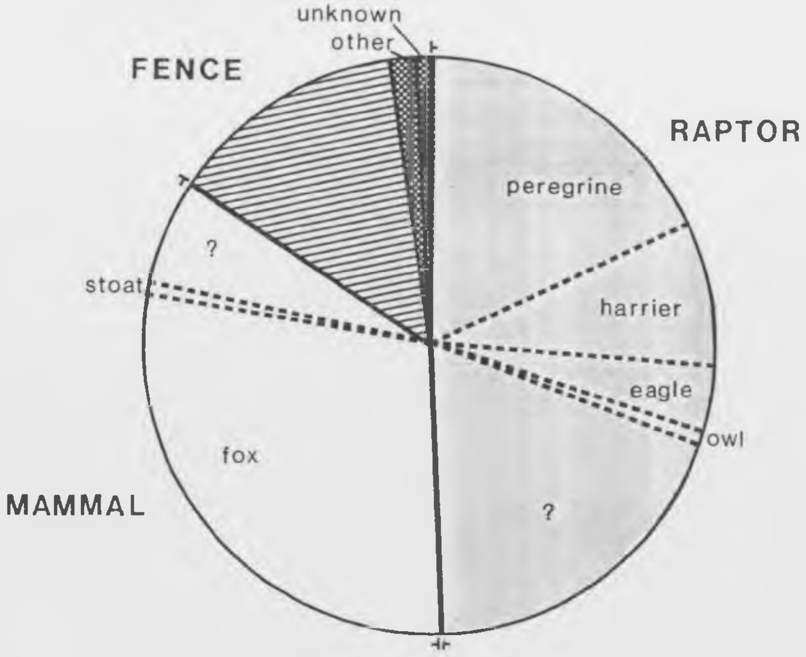
FIGURE 3.4 Causes of mortality on (a) the six study sites and (b) all other moors in Scotland. Mortality divided into kills by raptors, mammals, fences, others (eg car) and unknown, then subdivided into predator species. Shooting mortality is not included.

a. N = 272



unknown
other
FENCE
RAPTOR
peregrine
?
cat
stoat
harrier
eagle
fox
MAMMAL
?

b. N = 237



unknown
other
FENCE
RAPTOR
peregrine
?
stoat
harrier
eagle
owl
fox
MAMMAL
?

FIGURE 3.5 Monthly variation in the number of grouse killed by raptors, mammals and fences. Data exclude the seasonal kills. Top graph shows all kills and lines above graph represent the winter period.

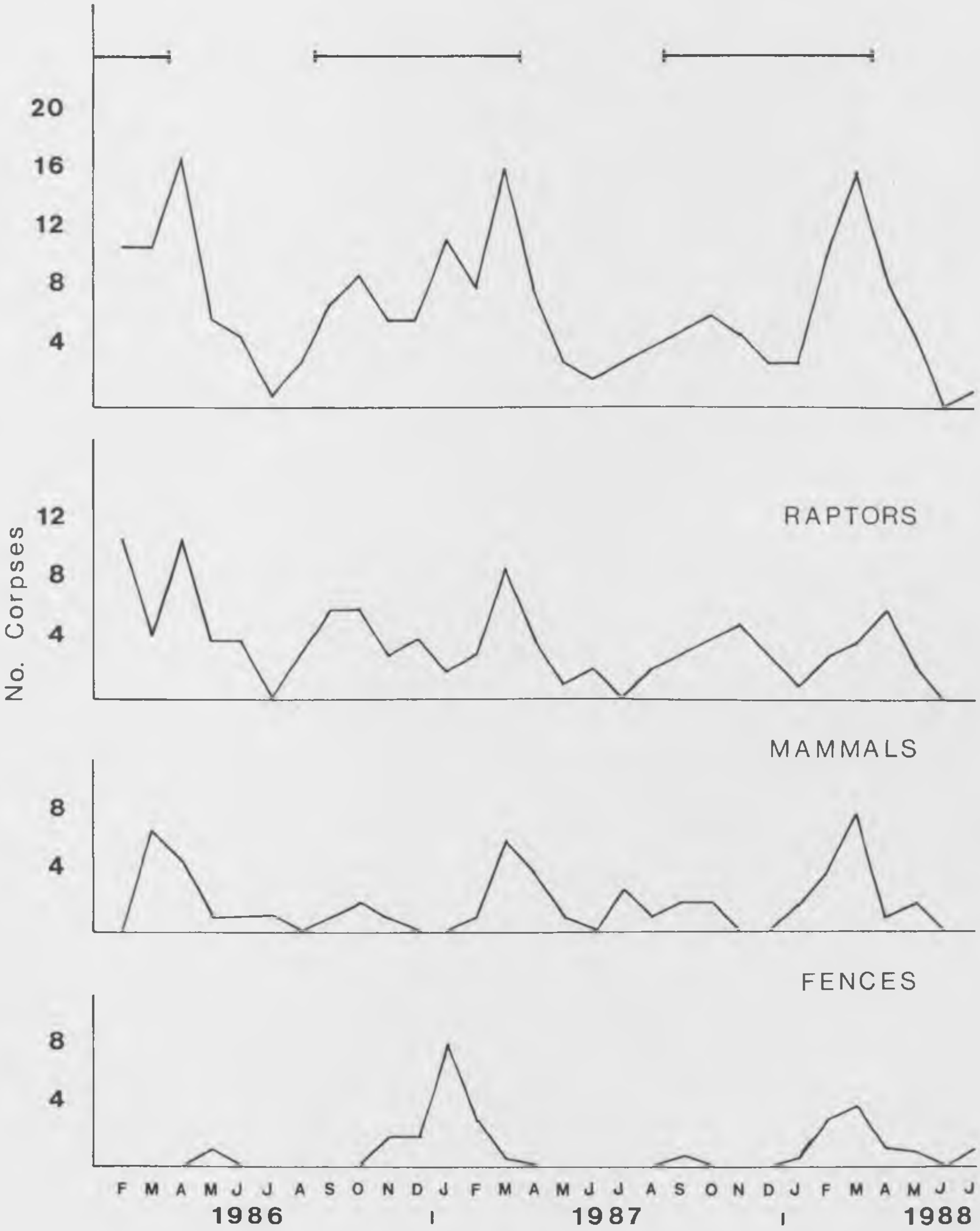

20
16
12
8
4
12
8
4
RAPTORS
No. Corpses
MAMMALS
8
4
FENCES
8
4
F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J
1986
1987
1988

FIGURE 3.6 Variation between moors (a) and years (b) in the percentage of kills attributed to raptors (R), mammals (M) and fences (F).

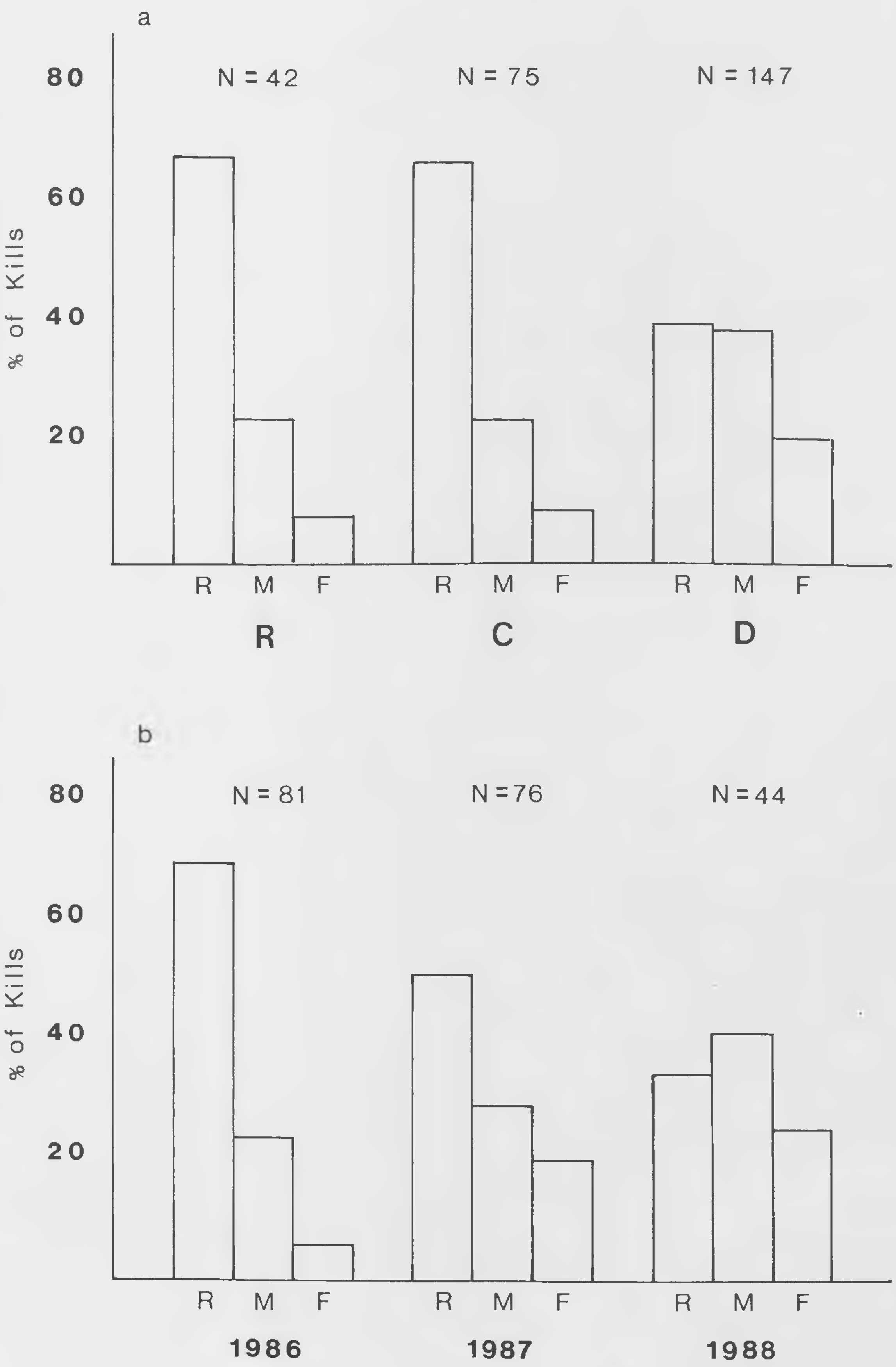

a
80
60
40
20
% of Kills
N = 42
N = 75
N = 147
R M F
R M F
R M F
R
C
D
b
80
60
40
20
% of Kills
N = 81
N = 76
N = 44
R M F
R M F
R M F
1986
1987
1988

TABLE 3.2 Numbers of male and female grouse killed on the three study moors in three years, from one spring to the next. Expected values are drawn from ratios of male : female counted in spring. Overall $\chi^2 = 2.40$ NS, Heterogeneity $\chi^2 = 2.27$ NS.

	MALES		FEMALES		SIGNIFICANCE	
	OBS	EXP	OBS	EXP	χ^2	P
1986	65	65.7	49	48.3	.02	NS
1987	40	49.2	42	32.8	4.3	$<.05$
1988	12	13.4	11	9.6	.35	NS

FIGURE 3.7   Seasonal variation in the age of grouse killed throughout the year on the study sites (all years combined).

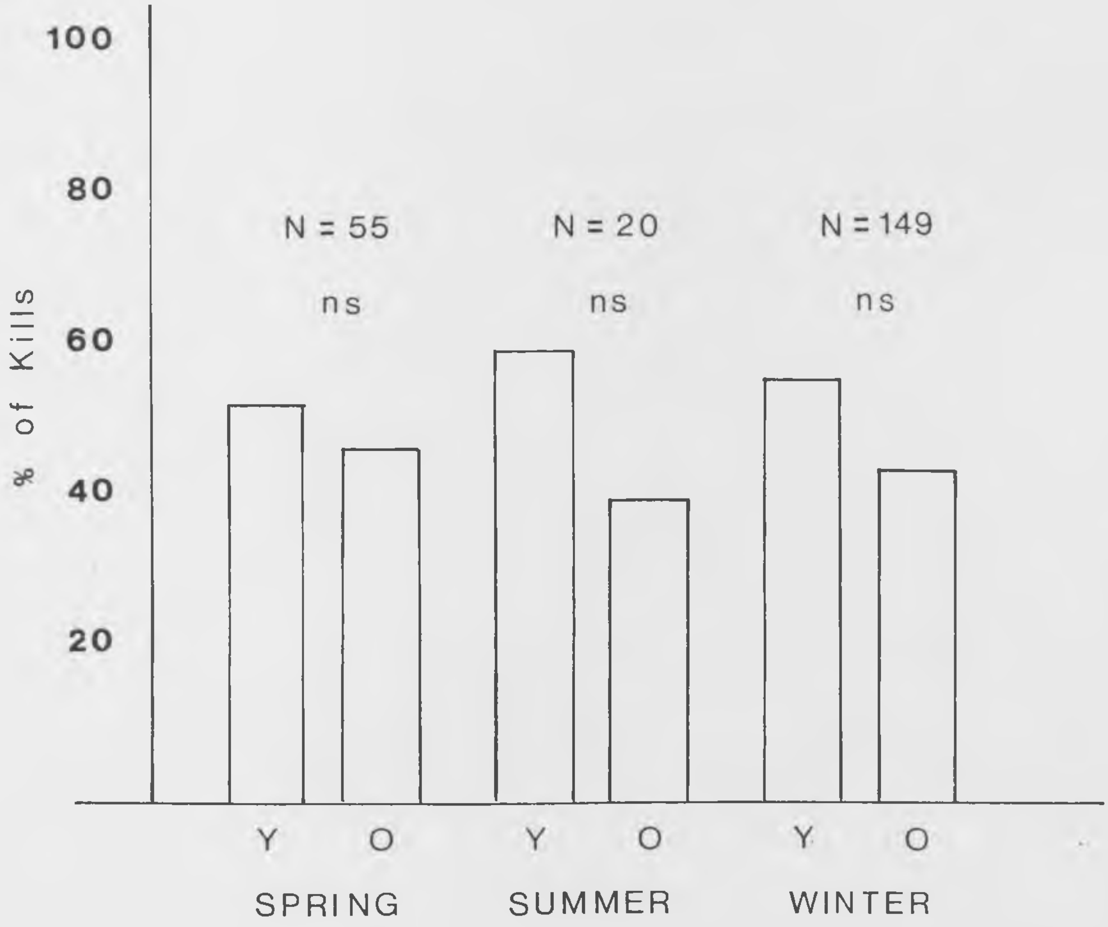

100
80
60
40
20
% of Kills
N = 55
ns
N = 20
ns
N = 149
ns
Y
O
Y
O
Y
O
SPRING
SUMMER
WINTER

TABLE 3.3 Variation between ratio of young:old grouse counted in autumn and killed overwinter. Data for three moors combined.

	YOUNG : OLD COUNTED	YOUNG : OLD KILLED	SIGNIFICANCE.
1985/86	1.9 : 1 (N = 87)	0.15 : 1 (N = 23)	$\chi^2 = 56.2$ $p<0.001$
1986/87	2.6 : 1 (N = 200)	3.8 : 1 (N = 67)	$\chi^2 = 0.7$ NS
1987/88	3.1 : 1 (N = 382)	0.9 : 1 (N = 56)	$\chi^2 = 20$ $p<0.001$

TABLE 3.4 Age and sex of grouse found killed by peregrines, harriers, foxes and fences. Data from all moors.

	SEX				AGE			
CAUSE OF DEATH	Male	Female	χ^2	p	Young	Old	χ^2	p
PEREGRINE	42	39	0.05	NS	33	34	0.0	NS
HARRIER	11	15	0.35	NS	20	7	5.33	*
FOX	49	30	4.10	*	38	46	0.58	NS
FENCE	23	17	0.62	NS	29	10	8.31	**

$p<0.05$) and fences ($\chi^2=8.31$, $p<0.01$) killed more young than old. From March to June, harriers killed more females than males (8:4), but the sample size was too small to test.

3.3.4 Raptor numbers

The number of raptors seen hunting the study areas varied depending on the time of year and the type of work being performed by the observer (see chapter 2). The number of raptors seen overwinter appeared to vary inversely to the density of grouse (Fig. 3.8), both between estates and within two of them.

3.3.5 Parasites and condition of grouse corpses

Seventeen intestines were examined for worm burdens (Table 3.5). These gave an average burden of 323 worms per bird, far below the 3500 at which grouse are deleteriously affected. Similarly, when chest index was examined (Table 3.6), over 90% of corpses (N=22) had an index of three or more, indicating good condition. Two kills were in slightly poorer condition, whereas none of the birds caught at random at night had an index below three. Overall, there was no difference between the chest index of those grouse killed and those dazzled ($\chi^2=0.4$, NS).

3.3.6 Comparison of studies

The aim of this section is to compare patterns of predation between similar studies in different areas and at different grouse densities. Some of the data come from population studies of willow ptarmigan (<u>Lagopus lagopus</u>), a subspecies which inhabits willow scrub elsewhere in Europe and North America. Methods of corpse finding varied, this study being the only one where corpses were systematically searched for. A higher proportion of kills may have been located during this work, than the others, and this should be borne in mind during the comparison. All data from the six study sites have been combined for the analysis.

This study was the only one carried out at low density (Table 3.7), with an average spring density at least 3.6 times lower than all the other investigations. An examination of numbers of corpses (Table 3.8) shows that the proportion of the population killed by predators is inversely related to the autumn density ($N=4$, $r=0.98$, $p=0.01$),

FIGURE 3.8 Relationship between raptor density (in winter) and grouse density (autumn) over four years, for three estates (excluding data for less than 20 hours field work). ★ - moor R; ● - moor C; ▲ - moor D. Regression: $Y = 15.44 - 0.14\ X$, $r=0.58$, $p=0.08$.

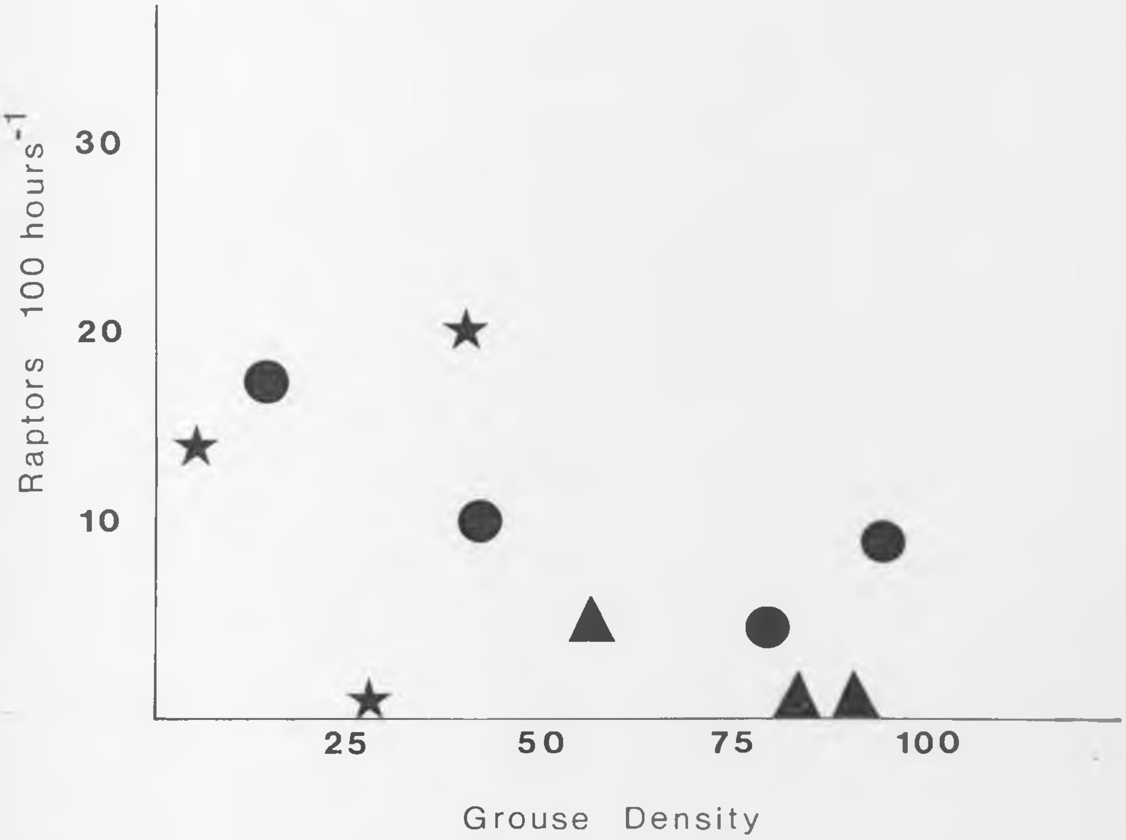

Raptors 100 hours^{-1}
30
20
10
25
50
75
100
Grouse Density

TABLE 3.5 Numbers of the roundworm _T. tenuis_ in the caecae of dead grouse showing when killed, age of grouse and presumed cause of death.

MONTH KILLED	AGE	PREDATOR	NO. WORMS
DECEMBER	Y	PEREGRINE	60
NOVEMBER	Y	PEREGRINE	40
APRIL	Y	?	140
MAY	Y	STOAT	280
MAY	Y	PEREGRINE	1720
APRIL	Y	HARRIER	220
WINTER	Y	FOX	1160
OCTOBER	Y	HARRIER	0
APRIL	Y	STOAT	340
SPRING	Y	FOX	0
JULY	Y	HARRIER	80
JULY	O	FOX	640
JUNE	O	PEREGRINE	380
APRIL	O	FOX	260
JUNE	O	PEREGRINE	0
FEBRUARY	O	FENCE	100
FEBRUARY	O	FENCE	80

<u>MEAN</u> 323 WORMS PER BIRD

TABLE 3.6 Chest index of birds killed by predators and dazzled at night. Index varies from 1 (very poor) to 5 (excellent condition). $\chi^2 = 0.44$, NS.

INDEX	KILLS (N=22)		DAZZLED (N=38)	
	NO.	%	NO.	%
1	0	0%	0	0%
2	2	9%	0	0%
3	7	32%	13	34%
4	12	54%	22	58%
5	1	5%	3	8%

TABLE 3.7 Size of different study areas and the average densities of grouse km^{-2}.

STUDY	YEARS	AREA KM^2	MEAN SPRING DENSITY	RANGE	MEAN AUTUMN DENSITY
1	1986-88	6.0	18	6-32	57.7
2	1987-88	5.0	76	14-104	250
3	1957-61	4.5	65	34-84	148
4	1958-61	4.0	69	34-100	122
5	1979-87	2.5 - 4.5	69*	42-86	--

* - Approx. densities estimated from Hannon and Gruys (1988).

STUDIES :

1 - Present study, Speyside, Scotland.
2 - Swaledale, North England (Hudson & Newborn unpub).
3 - Glen Esk low site, Angus, Scotland (Jenkins *et al.* 1963 + 1964).
4 - Glen Esk high site, Angus, Scotland (Jenkins *et al.* 1963 + 1964).
5 - Chilkat Pass, Canada (Hannon and Gruys 1988).

TABLE 3.8 Numbers of predator kills found in each study from one autumn to the next. Expressed as kills year^{-1} km^{-2}. Study areas as in table 3.7.

STUDY	AUTUMN DENSITY	MEAN No. CORPSES	RANGE	% AUTUMN POPULATION FOUND DEAD
1	57.7	15.1	12.7 - 19.1	27%
2	250.0	5.8	*	2.5%
3	148.0	26.5	13.6 - 35.2	18%
4	122.0	20.9	11.9 - 37.0	17%
5+	--	14.4	11.6 - 21.3	12%

+ These data estimated from Hannon and Gruys (1988).

* Only one full winter studied

although comparisons of mortality may not be accurate.

Many more raptors were seen in this study than any of the others (Table 3.9) possibly because I spent more time looking for them than the casual observations of the other studies. To allow for this I used only data collected during general grouse work and not during periods of intensive observation, though these differed only with respect to harriers (chapter 2). Even accounting for this, numbers were still higher in this study, indicating that more birds of prey were present. There was little difference in raptor numbers in summer and winter apart from the harrier, which were more frequently seen in summer (Chapter 1). In Upper Speyside, large areas consisted of unkeepered land and predators could hunt from these areas during the summer. Fox numbers were unknown in the area, although their scats were collected and numbers compared to those from the English moors. Between May and December 1986, 78 scats were collected from 5 km ^{2} in Scotland as opposed to 5 scats from 5 km^2 in England (Hudson & Moore 1987).

In all studies, raptors killed similar proportions of grouse and this was consistently higher than mammals (Table 3.10). A major difference between this and the Glen Esk study was the number of peregrines present. In six years, covering 8.5 km^2, Jenkins et al. found only three suspected peregrine kills, compared to a minimum of 57 from 6 km^2 in three years. Apart from this difference, estimated losses to other species were similar, with harriers compensating for the lack of peregrine kills in Glen Esk.

Interestingly, in the Canadian studies, predators were not killed and yet willow ptarmigan densities still rose to high levels. These populations exhibit 8 to 11 year cycles (Mossop 1985), whereas English populations peak every four years (Potts et al. 1984) and some Scottish populations every 6 to 7 years (Williams 1985). It is possible that predators may lengthen the cycles by slowing the increase in density. Such extensions of low densities, associated with predation, are thought to occur in some small mammal populations (Hansson 1984; Henttonen 1985; Jarvinen 1985).

Hannon found little numerical response in raptor density to changes in ptarmigan numbers, suggesting that they could have a greater effect at low density than at high. Foxes appeared to show a two year time-lag

TABLE 3.9 Numbers of raptors (Harriers, Eagles and large Hawks/ Falcons) seen 100 hours^{-1} in each study during general work in spring and summer (May to August) and overwinter (September to April after Jenkins *et al.* 1963). Study areas as in Table 3.7.

STUDY	SUMMER	WINTER
1	25.1	24.8
2	--	1.0
3	--	4.6
4	--	5.4
5	8.1	--

TABLE 3.10 Variation in proportions of raptor and mammal kills found in each study. Study areas as in Table 3.7.

STUDY	% OF PREDATOR KILLS				
	ALL RAPTORS	EAGLE	PEREGRINE + HARRIER	ALL MAMMALS	FOX
1	60%	3%	27%	40%	23%
2	62%	0%	---	38%	---
3	53%	3%	22 - 23%*	47%	22 - 23%
4	59%	14 - 15%	5%*	41%	14 - 15%
5	51%	---	---	49%	---

* Mostly harrier kills, but some sparrowhawk and buzzard.

in response to density, which could also delay population growth. In the Chilkat study, predators under natural situations were unable to suppress grouse populations, although the habitats may have provided more cover than the heather moors in Britain.

Another important difference is in the level of mortality due to parasites. Both Jenkins et al. (1964) and Hudson (1986a) found large numbers of parasitised birds dead in some years. In this study no grouse were found killed by parasites and workers on willow grouse have similarly found little parasitism (Hudson & Steen unpub). In the studies where predators were more common, mortality to parasites is low, suggesting that parasites only become important once predators are reduced.

3.4 Discussion

3.4.1 Grouse mortality and dispersal

Over the three years of this study an average of 36% of the autumn population was found dead on the study sites up to the next autumn. However, this mortality could not account for all of the losses from the sites. Overwinter, grouse numbers decreased by 57%, of which 49% was accounted for by kills found. This indicates that either 29% of birds present in autumn dispersed from the areas, and were not offset by immigrants or that their corpses were not found. It is unlikely that so many corpses (>100) were not recovered, so dispersal into low density areas is the likely cause of the loss. This was supported by the finding that the numbers of grouse on the lowest density areas increased overwinter.

More adult grouse died in the winter than at any other time of year. This could partly be explained by the increase in grouse numbers from breeding, but dispersal and the pattern of mortality suggested that other factors were involved. From the predators point of view there were fewer prey species on the moors during winter (see chapter 2), so grouse became a more important prey item. During the summer grouse were protecting their eggs and chicks and were rarely seen. Also there were more alternative prey on the moors and predators (mainly foxes and crows) were killed in the spring. Consequently few adults were killed at this time of year, although the chicks formed an important part in some predators' diets (Chapters 4 & 5).

During early winter (August to November), grouse divide into two social classes, with some becoming territorial, whilst others remain in small non-territorial packs (Jenkins *et al.* 1963). In mid-winter, both groups join together in snowy conditions to form large packs. Then, from February onwards, territories are reformed and the small packs disappear. During both these periods of territorial activity, some dispersal takes place, though this appears to be largely confined to the early-winter period.

In line with the findings of Jenkins *et al.* (1964), mortality to predators in this study was highest during these periods of territorial activity and dispersal, in particular the late-winter phase. In mid-winter grouse formed into large mobile packs which were associated with snow cover (Hudson unpub) and, as suggested by Jenkins *et al.*, were relatively invulnerable to predation, probably due to increased vigilance (eg. see Kenward 1978). However, it was during this period when fences killed most grouse, probably due to the movement of the packs over the moors.

3.4.2 Additive versus compensatory mortality

An important issue in any study of predation is whether mortality was compensatory, as indicated by Jenkins *et al.* (1963), or additive (see chapter 1). They suggested that predators kill grouse made vulnerable by their social status, i.e. those without territories. Therefore any observed mortality is merely a function of social behaviour and not the ultimate cause of death, and so social behaviour and not predation determines breeding numbers.

An alternative hypothesis is that grouse are faced with the decision of whether to stay on a territory or join a waiting flock (Mossop 1985). Here the non-territorial birds are not simply 'surplus' grouse, but include individuals that may survive and breed; i.e. mortality is additive. The advantage of being in a group is that individuals may have a reduced risk of predation due to increased vigilance (see Krebs & Davies 1984 for review), whilst an advantage of territorial behaviour is conferred if these birds are able to maintain their territories to the following breeding season. Some dispersal may take place in autumn to prevent inbreeding (Hamilton & May 1977) and in snowy conditions an increase in the vulnerablity of territorial birds or a decrease in food availability will force all birds into large packs. In late winter grouse without territories must decide when to leave the packs and become territorial. If there is no space on the moor then birds can be expected to disperse. The costs and benefits of these decisions are likely to vary, both with the density of grouse and the density of predators.

Assuming that these two groups of non-territorial and territorial grouse are present on the moorland in winter, then there are two important differences between these hypotheses. The first lies in the mortality of territorial birds. The findings of Jenkins _et al._ (1963) and Watson (1985) indicated that territorial birds were rarely killed, whereas the alternative gives no _a priori_ reason why they should not be, although there may be slight differences in vulnerability between the two groups. It is likely, for example, that non-territorial, dispersing birds are more vulnerable to predators, but it could also be argued that grouse involved in territorial activity have less time for vigilance and therefore have increased vulnerability. The second difference depends upon whether or not the non-territorial birds that were not killed would survive and breed; i.e. whether their mortality is additive or compensatory.

Results from Speyside differ from those of Jenkins _et al._ (1963). Whilst they showed that territorial birds were rarely killed, Hudson (unpub) has recently shown that territorial and non-territorial radio-tagged grouse were equally likely to be killed by predators on these sites. He went on to show that on these low density moors, territories were available, because birds transferred from other moors subsequently settled and bred, although it was not known whether these birds displaced previous territory owners.

Why should these two studies differ? A possible answer is put forward by Jenkins _et al._ (1964) when they showed that in one year, the grouse population was "..well below the maximum possible level.." and predation levels were low because birds were able to find territories. In other words there were very few non-territorial birds present on the moor to be killed by predators. This study was carried out at low grouse density with high numbers of predators (see section 3.3.6). Many, if not all, the birds killed may have been able to get territories in the spring. At higher densities, those birds which had difficulty obtaining a territory were relatively more susceptible to predation, and therefore suffered increased mortality. At low density, mortality will tend to be additive and at high density compensatory, though the 'carrying capacity', or amount of space available for territories, will vary with moorland management and intrinsic factors influencing grouse behaviour (chapter 1).

As this study was carried out for three years, only trends in population changes and their effects can be observed. With regard to predation, the number of kills appeared to be inversely density dependent, with a greater percentage of the population being found dead on the low density areas. This supports the view that predation in this study is additive. Were predation compensatory, losses would be expected to increase proportionately with density, as more birds are without space to breed. This inverse relationship ties in with the finding that raptors were more frequently seen at low density (section 3.4.5), suggesting that predator numbers were not determined by grouse numbers, but by the total prey of all species.

3.4.3 Causes of mortality and selection by predators

Within the six study areas raptors killed more grouse than any other form of mortality, although mammal kills may have been underestimated. The fox and peregrine were the major predator species, accounting for a minimum of 23% and 21% of all corpses respectively. It is noticeable how few birds were killed by harriers (6%) and by eagles (3%), indicating that neither of these raptors was a major predator of adult grouse in winter. These figures were similar to those from other moors, suggesting that the data were representative. Raptors killed most grouse in early winter and late winter/early spring, whereas foxes killed most in March and fence lines in mid-winter. Raptors killed a greater proportion on low density moors, with mammals and fences increasing in importance at high density. These trends were also similar between years.

One of the problems of examining kills for age and sex selection by predators is that biases in availability may occur undetected. The only time when these ratios are known is from counts in April (male:female) and July (young:old).

Whilst male and female grouse were killed in proportion to their relative densities on the moor, fewer young grouse than expected were killed in the winters of 1985/86 and 1987/88. One possible reason for this difference was that there was more dispersal of young birds from the study areas in these years. This is supported by the finding that observed mortality could account for much of the loss in 1986/87 but only 35% in 1985/86 and 36% in 1987/88. Why dispersal rates should vary remains unclear. If young birds were dispersing (Hudson 1986a), then the fact that so few were killed by predators supports the idea that territorial birds may have been killed.

The finding that fences killed more young birds than old suggests that packs in mid-winter may have contained more young. However, the age structure of these packs is unknown and it is uncertain whether fences killed a higher proportion of young than were actually present. Harriers also killed more young than old, though the reason for this difference is unknown. They caught grouse on the ground by pouncing on them. Birds could possibly have avoided capture, either by flying away or by 'bouncing' beneath the harrier (Watson 1977). It is possible that young grouse were inexperienced in knowing how to avoid harriers.

3.4.4 Condition of corpses

Birds which were killed were in good condition, with over 90% of grouse having a chest index of three or more and no corpse having more than 2000 T.tenuis worms. Predators were not simply selecting birds in poor condition. Temple (1987) showed that predators took substandard individuals only when the rest of the population were relatively difficult to capture. These data suggest that predators do not simply take diseased birds from the population, indicating that they have no difficulty in killing individual grouse. In England, predators (in particular foxes) did select diseased birds (Hudson 1986a). This occurred particularly during the breeding season when grouse were less vulnerable to predation, but high parasite burdens increased their scent emission, thereby increasing their relative vulnerability to foxes. In this instance, the individuals without disease were difficult to locate whereas diseased grouse were vulnerable and therefore suffered increased mortality.

3.4.5 Raptor numbers

Jenkins et al. (1964) found a correlation between raptor numbers and grouse density and the number of grouse dispersing between years, but limited data from this study did not follow that trend. Indeed, raptors appeared to be inversely related to grouse density on two of the estates and this tied in with the observation that raptors were the main predators on the lowest density moors. The reason for this is unclear; there must be some factor other than grouse numbers governing the density of raptors in the winter. Whatever the reason, this has potentially important consequences for low density moors, if the trend is real, as predation pressure will be greater. On the lowest density estate in 1986, where raptor numbers and the proportion killed were highest, grouse stocks can only have been maintained by dispersal from surrounding moors, assuming that territorial birds were killed. However, the high predation levels were not enough to prevent the population from increasing. Had dispersal rates been lower, due to poor grouse stocks on surrounding moors, then the impact of such predation levels could have been severe.

3.5 Summary

This study was carried out on populations of grouse at low density, with high numbers of predators. A greater proportion of the population was found dead than in any other study, but mortality could not account for all losses from the population. Birds killed were in good condition and not heavily parasitised. Two peaks in mortality occurred and these were associated with periods of dispersal and territorial behaviour. There is contradictory evidence as to which groups of birds get killed over the winter and this is likely to be dependent on the densities of grouse and their predators. Initial findings by the Game Conservancy suggested that territories were available during this study and many of the birds therefore may have been potential breeders. Peregrines and foxes were the major predators of adult grouse, whilst harriers and eagles were unimportant. Although predators may delay the increase in grouse densities, other studies suggest it unlikely that they could suppress a population at low densities.

CHAPTER 4

PREY AND BEHAVIOUR OF HEN HARRIERS IN THE BREEDING SEASON

4.1 Introduction

Chick loss is one of the key factors influencing red grouse population dynamics (Hudson 1986a). Although there is disagreement over its importance in regulating populations, the view that it is a significant force at low density is widely supported (see chapter 1). The impact of predation on red grouse chick numbers has not been directly examined, but studies on other gamebird species show that chick predation can affect overall breeding success (Potts & Vickerman 1974; Marcstrom et al. 1988).

One predator which could remove large numbers of red grouse chicks is the hen harrier (Picozzi 1978). The diet of nesting harriers was studied by Picozzi on moorland with high grouse densities, and he concluded that harriers removed approximately 15% of grouse chicks. He added: "...comparative investigations are needed on moors with less grouse to find if harriers would prey disproportionately on them...".

This chapter and the following two, examine the role played by hen harriers in reducing red grouse breeding success. In order to determine the impact of harriers it is important to study their behaviour, to see how factors such as food consumption and hunting success vary in relation to prey density and distribution.

Hen harriers feed on a variety of prey types during the breeding season (Breckenridge 1935; Schipper 1973; Barnard et al. 1986). In Britain, their commonest prey at this time of year are passerines (especially meadow pipits), together with red grouse, lagomorphs and in Orkney, voles (Balfour & Macdonald 1970; Picozzi 1978, 1980). Outside the breeding season, small mammals become more common as prey (Watson 1977). Harriers hunt less than 9 metres above the ground, using edges and shrubs to surprise their prey (Brown & Amandon 1968; Schipper et al. 1975.). Prey are caught with sudden strikes or pounces and the recorded frequency of hunting success is low with 5% - 15% of strikes successful (Schipper et al. 1975; Temeles 1985; Collopy & Bildstein

1987). Harriers hunt throughout the day, though their activity tends to decrease around mid-day, probably due to the activity patterns of their main prey (Schipper 1973).

This chapter investigates the behaviour of harriers in the breeding season on moorland managed for red grouse, and examines the following questions: (1) How important are grouse as prey when at low and medium density? (2) How does harrier feeding rate vary between nests and throughout the season? (3) How does hunting activity vary throughout the day and the breeding season? (4) How successful are hunting harriers in relation to other studies? (5) How are the main prey species distributed over the moor? (6) Do harriers gear their hunting to one prey type? (7) How do adult grouse defend their young?

4.2 Methods

4.2.1 Study Areas

Two areas of moorland were chosen for this study, Speyside (Fig 4.1) in 1986 and 1987 (Moor R) and Perthshire (Fig 4.2) in 1988 (Moor B). These moors were selected because they contained breeding harriers and had differing grouse densities. Within each moor, a study site was chosen; one 6km^2 (1500 acres) on moor R and one of 4km^2 (1000 acres) on moor B. These were considered representative of the moors concerned and were overlooked by good vantage points for observation.

4.2.2 Hunting Observations

Individual harriers were watched as they flew into view and their movements dictated into a continuously running tape recorder until they disappeared. The amount of time spent perching, soaring (defined as non-powered flight over 10m.), feeding and hunting was recorded, along with the type of habitat over which they hunted. The number and success of strikes, where each strike at a prey item was considered an independent attempt, was also noted.

4.2.3 Harrier prey

Harrier nest sites were located by watching the moor for displaying birds in April and food passes in May (see Watson 1977). Individual harriers could then be recognised during observations, as they left or returned from their nests. In 1988 hides were placed close to three

FIGURE 4.1 Map showing area of estate R, studied in 1986 and 1987. Position of study site (shaded) and harrier nests on estate and surrounding moorland are indicated.

KEY:

● - Harrier nest.
○ - Nest deserted.
●K - Nest probably destroyed.
★ - Vantage point.

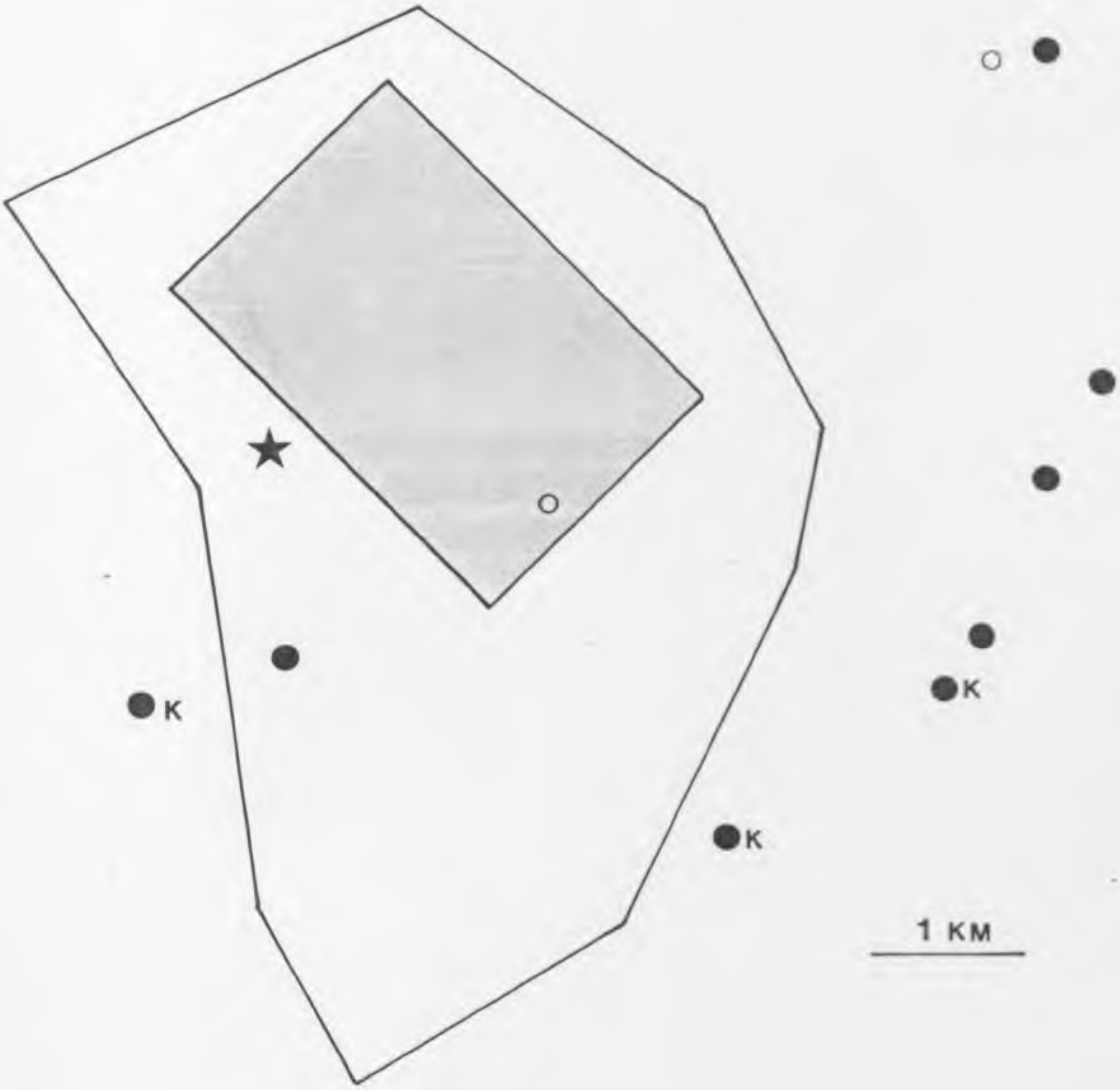

K
K
K
1 KM

FIGURE 4.2 Map showing area of estate B, studied in 1988. Position of study site (shaded) and harrier nests on estate and surrounding moorland are indicated. Nests linked all shared same male.

KEY:

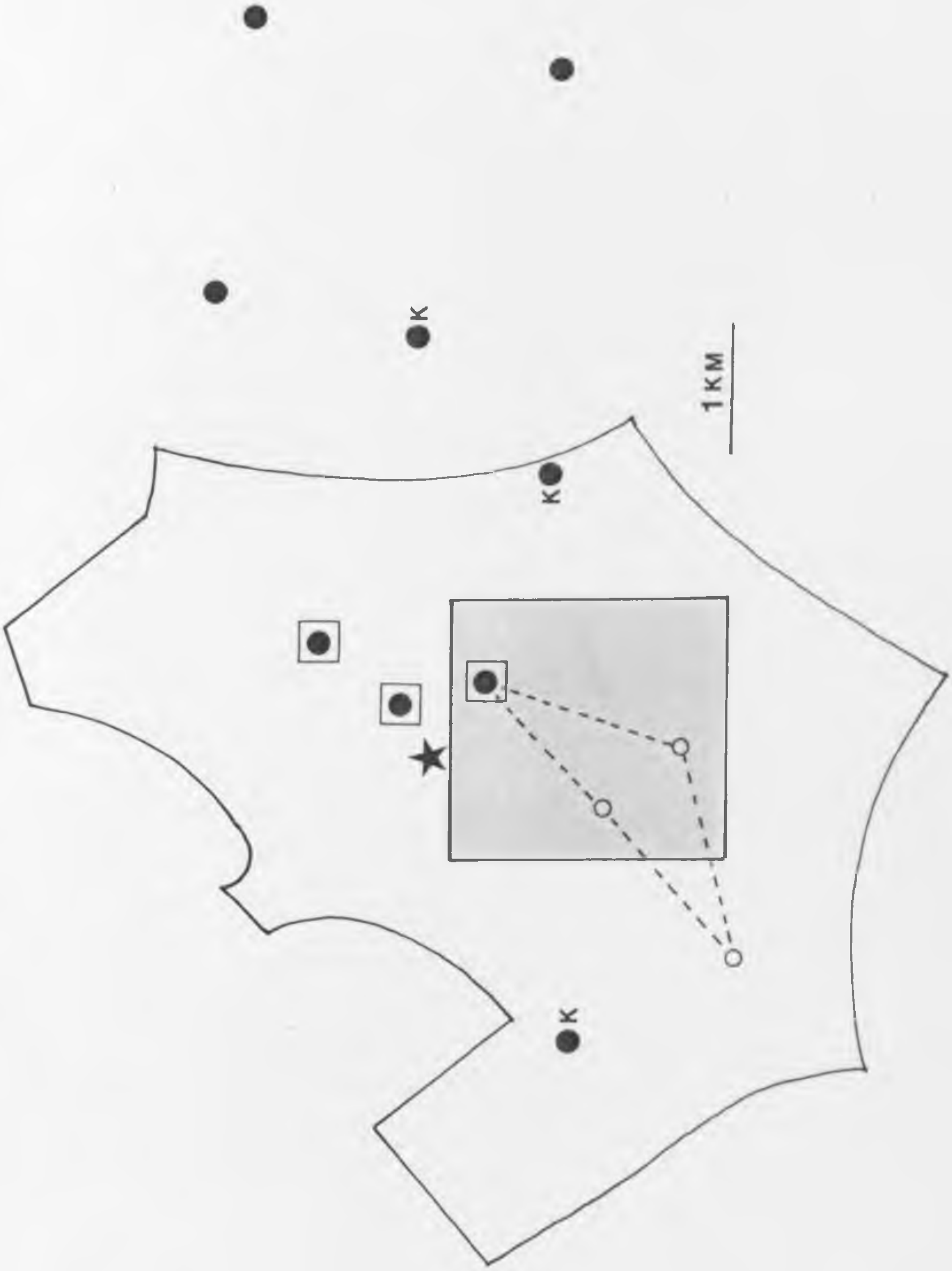
● - Harrier nest.

○ - Nest deserted.

●K - Nest probably destroyed.

⊡ - Nest with hide.

★ - Vantage point.


K
K
K
1 KM

harrier nests and moved over a one week period to between five and seven metres of each nest. At this distance prey species could be identified. Some nest observations were also carried out on a neighbouring estate to moor B in 1988.

Harrier prey, during the breeding season, were assessed in three separate ways. Firstly from hunting observations, which could only give information on grouse and lagomorphs in the diet, as other prey items could not be identified. Secondly, from analysis of remains and pellets located at or within 100m. of the nest. As some prey items in the pellets could not be identified to species, the items were divided up into five main prey groups: grouse chicks; wader chicks; passerines; small mammals and lagomorphs and their proportions were compared to those obtained using the other methods. Lastly, prey were identified by nest observations from the hides. Prey items from individual nests were compared to see whether any large differences occured. Of these methods, the first was used in 1986 and 1987 and all three in 1988.

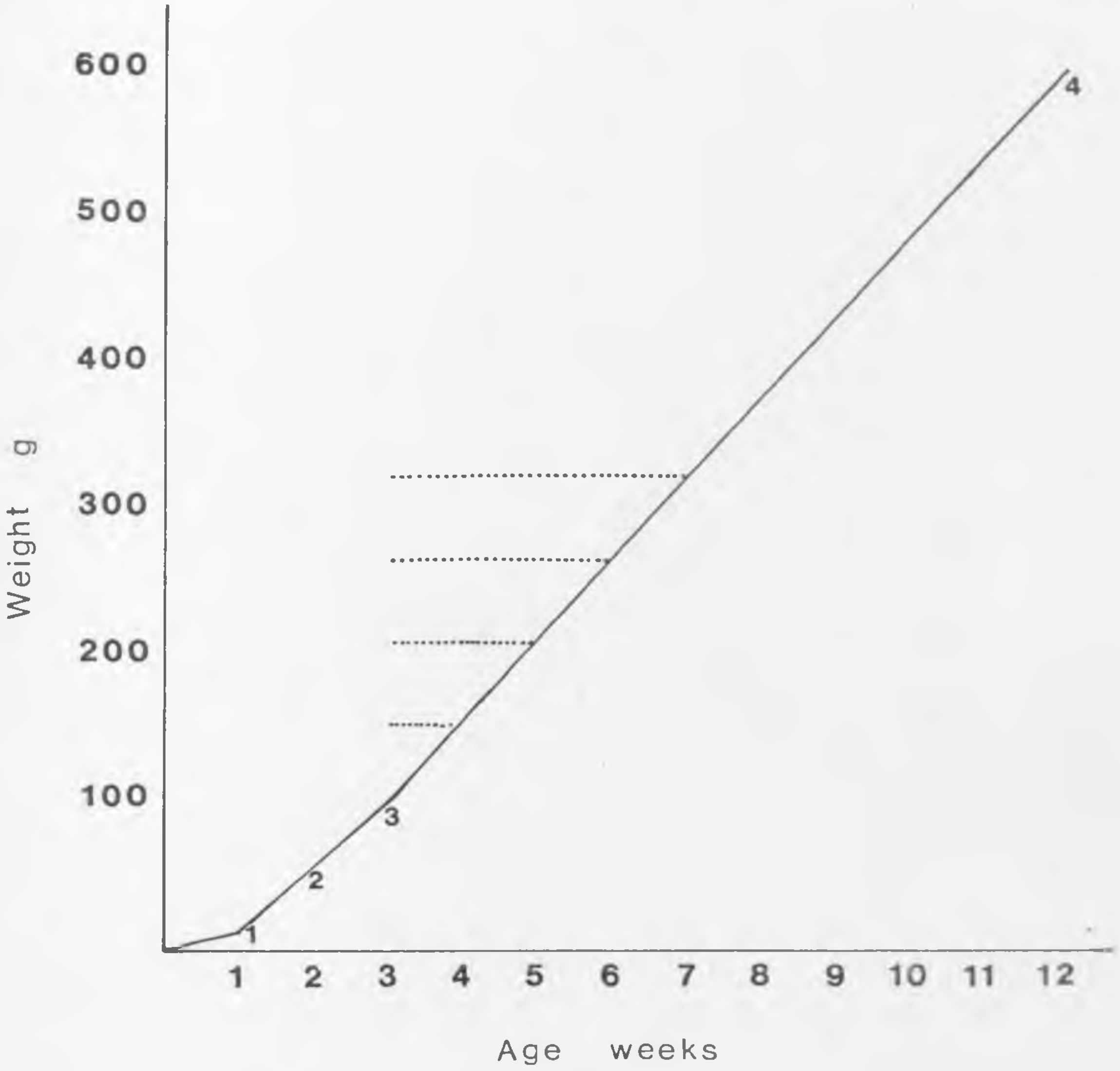
Prior to hatching, female harriers did not feed at the nest, and prey were identified either in the talons of flying harriers (see Barnard *et al.* 1986), or more commonly by watching where the bird fed on the prey, then going to that spot to collect the remains. Two observers were needed for this, to help locate the exact spot. In 94% (N=30) of cases, prey remains were found, and any bias for larger prey was therefore considered minimal.

Biomass data for prey species were not measured in the field and were taken (apart from grouse) from Schipper (1973). Grouse weights were estimated from Hudson (1986a) for the first three weeks and then by extrapolation to week 12 (Fig.4.3), by which time grouse chicks are fully grown (Watson & Miller 1970). Estimates of grouse weights for weeks four to seven were then read from this graph. Prey were grouped into six categories: red grouse chicks; waders and larger passerines (60g); passerines - mostly meadow pipits (20g); small mammals (25g); lagomorphs (250g) and others - mostly small unidentified prey (20g).

4.2.4 Habitat Selection

Within each study area the vegetation was divided into seven main types which could be distinguished from the vantage points: mature

FIGURE 4.3 Method for estimating the weight of grouse chicks, from one week after hatch, to 12 weeks. Points 1 - 3 from Hudson 1986a, point 4 from Jenkins *et al.* 1963. Dotted lines show the weights estimated for weeks four to seven.


600
500
400
300
200
100
Weight g
1
2
3
4
1
2
3
4
5
6
7
8
9
10
11
12
Age weeks

heather (MH); young heather - <10cm. high approximately (YH); mature heather/ bog myrtle mix (BOG); bog flush (BF); reeds/grasses (MARSH); burnt heather (BURN) and distinct edges 2m. either side of a boundary (EDGE). Edges could be clearly determined only along distinct boundaries between young heather or burn patches and other habitats. Streams and tracks were ignored as they were difficult to see from the vantage points and consisted of less than 1% of the study areas.

The relative presence of each habitat type in the study area and the association between prey species and habitat was recorded during transects with a dog. The number of transects required to give an accurate estimate of these measurements was determined in 1987 (Fig.4.4). Here a running mean for the proportion of various habitats and prey recorded during each transect was examined to find the number of transects needed, beyond which no further change was recorded. To determine accurately the proportions of habitats on each study area 20 kilometres were walked. Passerine and lagomorph density indices were determined approximately in 1987 and 1988 during the transects with the dog and are given as number seen km^{-2} with each transect covering a 100m strip (50 metres either side of the transect was covered by the dog).

A possible bias in these results may have occured if the various prey types did not flush equally, thereby allowing the relative importance of certain species to be overemphasised. However, this does not affect the between moor comparison, as the bias should be consistent between areas.

The selection of habitat types by harriers and their prey was examined using the following equation:

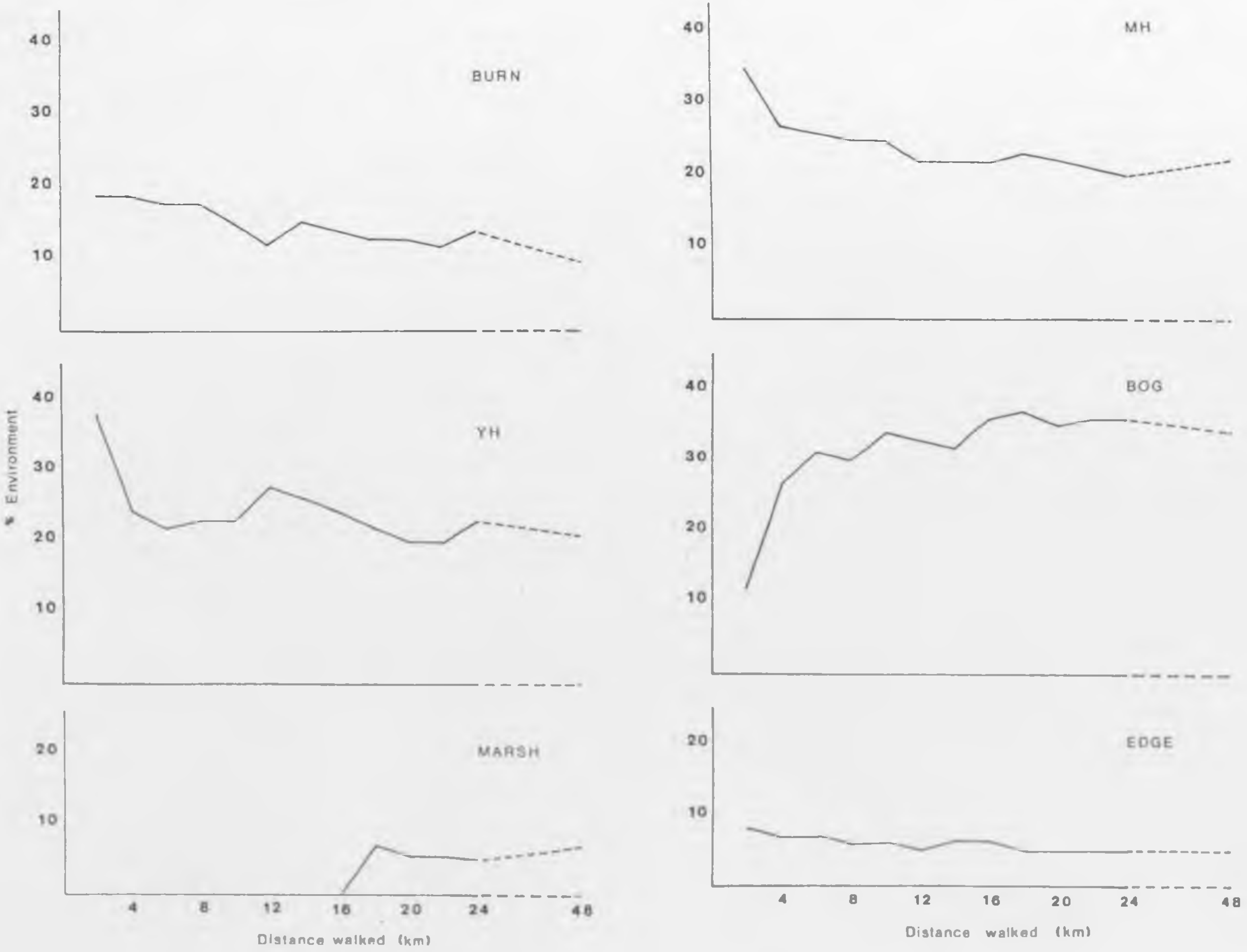
$$HS = (Bo-a)/((Bo+a)-2(Bo-a)a)$$ (Barnard & Thompson 1985)

Where: Bo = No. of obs. in given habitat/ No. obs. in all other habitats.

a = area of habitat/ area of all other habitats.

This method was similar to Dunnet & Paterson (1968) but was preferred as it gives a clearer picture of habitat selection (+ve values) and

FIGURE 4.4 Changes in the percentage of habitat types in the study areas in relation to total length of transect walked. MH - mature heather, BOG - bog myrtle/heather mix, BF - bog flush, BURN - burnt heather, YH - young heather, MARSH - reeds/grasses, EDGE - edge between habitats.


BURN
MH
YH
BOG
MARSH
EDGE
% Environment
40
30
20
10
4
8
12
16
20
24
48
Distance walked (km)
Distance walked (km)

avoidance (-ve values). The further the value from zero, the stronger the preference or avoidance.

There are two likely sources of error in these data. Firstly, it was possible that the habitats over which the harriers were hunting were wrongly identified. When harriers were furthest from the vantage points it was sometimes difficult to see how high they were flying and therefore which habitats they were over. Secondly, prey habitat selection was measured in late May and could change over the six week period (see Hudson 1986a). The findings should be considered with these biases in mind.

4.2.5 Grouse Behaviour

The behaviour of grouse broods, when discovered by harriers, was analysed with the reaction of the adult grouse, length of interaction and number of strikes by the harrier recorded.

4.3 Results

The two study areas used differed in prey composition (Table 4.1). Although passerine densities were similar, densities of other main species were higher on moor B. Of the small mammals caught (chapter 2), very few were voles on moor R (6%), but they were relatively common on Moor B (72%). In all three years the main grouse hatch occured towards the end of May.

4.3.1 Harrier prey - by number

In 1988, 299 prey items were identified from the three hides (A, B and C, Table 4.2), of which 32% were red grouse chicks. The proportion of grouse chicks in the diet was seen to vary considerably between harriers (Table 4.3). The prey composition differed significantly between nests (χ^2=44.0, $p<0.001$) with nest B receiving proportionately over twice as many grouse as A or C. When this method of prey analysis was compared against proportions of prey determined by the other methods in 1988 (Table 4.4), hunting observations gave no significant difference in the proportion of grouse in the diet (and lagomorph estimates were also similar), but pellet and remains analysis gave a lower proportion of passerines (χ^2 =15.6; $p<0.001$) and a higher

TABLE 4.1 Relative densities of prey species on moor R in May 1986 and 1987 and on moor B in May 1988. Grouse, passerines and lagomorphs are given as number km^{-2} and small mammals as the number caught per 100 trap nights (in spring).

	MOOR R		MOOR B
	1986	1987	1988
Red Grouse	2.0	4.0	14.5
Passerines	141	151	132
Lagomorphs	3	3	33
Small mammals	.001	.600	2.00

TABLE 4.2 Numbers of prey items identified at three harrier nests, from hides (A, B and C) placed 5 to 7m. away on moor B and one (D) on an adjacent moor (D) in 1988.

	A	B	C	TOTAL	D
GROUSE CHICKS (*Lagopus lagopus scoticus*)	35	30	32	97	8
MEADOW PIPITS (*Anthus pratensis*)	45	5	36	86	6
SKYLARKS (*Alauda arvensis*)	2	0	11	13	0
WHEATEAR (*Oenanthe oenanthe*)	1	0	2	3	1
BLACK GROUSE (*Tetrao tetrix*)	1	0	0	1	0
SONG THRUSH (*Turdus philomelos*)	1	0	0	1	0
RING OUZEL (*Turdus torquatus*)	1	0	0	1	0
CHAFFINCH (*Fringilla coelebs*)	0	0	1	1	0
BLUE TIT (*Parus caeruleus*)	0	0	1	1	0
GOLDCREST (*Regulus regulus*)	0	0	1	1	0
LAPWING (*Vanellus vanellus*)	0	0	1	1	0
COMMON SANDPIPER (*Actitis hypoleucos*)	0	1	0	1	1
TWITE (*Carduelis flavirostris*)	0	1	0	1	0
CUCKOO (*Cuculus canorus*)	0	0	0	0	1
WADER CHICKS	5	2	2	9	0
PASSERINES	11	4	8	23	1
UNKNOWN	22	18	12	52	1
SMALL MAMMALS	27	4	11	42	3
LAGOMORPHS	2	1	14	17	4
TOTALS	153	66	132	351	26
IDENTIFIED	131	48	120	299	25

TABLE 4.3 Differences in percentages of prey types (by number) identified at each harrier nest on moor B. There was a significant difference between nests ($\chi^2=44.0$, $p<0.001$).

	A	B	C
N =	131	48	120
GROUSE CHICKS	28.6%	62.5%	26.4%
PASSERINES	47.3%	20.8%	49.6%
SMALL MAMMALS	20.6%	8.3%	9.1%
LAGOMORPHS	1.5%	2.1%	11.6%
WADER CHICKS	4.5%	4.2%	3.3%

TABLE 4.4 Estimates of prey in the harrier diet from hunting observations (H) in 1986 and 1987 and from analysis of pellets and remains (P.R.) and nest observations (N) in 1988. Significance levels are for a comparison of H and N (1); P.R. and N (2) in 1988.

	1986/87	1988				
	H	H	P.R.	N	SIGNIF.	
PREY TYPES					(1)	(2)
RED GROUSE CHICKS	20%	41%	31%	32.4%	NS	NS
PASSERINES	--	--	23%	43.0%		***
SMALL MAMMALS	--	--	28%	14.0%		***
LAGOMORPHS	0%	7%	18%	5.7%	NS	***
WADER CHICKS	--	--	1%	4.0%		--
N	35	29	74	299		

proportion of mammals in the diet (small mammals: $\chi^2 = 11.05$; $p<0.001$; lagomorphs $\chi^2 = 16.68$; $p<0.001$).

Observation time was not equally allotted to each nest and therefore one problem of grouping the prey data from the three nests is that the proportion of prey in the diet at those nests where more time was spent will be overemphasised. If this is taken into account, then grouse chicks formed 39% of the diet by number. So 32% can be considered an underestimate of grouse in the harriers diet in 1988.

Male B was the only polygynous male and attempted to breed with three other females, none of which successfully hatched young. As discussed below, this had no apparent effect on the rate with which the male brought food to the nest.

Harrier chicks were associated with the nest for approximately five weeks after they hatched. However, in the fourth week the harrier chicks tended to move into the surrounding vegetation where they were fed, and it became increasingly difficult to identify the prey. The rates at which prey were brought to the nest were compared by examining the rate of prey intake per hour for each observation period. These nest watches varied from 1.5 to 17 hours (mean 5.8 hours) and were not different between nests (F=1.5, d.f.=2, p=0.23). Delivery rates varied significantly between nests (F=6.54, d.f.=2, $p<0.01$), with nest A receiving over 36% more items than either B or C (Table 4.5).

Nest C, which was watched for 73 hours before the chicks hatched, showed no difference in prey delivery rate before and after hatch (t=1.25, p=0.22). Similarly, for all nests, there was no diurnal pattern in the rate with which food was brought to the nest (Fig. 4.5). Females provided 14% (N=51) of the prey items brought to nests in 1988 and 37% of these were grouse chicks. Although providing fewer items, a greater proportion of these items were lagomorphs and grouse chicks (Females - 59% large prey, Males - 36%, $\chi^2=7.44$, $p<0.01$).

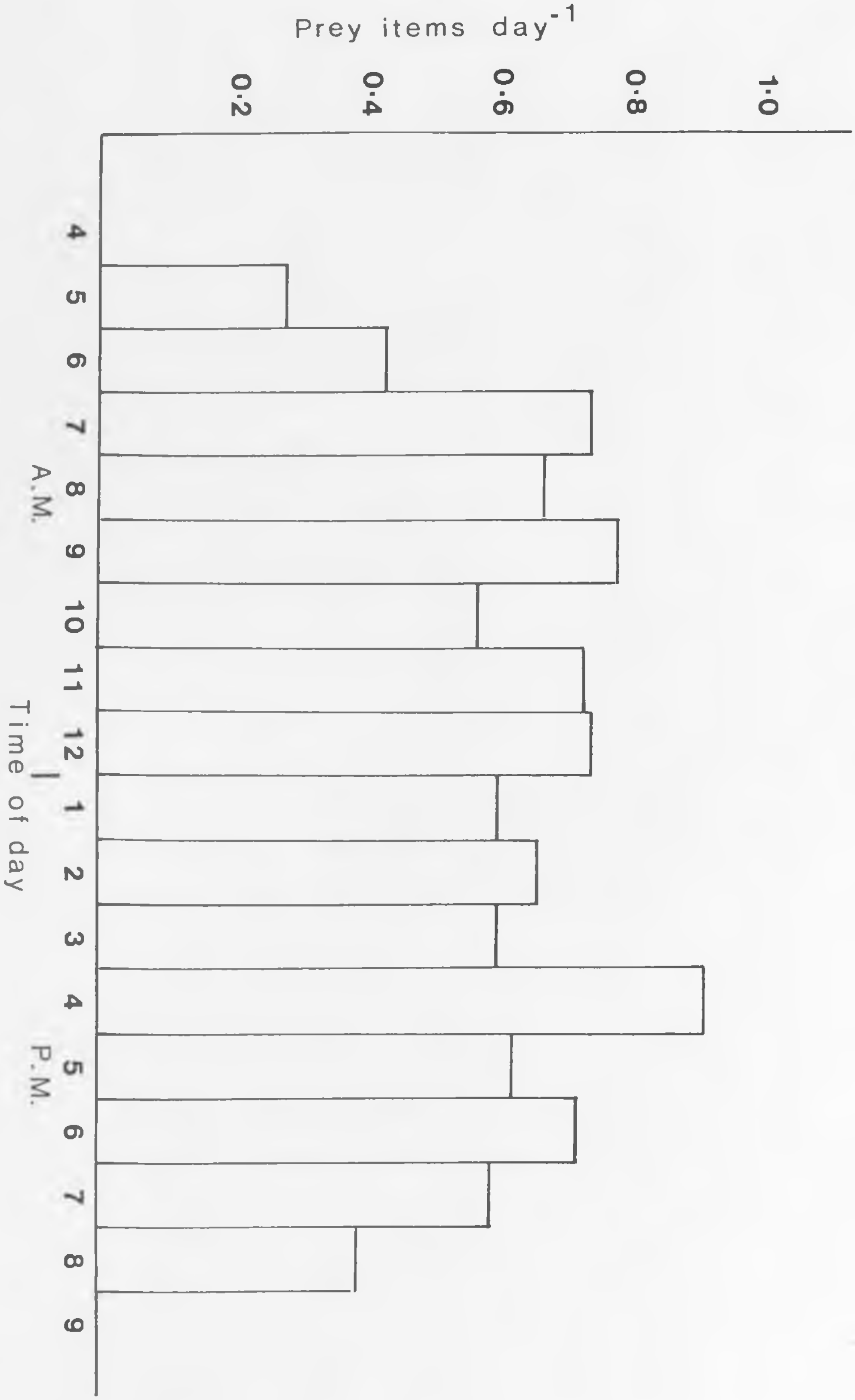
4.3.2 Harrier prey - by weight

Although the number of food items per hour differed between nests, rate of biomass (measured as g hour^{-1}) did not, either for all data (F=0.62, d.f.=2, p=0.54), or for data after hatch (F=2.26, d.f.=2, p=0.11). However, the rate, by biomass, for nest C was higher than for

TABLE 4.5 Observations on three nests in 1988, showing differences between nests. Male status is either monogamous (M) or polygynous (P). Rates are presented as number per hour or grams per hour ± 1 s.e.

	NEST		
	A	B	C
MALE STATUS	M	P	M
NO. EGGS	4	5	4
HATCH DATE	4.6.88	4.6.88	22.6.88
NO. CHICKS	2	2	3
HRS. OBSERVATIONS	198.7	115.7	221.3
PERIOD OF OBSERVATIONS	29.5 - 9.7	29.5 - 6.7	31.5 - 15.7
PREY ITEMS (N hr^{-1})	0.82 ± .07	0.59 ± .07	0.60 ± .06
PREY ITEMS (g hr^{-1})	52.9 ± 5.6	54.2 ± 9.4	78.6 ± 9.2

FIGURE 4.5 Diurnal variation in the number of prey items brought per hour to three nests by male and female harriers in 1988. The first prey were brought in after 5 AM and the last before 9 PM, between 7 AM and 7 PM there is no diurnal activity pattern.


Prey items day^{-1}
0·2
0·4
0·6
0·8
1·0
4
5
6
7
8
9
10
11
12
1
2
3
4
5
6
7
8
9
A.M.
P.M.
Time of day

A or B, and when measured as g $chick^{-1}$ $hour^{-1}$, figures were similar (A: 26.5 g hr^{-1}, B: 27.1 g hr^{-1}, C: 26.2 g hr^{-1}).

For all nests combined the rate, by biomass, was significantly higher after hatch than before ($t=3.32$, $p<0.01$). After hatch both A and C showed an increase in rate with time (Fig. 4.6 :A - $b=2.33$, $r=0.6$, $p<0.01$; C - $b=4.12$, $r=0.47$, $p<0.05$), but rate remained unchanged for B ($b=1.0$, $r=0.23$, $p=0.32$). The slope of this line was greater, but not significantly so for nest C (Ancova $F=0.97$, d.f.=1, $p=0.66$) which contained one more chick. As the chicks grew older the females provided more prey and when prey rate provided by males alone was examined there was no significant trend with time for any nest (A - $b=1.0$, $r=0.24$, $p=0.26$; B - $b=1.0$ $r=0.22$, $p=0.65$; C - $b=0.9$ $r=0.11$, $p=0.62$). The increase in prey capture as the young grew was due to the females.

4.3.3 Harrier hunting behaviour

The study areas were hunted by three pairs of harriers in 1986, two in 1987 and 3-5 pairs in 1988 (two pairs were suspected to have been shot halfway through the summer). Birds were not strongly territorial, except at the nest and their hunting ranges overlapped. In 1988 five separate males were seen to regularly hunt less than one kilometre from a nest without either of the territorial birds responding. During the three years, interactions between breeding birds were seen only three times, (all < 1 km. from the nest) and took the form of a male escorting another male from the area (see Cramp and Simmons 1980).

As in other raptors, male harriers did all the hunting whilst the female was on eggs and the chicks were young. However, as the chicks grew older the frequency of observations of females hunting increased (Fig. 4.7). During the six week observation period, males hunted further from the nest than the females. In 1986, when the nearest nest was three kilometres from the study area, males were regularly seen hunting, but there was only one observation of a female. In 1988 males were never seen hunting over three kilometres from the nest and females were rarely seen to go beyond one kilometre before the young fledged. Whilst the chicks were on the nest, females hunted intensively for a few minutes, then rose up and flew back over the nest before continuing. After fledging, the female and her young were seen in the vicinity of the nest for one to two weeks.

FIGURE 4.6 Seasonal variation in the weight of prey brought per hour to three nests by harriers (both sexes) in 1988. a) - nest A; b) - nest B; c) - nest C; b and c on following pages. HATCH indicates when the harrier nest hatched and regression lines after this time are drawn on. Day one is approximately a week after the main grouse hatch.

FIG. 4.6a

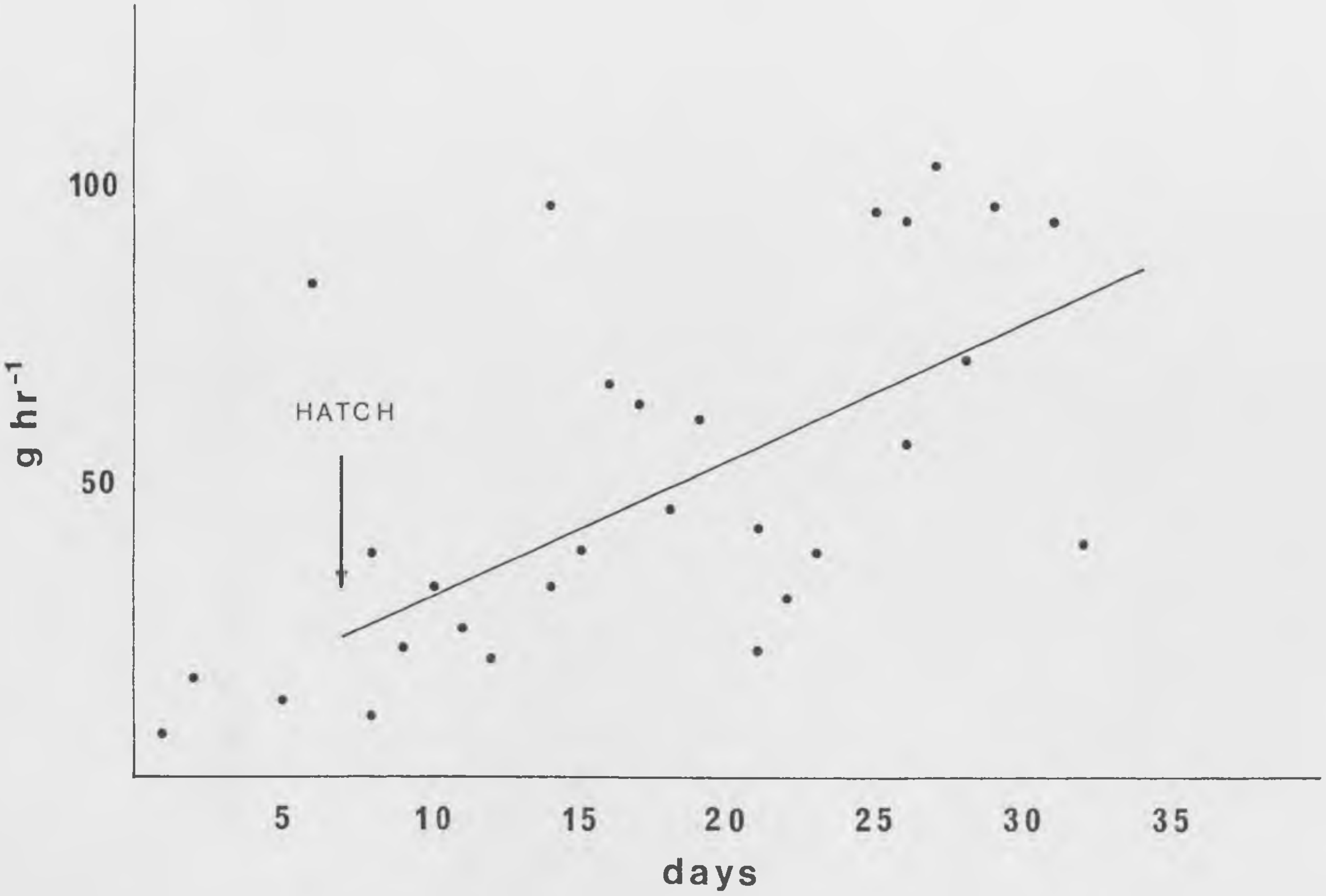


FIG. 4.6b

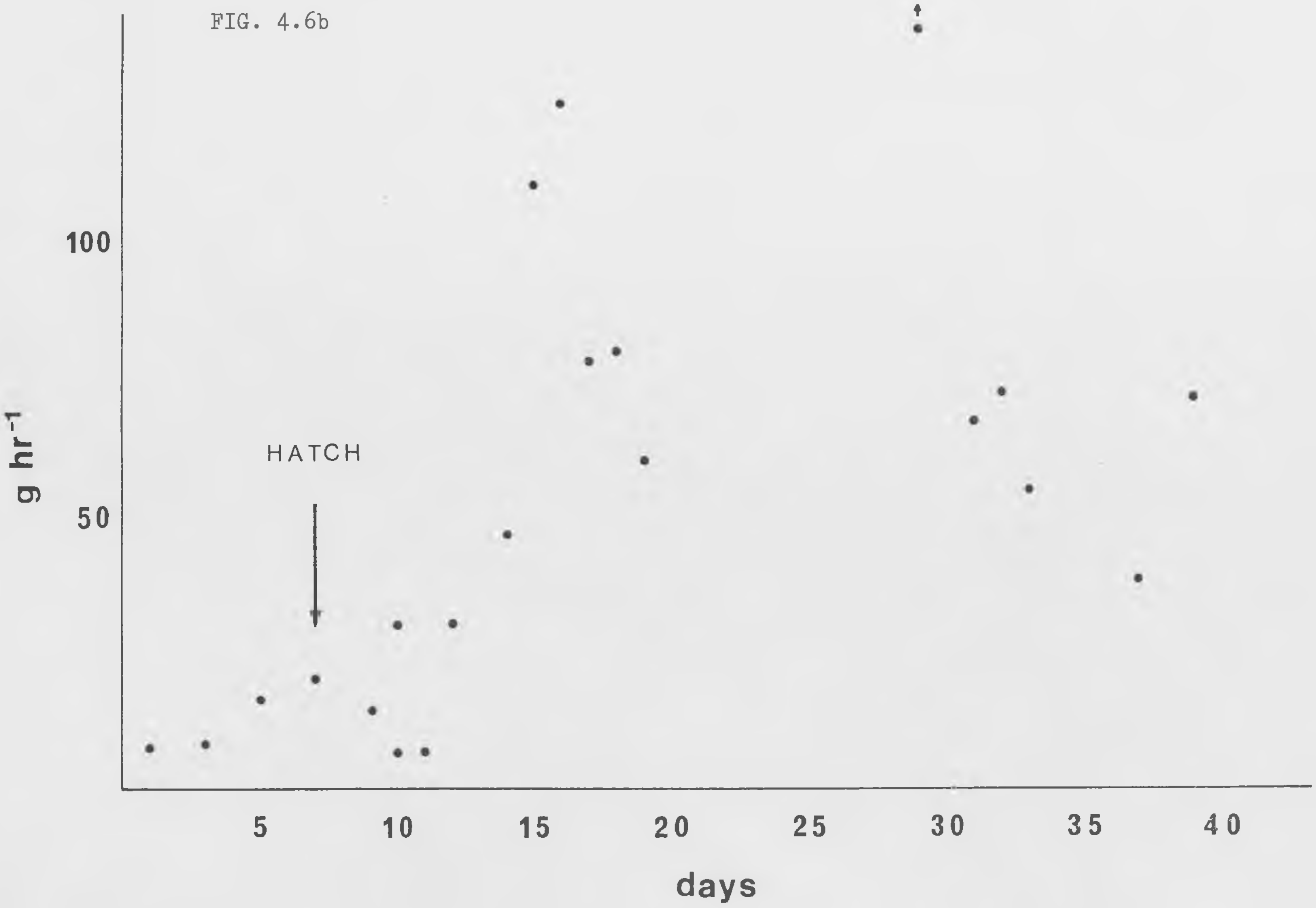


FIG. 4.6c

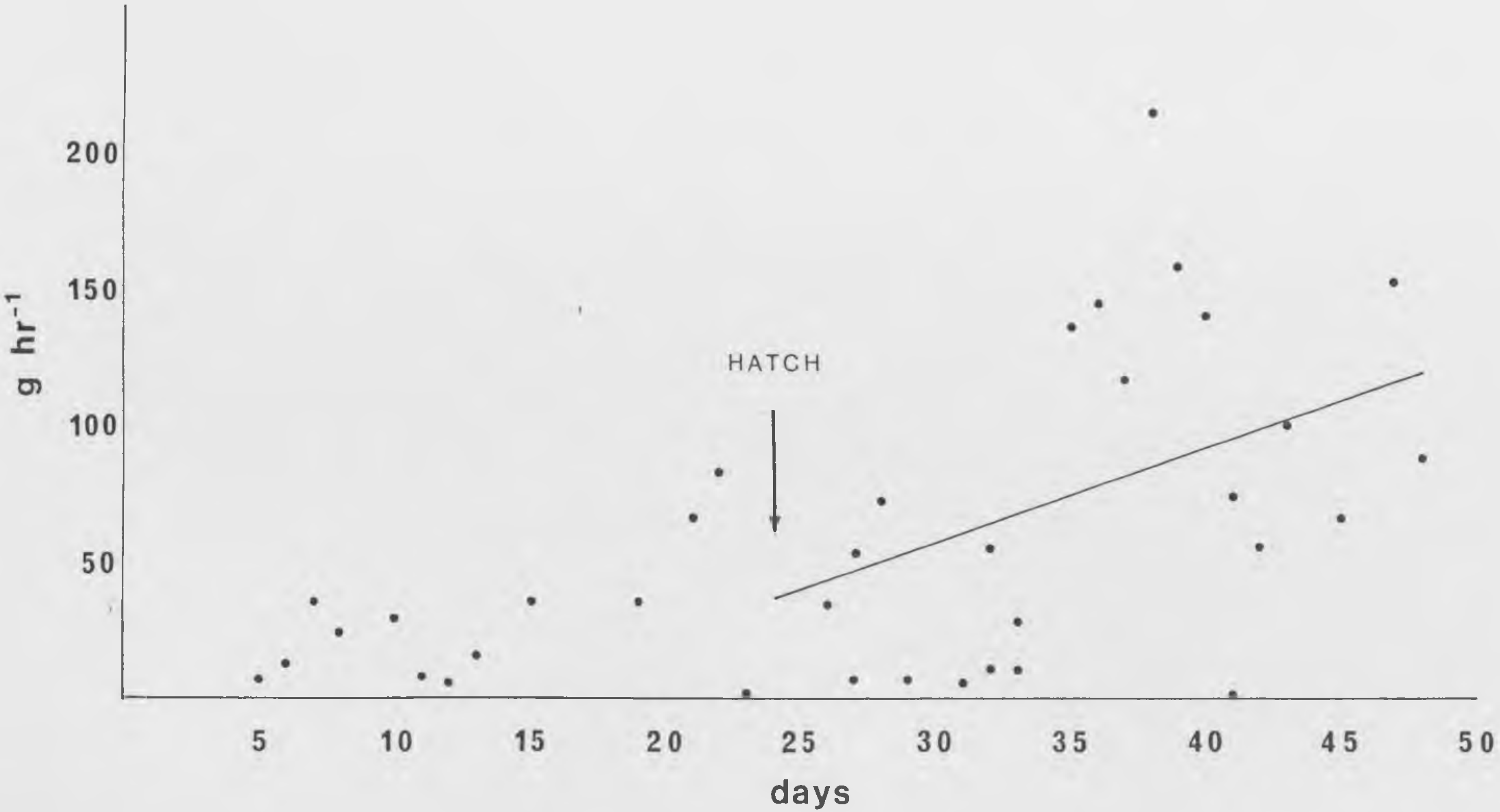
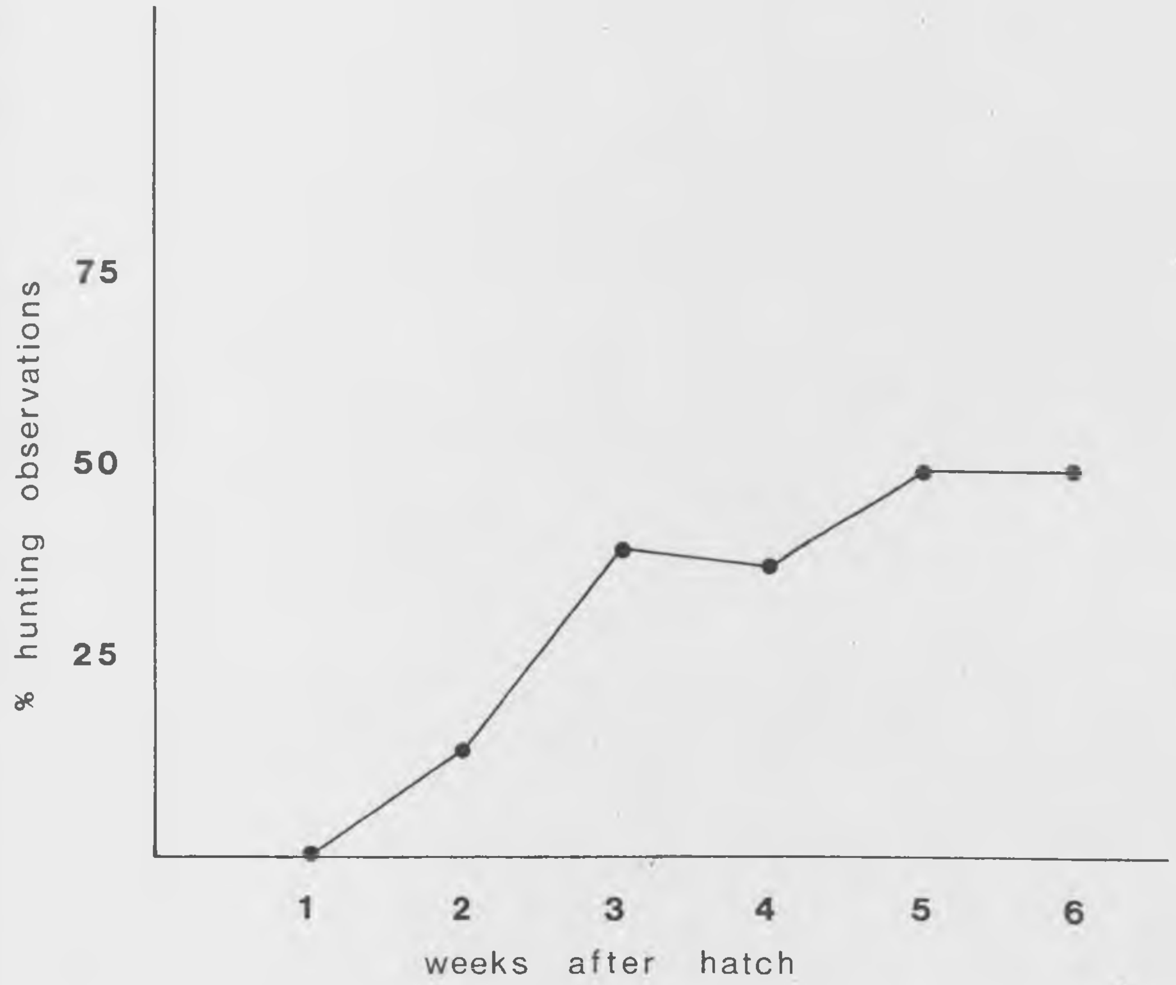


FIGURE 4.7 Seasonal variation in the amount of hunting performed by female harriers in 1988, measured as the percentage of all hunting observations per week. By week five males and females shared the hunting. Number of observations = 87.


% hunting observations
75
50
25
1
2
3
4
5
6
weeks after hatch

In 1988 the three nests were within 1.5 km. of each other and, judging from the prey, hunting was largely confined to open moorland, although the song thrush, blue tit and goldcrest taken by male C suggested that he spent some time hunting the conifer plantation adjacent to the moor. In 1986 and 1987 male harriers were seen to regularly hunt up to 5 km. from their nests. In 1988, when prey were more common, no male was seen to hunt over 3 km. From the 1988 data, when large sections of the hunting range could be observed for the three pairs, it was estimated that harriers had a maximum home range radius of 3 km. giving an approximate area of 28 km^2. A similar calculation gives a hunting area in the region of 78 km^2 in 1986 and 1987. So males hunted over a larger area on moor R, where prey were less abundant.

Males left the nest in two different ways: they either hunted as they left along general routes for a few hundred metres, or they rose up above the nest and glided to hunting areas over a kilometre away. Generally, when prey were caught they soared up and glided back to the female, although larger prey were taken to the nest with powered flight.

During the spring and summers of 1986-88, 578 hours were spent watching the moor for hunting harriers, in which time 17.96 hours of hunting observations were obtained. During this period 187 strikes at prey were observed, of which 45% were successful (Table 4.6). Females were less successful than males (Males: N = 159, Successful = 79; Females: N = 26, Successful = 6; $\chi^2 = 5.34$ $p<0.05$) and neither sex was successful at catching passerines once flushed from the vegetation at <10 metres (N=82; successful=0).

4.3.4 Hunting in relation to habitats and prey

Habitat compositions were different on the two moors (Table 4.7). Moor R had an area of marsh and a substantial amount of bog myrtle/ mature heather bog. Moor B had neither of these habitats, but had the richer bog flush and more pure stand mature heather. Grouse broods selected the EDGE habitat on moor R and avoided the BURN and MARSH (Table 4.8). On moor B they also strongly selected the bog flush (BF) habitat, not present on R. Passerines similarly selected the EDGE, but otherwise showed differences between moors especially with regard to young heather (YH) and mature heather (MH).

TABLE 4.6 Observations on harriers in three years on main study areas showing time spent observing, time harriers in view, strike rate and strike success.

	1986	1987	1988	TOTALS
OBS. TIME (HRS)	199.6	241.0	137.4	578.0
OBS. ON HARRIERS.	10.58	9.44	9.41	29.43
OBS. ON HUNTING HARRIERS	7.87	5.36	4.73	17.96
NO. STRIKES	59	78	50	187
NO. STRIKES SUCCESSFUL	26	31	27	84
% STRIKES SUCCESSFUL	44%	40%	54%	45%
NO. STRIKES (Hr^{-1} hunting) Both sexes.	7.50	14.55	10.57	10.41
NO. SUCCESSFUL STRIKES (Hr^{-1} hunting) Both sexes.	3.30	5.78	5.71	4.68
NO. SUCCESSFUL STRIKES (Hr^{-1} hunting) Males alone	3.30	5.72	6.76	5.26

TABLE 4.7 Relative proportions of various habitat types on study areas R (1986/87) and B (1988). No insect rich bog flushes were present on moor R and no bog myrtle bog or marsh on moor B.

	HABITAT TYPES						
	MH	YH	BURN	BOG	BF	EDGE	MARSH
MOOR R (1986/87)	22%	21%	10%	34%	0%	5%	7%
MOOR B (1988)	56%	18%	4%	0%	16%	6%	0%

HABITATS : MH - MATURE HEATHER
YH - YOUNG HEATHER
BURN - BURNT HEATHER
BOG - BOG MYRTLE / MATURE HEATHER MIX
BF - BOF FLUSH
EDGE - EDGE BETWEEN TWO HABITATS
MARSH - REEDS AND GRASSES

TABLE 4.8 Habitat selection values for passerines, grouse broods and hunting harriers on moor R in 1987 and moor B in 1988. Positive values denote selection and negative values avoidance. Habitats as for table 4.7.

	HABITATS						
MOOR R 1987	MH	YH	BURN	BOG	BF	EDGE	MARSH
PASSERINES	0.11	-0.39	-0.27	-0.07	--	0.58	0.13
GROUSE	-0.05	0.00	-0.82	-0.10	--	0.82	-0.86
HARRIERS	0.20	-0.35	-0.35	0.02	--	0.53	-0.14
MOOR B 1988							
PASSERINES	-0.15	0.01	-0.15	--	0.10	0.55	--
GROUSE	-0.26	-0.58	-0.23	--	1.26	0.45	--
HARRIERS	-0.18	-0.24	0.06	--	0.53	0.35	--

On moor R harrier hunting was concentrated on EDGE and MH and was related to habitat selection by passerines (Fig. 4.8), but not to grouse, though both passerines and grouse strongly selected the EDGE. On moor B harriers selected BF and EDGE and hunting was related to habitat selection by the grouse and not to passerines.

4.3.5 Harrier - grouse interactions

Nest observations indicated that the rate with which grouse chicks were caught per hour decreased slightly in July (Table 4.9), although this was not the case for nest C. This may have been due to the grouse chicks becoming less vulnerable to male harriers as they got larger. Males were seen to catch grouse throughout June and July, but the growing chicks may become increasingly difficult to handle. Female harriers are 10% larger (by weight) than males (Cramp and Simmons 1980), and able to handle larger grouse chicks. The percentage of grouse in the diet later in the season may have been largely dependent on female hunting ability.

Interactions with grouse broods were observed 41 times, of which 20 were successful, and lasted from 2 seconds to 597 seconds (Table 4.10). On two occasions grouse broods were observed as a harrier approached. Both times, the male pressed himself to the ground while the female gathered her chicks and moved to the nearest cover. When the harrier was overhead one or both of the adults (though rarely the female alone, Table 4.11) flew directly at the bird (JUMPS), occasionally making contact and once knocking a female harrier out of the air. Adult grouse were also seen pursuing harriers over 10 metres from the brood (CHASES).

There was no difference between moors, either in the reaction of the sexes ($\chi^2=2.67$, $p>0.1$) or between the types of behaviour ($\chi^2= 4.98$, $p>0.05$). The female grouse usually stayed close to her chicks, whilst the male actively defended the brood and was involved in 95% of JUMPS and 100% of CHASES, trying to force the harrier away. JUMPS appeared to prevent the harrier from striking at chicks, as harriers sometimes started a strike, but were blocked by this behaviour. The harrier would then fly 10-20m., turn, come back and repeat the attempt. Throughout these interactions, the grouse held their wattles erect; had their feathers puffed out, tails fanned, wings spread and produced

FIGURE 4.8 The relationship between habitat selection (Hs) by harriers and by passerines (top) and grouse (bottom) on moor R (a) and moor B (b - on following page). Harrier hunting was related to passerines on moor R and grouse on moor B.

FIG. 48a

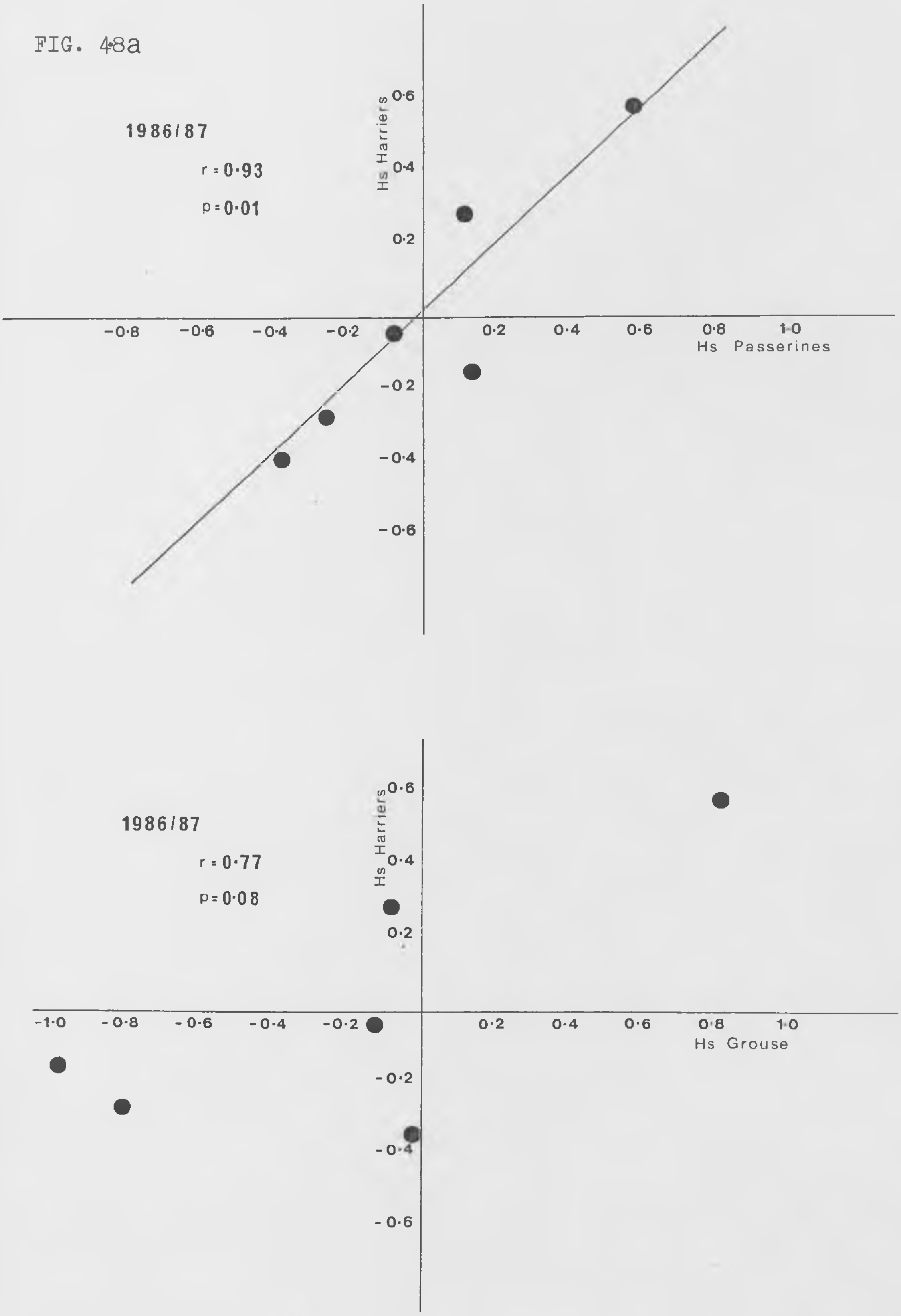

1986/87
r = 0·93
p = 0·01
Hs Harriers
0·6
0·4
0·2
−0·2
−0·4
−0·6
−0·8
−0·6
−0·4
−0·2
0·2
0·4
0·6
0·8
1·0
Hs Passerines
1986/87
r = 0·77
p = 0·08
Hs Harriers
0·6
0·4
0·2
- 0·2
- 0·4
- 0·6
-1·0
- 0·8
- 0·6
- 0·4
- 0·2
0·2
0·4
0·6
0·8
1·0
Hs Grouse

FIG. 4.8b

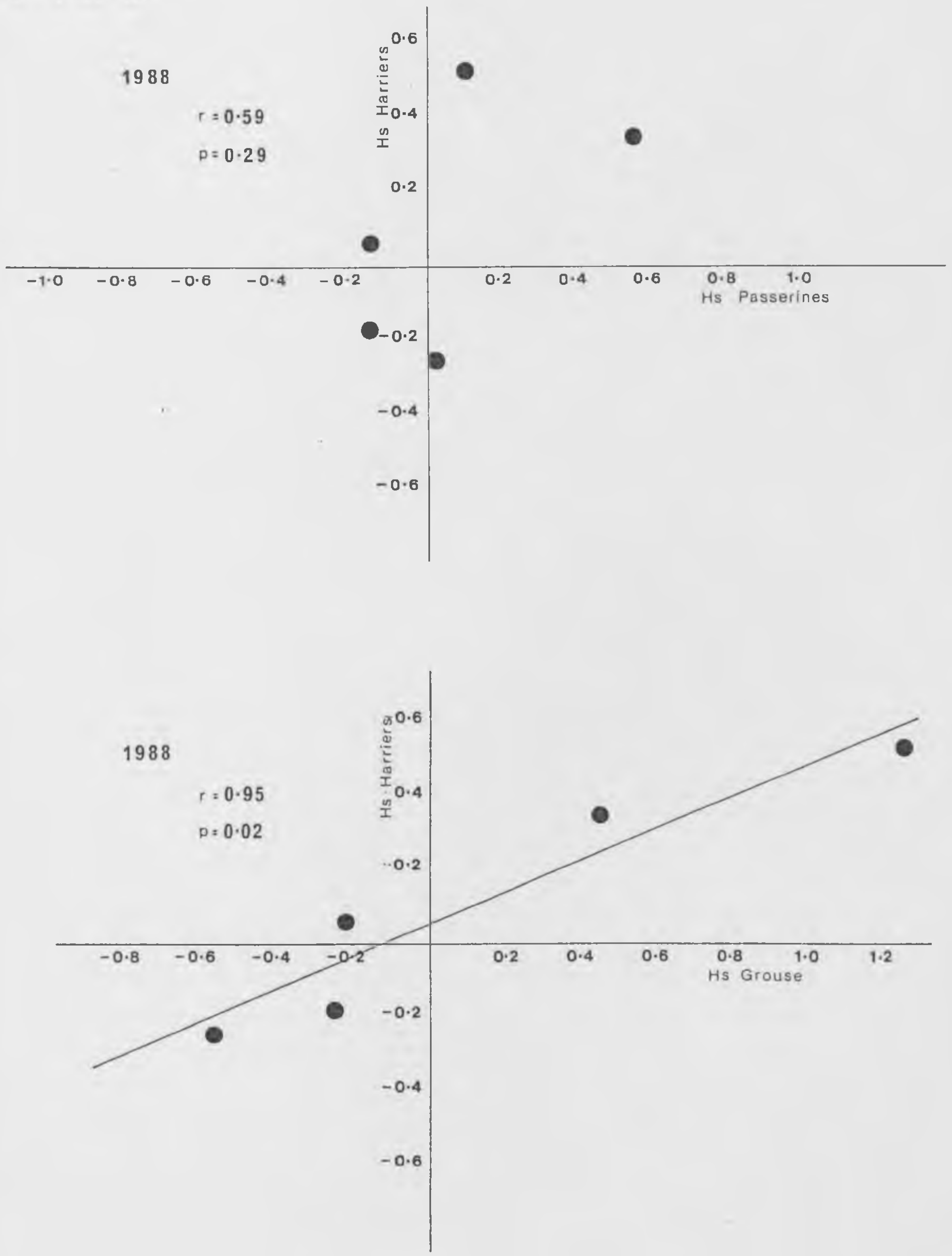

1988
r = 0·59
p = 0·29
Hs Harriers
0·6
0·4
0·2
−0·2
−0·4
−0·6
−1·0
−0·8
−0·6
−0·4
−0·2
0·2
0·4
0·6
0·8
1·0
Hs Passerines
1988
r = 0·95
p = 0·02
Hs Harriers
0·6
0·4
0·2
−0·2
−0·4
−0·6
−0·8
−0·6
−0·4
−0·2
0·2
0·4
0·6
0·8
1·0
1·2
Hs Grouse

TABLE 4.9 Seasonal variation in the rate (No. hr^{-1}) with which grouse chicks were brought to three harrier nests in 1988.

WEEKS AFTER MAIN GROUSE HATCH	NESTS			MEAN NUMBER PER HOUR	HOURS OF OBSERVATIONS
	A	B	C		
2-3	0.16	0.36	0.09	0.19	178
4-5	0.23	0.34	0.16	0.23	171
6-7	----	0.18	0.16	0.16	159

TABLE 4.10 Duration (in seconds) and outcome of harrier-grouse interactions observed over three years.

	1986	1987	1988
NO. INTERACTIONS	6	6	29
AV. LENGTH (SECS)	90s	129s	25s
RANGE	15 - 196s	2 - 597s	2 - 335s
NO. STRIKES	9	6	15
NO. SUCCESSFUL	4	4	12

TABLE 4.11 Behaviour of adult grouse when defending their young against harriers (where sex could be determined) (see text).

	JUMPS	CHASES	TOTAL
MALE	51	11	62
FEMALE	6	0	6
BOTH SEXES	34	11	45
TOTAL	91	22	113

a loud hissing/ clucking noise which was clearly audible at 500 metres. CHASES also occured once a chick had been caught: on one occasion a male chased a harrier for over 200 metres, sat about 50 metres away and watched for 3 minutes whilst the chick was eaten.

During the period when grouse chicks were present, adult grouse were never seen to be attacked by either the male or female harrier, though both take adults during the rest of the year (St. John 1893, Watson 1977; Pers. obs.). Although adult grouse were not seen to fly away on the approach of a harrier in the summer, on three occasions a buzzard (Buteo buteo) was attracted to a grouse brood which a harrier was attacking and on two of three observations both adults flew off. On the other occasion the female grouse was chased off by the buzzard whilst the male attempted (unsuccessfully) to protect his young against the harrier.

Of all 41 interactions, a harrier was only once seen to return to the area within two hours and then was unsuccessful. Six times a male was observed carrying a grouse chick back to the nest and then immediately fly off in the opposite direction to hunt. Birds were occasionally seen to return after two hours and briefly search the area, but by that time the grouse broods had moved on. Frequently harriers located a grouse brood, elicited a response from one or both of the adults, but did not attack and simply carried on hunting (10 of 41 interactions).

Blue hares also attacked harriers, in defence of their young. On two occasions a male was seen to hover over a leveret whilst the adult hares ran around their young. As soon as the harrier struck, the hares ran directly at it, forcing the male to take off. One of the two interactions was successful.

4.4 Discussion

4.4.1 Harrier diet and nest observations

In line with some other studies (Picozzi 1978; Barnard et al. 1986) avian prey formed the bulk (80%) of the harrier diet during the breeding season. In 1988, red grouse chicks formed a minimum of 32% of the diet (by numbers) of nesting harriers, although there were considerable differences between nests. If this difference is taken into account, grouse formed 39% of the prey. Harrier diet was examined by nest observations, hunting observations and analysis of pellets and remains. Observations from hides gave the most accurate picture of diet, although, as observed by Newton (1986), there is a potential bias in that a disproportionate number of large prey items are brought to the nest. However, the proportion of grouse as prey did not differ significantly between methods. As observed by Redhead (1968) and Schipper (1973), there were differences in the proportions of mammals and passerines from the pellet analysis. One difficulty with estimating diet from hunting observations is that sample sizes tend to be small and only large prey such as grouse and lagomorphs can be specifically identified.

The rate with which harriers brought prey items to nests, varied between nests, but at one nest did not vary before and after hatch. However, when weights of prey were estimated as grams per hour, this did not vary between nests. In other words, those males which supplied their females with fewer items compensated by providing larger prey. Before the hatch, smaller prey were provided and once the chicks hatched the rate (grams hr^{-1}) increased. This was due to the females hunting, since the rate with which males provided food remained constant. The highest rate was recorded at nest C, which had three chicks. When measured as grams per chick per hour the figures for the three nests were similar.

Specific daily activity patterns have been noted by Schipper (1973), and Martin (1987), which Schipper considered reflected prey availability. He showed that harriers tended to have peaks of activity in morning and early evening when passerines were main prey, though there was much variation between areas and years. In this study there was no apparent daily activity, other than a steady rise in the morning and a steady fall in the evening, with birds bringing food items equally from 7 AM to 7 PM, even though passerines were an important prey item. This may indicate that the main prey species showed no pattern in availability.

4.4.2 Harrier hunting behaviour and success

Several harriers were seen to hunt the same area and low levels of agonistic behaviour were observed, although a core area around the nest is often defended (Martin 1987), supporting the view that harriers do not defend exclusive hunting ranges (Newton 1979). This can increase their potential impact on prey densities, as several birds could deplete the population from an area. However, territorial behaviour may vary with prey type and availability.

Harrier home range estimates for males in previous studies have varied widely: 2.5 km^2, Breckenridge (1935); 2.1 km^2, Craighead & Craighead (1956); 66.4 km^2, Balfour (1962); 4.97 km^2, Schipper (1977); 14 km^2, Picozzi (1978); 15.7 km^2, Martin (1987), with individuals travelling up to 9.5 km. to hunt (Martin 1987). In this study, home ranges were relatively large and appeared to be related to prey availability, as predicted by MacArthur & Pianka (1966).

For the sparrowhawk, Newton (1986) has clearly shown that home range varies, depending on the food requirements of the individuals and their young, though this has to be balanced against the need to protect their young. Newton found that females hunted over a larger area than males, once the chicks had fledged. Before this time, as found in my study, males ranged over a larger area. Newton also showed, as did Martin (1987) for harriers, that differences in home range size are dependent not only on prey availability but also on habitat type. For example, if prey take evasive action when they see a harrier, an area might quickly become depleted of prey and the harrier must move on. The strength of such behaviour is likely to be related to cover and terrain. Where cover is good and terrain undulating, the harrier will be less visible and can therefore spend more time hunting a smaller area (see Schipper et al. 1975). Heather moorland is an open habitat with relatively poor cover. In such an environment, harriers may quickly deplete an area of available prey and so require a larger home range. Within any one habitat, home range will probably be related to prey availability.

Hunting harriers caught, on average, 4.7 items per hour of hunting, yet nest watches showed that only 0.67 items were brought to the nest. Throughout the day harriers could provide 10 items at this rate (based on 15 hours available, Watson 1977) and this indicates that they need only have spent 2.1 hours (14%) hunting to meet brood requirements. This figure is similar to that obtained by Martin (1987), who found that males spent 20% of their time hunting during the breeding season. For all observations in this study, this rate did not differ between areas where prey densities were different, but male success did vary, with birds most successful on the high prey density moor.

Prey mobility, abundance and habitat structure are thought to be important factors in determining hunting success (Temeles 1985; Baker & Brooks 1981; Newton 1979). Throughout the three years of this study, hen harrier hunting success was high (40%-54%), especially in comparison with other studies (Collopy & Bildstein 1987; Schipper et al. 1975; Temeles 1985). As passerines form a large proportion of the prey (43.8% in 1988), this does not fit the generalisation that mobile (i.e. avian) prey are more difficult to capture. These studies were carried out during the winter and this may account for the variation. A seasonal difference in success rate is also found in other species of raptors. Temeles (1985) lists several hunting studies and a comparison of those studies where the season is stated (Table 4.12) shows a clear difference in hunting success rate between birds in the breeding season and outside it, with breeding birds being more successful. There are various possible reasons for this:

1). Increased prey abundance. During the breeding season prey species will also be breeding and thereby provide a larger prey base for the predators. Also birds may migrate into breeding areas, thereby increasing the density (see chapter 2). The majority of the birds brought to the nest in my study were juveniles (also Picozzi 1978). However, when hunting success was examined before June in 1987 before juveniles were available it was also high (41%). It seems unlikely that prey abundance alone influences hunting success.

2). Decreased prey vigilance. During the winter, prey are mainly concerned with feeding and survival and can spend more time being vigilant for predators. In spring and summer, time is taken up by

TABLE 4.12 Differences in hunting success (% of observed strikes successful) in summer (breeding season) and rest of year for various raptors. Data from Temeles (1985), unless otherwise stated.

MAIN PREY TYPE	OUT OF BREEDING SEASON	BREEDING SEASON
MAMMALS	8.3	29.2
	7.7	78.8
	(Collopy and Bildstein 1987) 5.8	16.0
	mean = 7.3	mean = 41.3
BIRDS	5.0	11.1
	5.0	13.2
	12.8	15.9
	7.5	51.7
	7.7	84.0
	(Collopy and Bildstein 1987) 15.1	40.0
		(This study) 44.1
		(This study) 39.7
		(This study) 54.0
	mean = 8.8	mean = 39.3
INVERTEBRATES	82.0	90.0

breeding and territorial behaviour, so prey have less time to be vigilant and may therefore be more vulnerable.

3). High intensity hunting. Treleaven (1980) suggests that raptors hunt at low or high intensity depending on their requirements. During the breeding season male raptors have to hunt for their mate, young and themselves so their requirements are higher than at any other time of the year. Perhaps therefore, more effort is put into catching larger prey items, such as grouse chicks.

These are thought to be the main factors influencing hunting success, though other considerations, such as experience of hunting birds (more immatures hunting in winter), the alteration of habitat structure between the seasons and decreased food availability for prey species in the winter, are also likely to play a part. Overall success rate will be dependent, to a certain extent, on all these factors. The observed increase in hunting efficiency during the breeding season means that the relationship between success rate and prey agility is less well defined.

4.4.3 **Habitat selection**

Other studies have shown that harriers are selective in the habitats they chose for hunting (Schipper 1973, Martin 1987). These studies examined hunting over large scale patches, i.e. which fields harriers hunted in. In this study patchiness occurred on a finer scale. Moorland vegetation consists of a mosaic of habitat types, largely created by the burning of patches of heather (see Miller 1964) and the presence of insect-rich bog flushes (Hudson 1986a). Burning creates areas of nutritious young heather shoots which are easily available to grouse. In this study, the edges created by burning and bog flushes attracted both passerines and grouse, although grouse broods preferred the bog flushes when available. Other habitats, such as burns and young heather, were avoided. It is suspected that, although these areas provide nutritious food, they have very poor cover and are avoided because of increased predation risks. Edges allow birds to forage in these patches and afford them the cover of mature heather stands.

Harriers select habitats for hunting, such as edges, that contain potential prey and allow them to surprise their quarry (Schipper 1973, Schipper *et al.* 1975). Hunting harriers selected the habitats favoured by passerines on moor R in 1986 and 1987 and by grouse broods on moor B in 1988 and this reflected the density of grouse on the two moors, but not the density of passerines. One important feature of these observations was that at low density, both passerines and grouse selected the EDGE habitat. Harriers, which appeared to hunt for passerines at low density, also selected the EDGE and therefore located more grouse broods. In other words grouse may have been killed disproportionately because they selected the same habitats as passerines.

4.4.4 Harriers and grouse

Red grouse chicks are an important prey item of harriers in Scotland, being of large biomass and relatively easy to kill. Differences between nests in the percentage of grouse in the diet appeared to be largely due to individual preferences. This was supported by the finding that although two nests hatched at the same time, within 1 km. of each other, large differences in diet occurred, indicating that changes in availability were not the cause. However, the availability of grouse chicks will vary depending on when the harrier chicks hatch. In this study the number of grouse chicks taken decreased slightly in July, possibly because they become less vulnerable to male harriers. Most harrier nests hatched about a week after the main grouse hatch, so by the time the grouse chicks were becoming too large for the male harriers, the females started hunting. Barnard *et al.* (1986) have suggested that harriers may time their hatching to coincide with passerine availability; in a similar way it is possible that they may take advantage of the arrival of grouse chicks on the moor. A similar relationship has been suggested for sparrowhawks feeding on songbird fledgelings (Newton & Marquiss 1982).

Once harriers had caught a grouse, they were never seen to return to the brood and successfully catch another chick. One explanation for this is that, once a brood had been attacked, the grouse become more vigilant and could warn their offspring to take cover. This agrees with the two observations of females taking their chicks into mature heather on the approach of a harrier. It may therefore be harder to find and catch a chick from a recently attacked brood. Similarly it is possible that the broods that were discovered but not attacked were ignored because they had spotted the harrier and were able to hide their young. Picozzi (1978) stated that he saw a brood of grouse removed over a three day period. In 1988 I twice saw a harrier return to the position of a brood, two to three hours after it had killed a chick. By that time the brood had moved on (broods can move up to 400m. per day Hudson 1986a) and the harrier was unable to find them, even though it quartered the precise area where the attack took place intensively.

4.5 **Summary**

The prey and behaviour of harriers was observed in the breeding season in Speyside and Perthshire. Avian prey formed the bulk of the prey in 1988 and of all items, 32% (by number) were red grouse chicks. There were considerable differences in the numbers of prey items brought to the three nests in 1988, though the weight of food brought to each chick was similar. Males provided prey at a constant rate throughout the season, with females providing more as the chicks grew older.

Home ranges overlapped widely, with up to five males seen hunting the same area. Hunting harriers were more successful than those recorded in other studies and this was thought to be due to seasonal differences between studies. Harriers selected the habitats favoured by passerines in 1986 and 1987 and habitats favoured by grouse in 1988. Judging by their numbers in the moorland, grouse chicks were the preferred prey of harriers. Grouse actively defended their brood when being attacked and in 51% of cases, the harriers were unsuccessful. Harriers rarely returned immediately to a brood, possibly because of the vigilance behaviour of the grouse.

CHAPTER 5

HEN HARRIERS AND RED GROUSE CHICK LOSSES.

5.1 **Introduction.**

In the previous chapter, findings on the importance of grouse in the diet of hen harriers were reported, along with observations of aspects of their hunting and feeding behaviour. In this chapter their impact on grouse chick numbers is examined, through the use of extensive and intensive studies. Estimates of chick mortality are derived from observations of hunting harriers to see whether they could account for chick losses. Data on harrier diet and findings from other studies are combined to examine the functional response of harriers and to assess the impact of harriers on red grouse breeding success.

The effect that such losses could have on the number of grouse shot in autumn and the possible consequences for the breeding population in the following year are examined in chapter 6.

5.2 **Methods.**

Brood size was recorded on 12 moors in 1987 and 14 moors in 1988 (Fig. 5.1) and was measured as the number of young per female (excluding chicks found without hens). Each moor was one of a pair, with a distance between them of approximately 15 km., and differed in that one of the pair had breeding harriers, whilst the other, the control, did not. Harriers were suspected to have been killed on or near all the "control" moors. Brood size was examined during the last two weeks in July, and the number of pairs of breeding harriers in each area was estimated through information from local gamekeepers and birdwatchers.

A more intensive study was conducted on one of the pairs of moors in Speyside during 1986/87 (moor R and control) and in Perthshire during 1988 (moor B and control). On these moors, mean grouse brood size was estimated in early June (over one week after the main grouse hatch)

FIGURE 5.1 Approximate positions of matched-pair moors, studied in 1987 and 1988 in Scotland, in relation to the main hen harrier distribution (shaded - from Sharrock 1976). Moors without harriers - ● ; moors with harriers - ○. Pair 1+2 in Sutherland, 3 in Moray, 4+5 in Speyside, 6 in Angus and 7+8 in Perthshire. Also one pair in the North of England (not shown).


1
2
3
4
5
6
7
8

and six weeks later in July, using a pointing dog. The difference in values gave an assessment of chick loss. Harrier predation throughout this period was monitored, through detailed hunting observations in all years and through nest observations in 1988 (chapter 4). Brood size was examined one week after the main grouse hatch as most mortality occurs within the first 10 days (Hudson 1986a). On these moors, study areas were chosen (see chapter 4) over which 3 pairs of harriers hunted in 1986, 2 pairs in 1987 and 3-5 Pairs in 1988 (2 pairs were suspected to have been killed halfway through the summer). Gamekeepers were employed on both areas and any fox families or crow nests found were destroyed. Harriers were still occasionally seen on the control area, but only rarely. In 1986 and 1987, 21.5 harriers were seen per 100 hours field work on the intensive study areas as opposed to 1.3 on the control.

The frequency distributions of brood sizes were examined on the intensive areas and their controls in July 1986 and 1987, in an attempt to discover whether harriers preyed on grouse broods in a density dependent fashion, i.e. whether the distribution was skewed on the harrier area but not the control.

Hunting observations were used to estimate chick losses, to see whether harriers could account for observed differences in brood sizes between June and July. In 1986 and 1987, observations of hunting birds were also used to estimate the percentage of grouse in the harrier diet. The accuracy of this method was tested against information derived from nest watches in 1988 (see chapter 4) and was shown to give a slightly higher percentage, though not significantly so. In 1986 and 1987, the numbers of chicks seen killed were small and the accuracy was uncertain, but 1988 data suggest that hunting observations gave an accurate estimate of the proportion of grouse in the diet. The response in harrier diet to variations in grouse density was examined by comparing data from this study with those from other similar surveys. Grouse density was measured as the number of females km^{-2} (ie. the number of broods) and in the two studies where density was not measured, it was estimated from count data carried out two years later for one point (1. Hudson pers. comm.) and from Picozzi (2. pers. comm. approximate estimate) for the other. Both of these are from very low grouse densities, in areas not managed for red grouse, and are thought to be representative.

5.3 Results.

5.3.1 Extensive Studies.

Counts carried out on the pairs of moors in July (Figs. 5.2 a+b) showed that in 13 of the 14 cases, moors with harriers produced fewer young grouse per hen than moors without harriers (1987 $p<0.05$; 1988 $p<0.05$ Sign test). Over the two years, the harrier moors produced on average 17% less grouse chicks. One of these pairs was monitored for three years, during which time the number of harriers on one moor changed from 3 pairs in 1986 to being partly hunted by a pair in 1988. Its control had no harriers in 1986 and 1987 but was on the edge of one pairs' range in 1988. The results show (Fig. 5.3) that a significant difference in young per hen was observed in 1986 and 1987 but not in 1988 when predation pressure from harriers was similar. There was no apparent difference in keepering activity between the years.

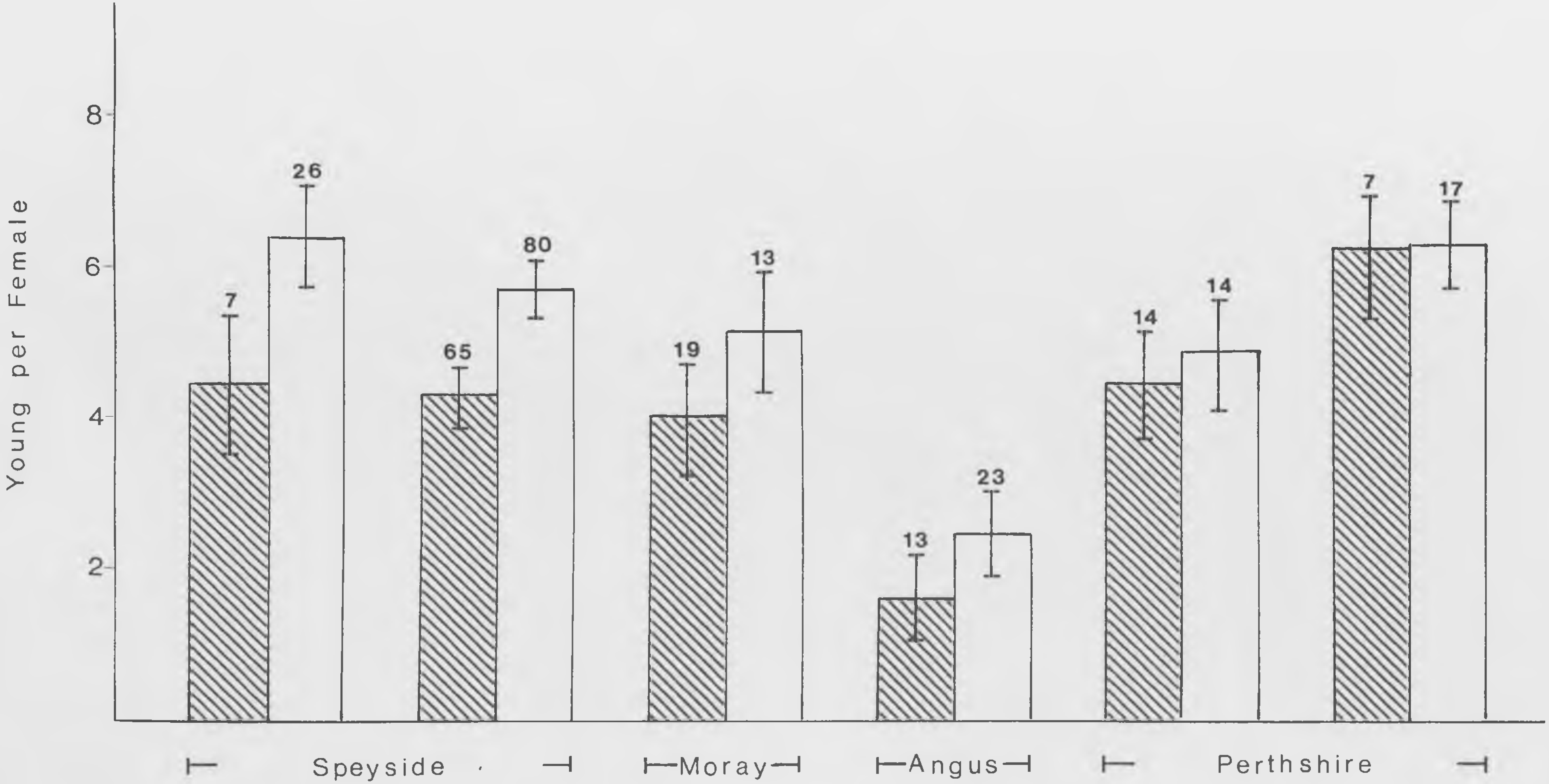
5.3.2 Intensive Studies.

Brood size in June was not significantly different between study area R and its control, but was different in July, when the moor with harriers had fewer young : hen (Table 5.1: 1986 $t=2.62$; $p<0.01$: 1987 $t=3.09$; $p<0.01$). In order to increase sample size in June, when broods were harder to find (see below) data were used from an adjacent moor to the control, where there were also no harriers. In 1988, the control moor was infected by an outbreak of *T. tenuis* and the grouse on part of the moor were treated using an anthelmintic to kill the parasites (P. Hudson pers.comm.). In June, brood sizes on treated and untreated areas were not significantly different from study area B (though the treated area was higher). However, in July, brood size was significantly larger on the treated area but not on the untreated. There was no evidence of an outbreak occurring on the main study area, although gut samples were not examined for worms in autumn.

When brood size frequencies were examined on moor R in 1986 and 1987 (Fig. 5.4), there was no significant skewness or kurtosis, suggesting that harriers were preying randomly on grouse broods and were not selecting the larger broods to feed upon. (With harriers, skewness = 0.18 ± 0.25, $p=0.5$: kurtosis = -0.76 ± 0.5, $p=0.12$. Without harriers,

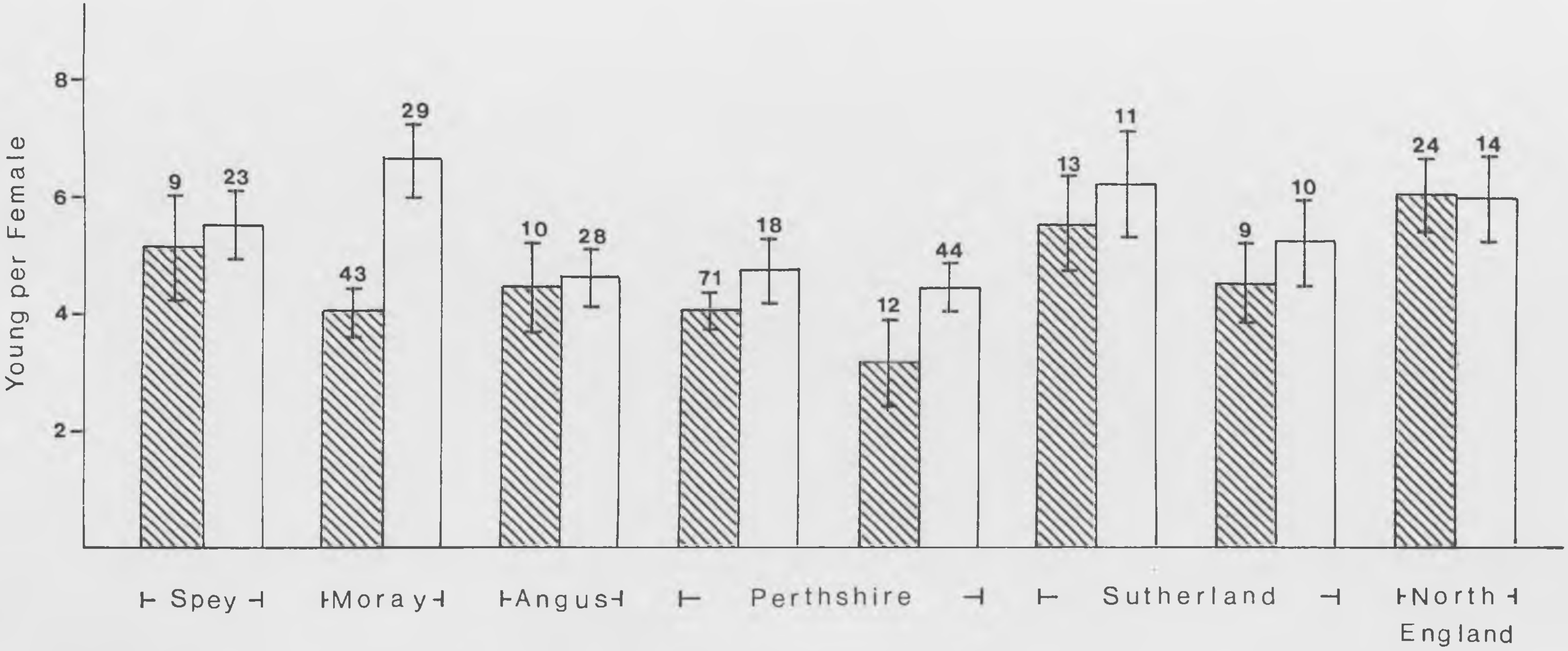
FIGURE 5.2 Number of young grouse per female counted on matched pair moors in July 1987 (a) and 1988 (b - on following page). Shaded bars represent those moors with breeding harriers and open bars without. Data presented as means ± 1 s.e and sample sizes. $P<0.05$ for both years - Sign test.

FIG. 5.2a



Young per Female
8
6
4
2
7
26
65
80
19
13
13
23
14
14
7
17
Speyside
Moray
Angus
Perthshire

FIG. 5.2b



Young per Female
8
6
4
2
9
23
43
29
10
28
71
18
12
44
13
11
9
10
24
14
Spey
Moray
Angus
Perthshire
Sutherland
North England

FIGURE 5.3 Number of young grouse per female counted in July on one pair of moors over three years, with varying numbers of breeding harriers. Data presented as means ± 1 s.e. and sample sizes. Numbers in the columns represent the number of breeding harriers on or near the moor. 1986: $t=2.62$, $p<0.01$. 1987: $t=2.61$, $p<0.05$. 1988: $t=0.48$, $p=0.6$.

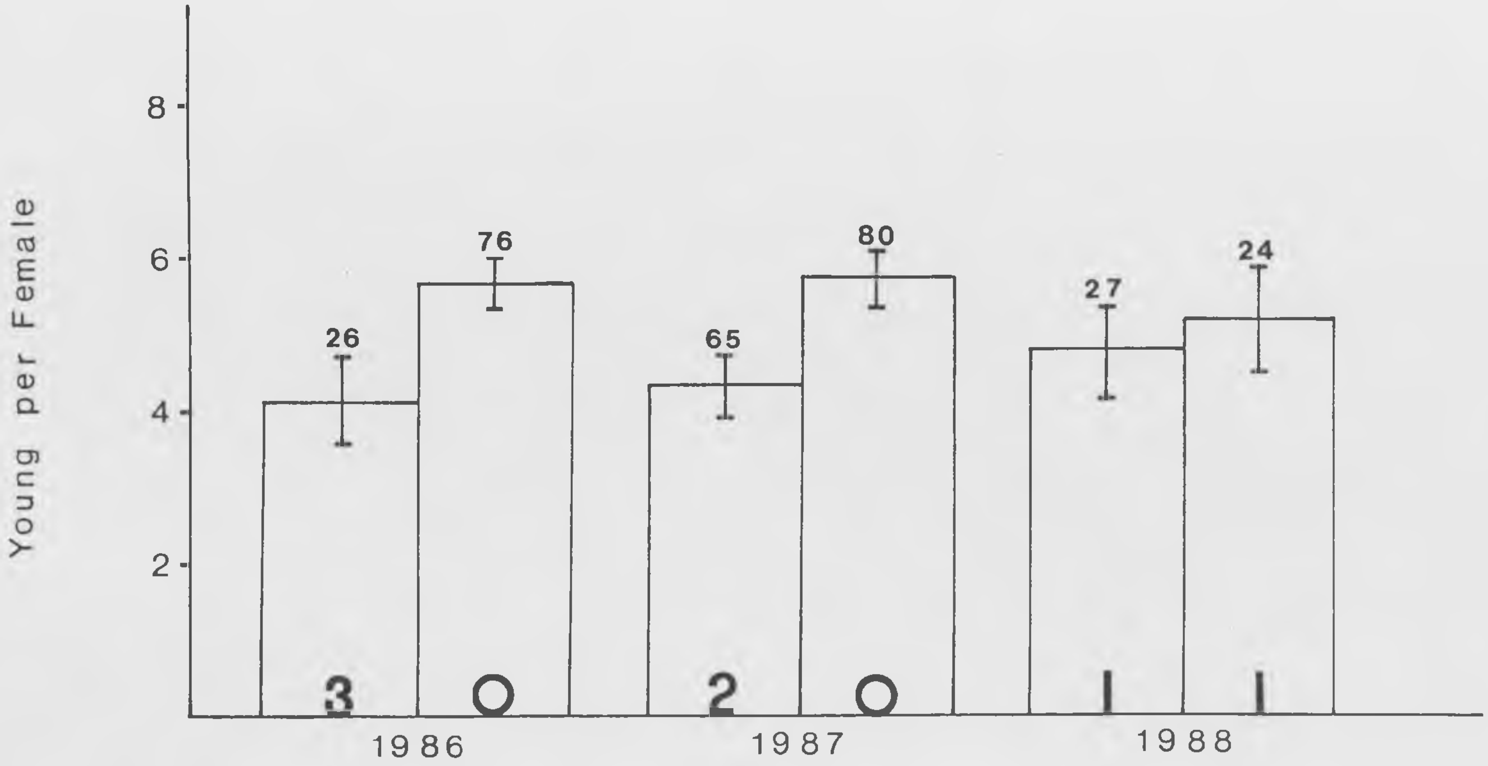
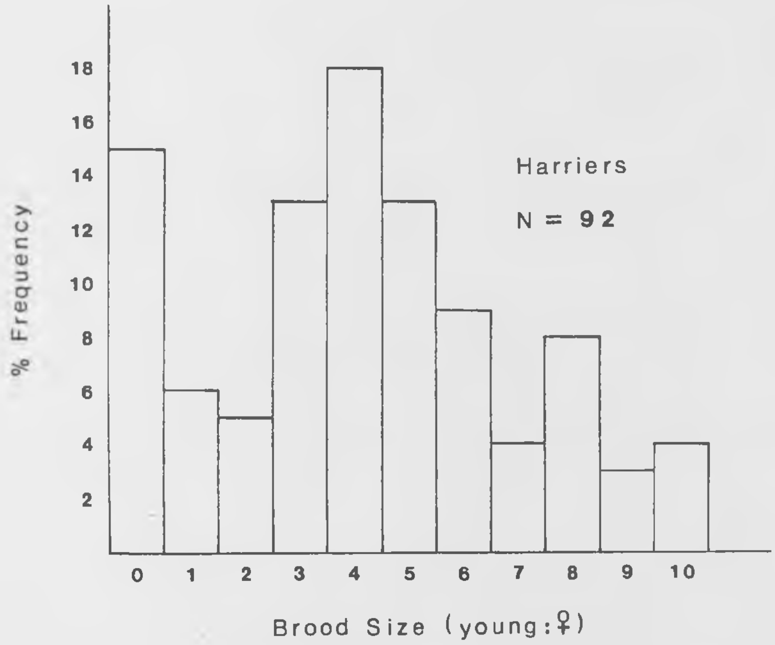

Young per Female
8
6
4
2
26
76
65
80
27
24
3
O
2
O
I
I
1986
1987
1988

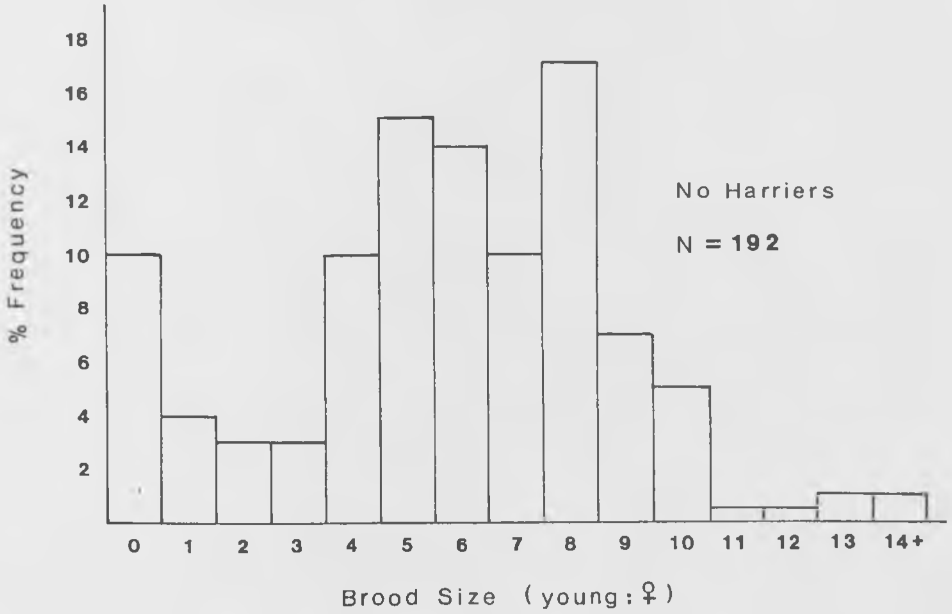
TABLE 5.1. Comparison, using student t-test, of brood sizes on the intensive study areas (with harriers) and the control areas (without) in June and July 1986-1988. Data are presented as grouped means ±1S.E. In 1988, the control moor data are divided into two: A - treated for parasites, B - untreated (see text).

		MOOR R		CONTROL		SIGNIFICANCE	
		Mean	N	Mean	N	t	p
1986	JUNE	4.75±0.73	12	5.32±0.55	28	0.57	NS
	JULY	4.08±0.52	26	5.65±0.30	91	2.62	**
1987	JUNE	5.78±0.58	28	5.81±0.62	26	0.03	NS
	JULY	4.26±0.36	65	5.87±0.34	106	3.09	**

		MOOR B		CONTROL				
1988	JUNE	4.80±0.45	40	A	6.00±0.58	10	1.27	NS
				B	4.20±0.70	15	0.57	NS
	JULY	3.99±0.29	71	A	5.62±0.54	21	2.59	**
				B	3.30±0.40	23	0.74	NS

FIGURE 5.4 Frequency distributions of grouse brood sizes on moor R (a) with harriers (skewness=0.18, p=0.5, kurtosis=-0.76, p=0.12) and control (b) without (skewness=0.07, p=0.67, kurtosis=0.51, p=0.14) in 1986 and 1987.


% Frequency
18
16
14
12
10
8
6
4
2
Harriers
N = 92
0
1
2
3
4
5
6
7
8
9
10
Brood Size (young:♀)


% Frequency
18
16
14
12
10
8
6
4
2
No Harriers
N = 192
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14+
Brood Size (young:♀)

skewness = 0.07 ± 0.17, $p=0.67$: kurtosis = 0.51 ± 0.35, $p=0.14$.)

In order to estimate whether harriers could account for the observed variation in grouse breeding success on the study areas, the difference in young per female counted in June and July was compared to expected losses, derived from observations of hunting harriers. Hunting harriers were observed on the main study area in the six weeks between counts and the number of grouse chicks observed to be taken from a known area in a known time (Table 5.2) was recorded. Standard errors for hunting observations were obtained by examining the number of grouse chicks taken in each km^2 of the study area. The number of chicks killed km^{-2} was then determined on the following assumptions:

a.) The time spent hunting was 630 hours in six weeks, based on 15 hours hunting a day. (See chapter 4 and Picozzi 1978).

b.) The young:hen measurement in June gave an accurate representation of the number of chicks available to the harriers. During 1986 and 1987, brood size on the control area was higher in July than in June (though not significantly), emphasising one of the problems of examining broods less than 10 days of age. This difference was thought to be due to the fact that young chicks were harder to detect than chicks over six weeks old. In early June when a brood was encountered, the chicks would frequently run and hide in the vegetation and were difficult to locate. Also, the adult grouse performed distraction displays during this period (Watson and Jenkins 1964, Hudson 1989) which, depending on intensity of display and the inexperience of the dog, hindered its ability to search. In late July, chicks were easier to flush as a brood, making them easier to count. The difference was small in 1987 and this may have been due to the increased experience of the observer and dog, or alternatively to the masking of any difference by other losses which occurred during the six week period, such as seen in 1988 on the control area where there was a parasite infection.

c.) All attacks on grouse chicks during the observation period were seen. In 1988 two of the 26 harrier-grouse interactions which occurred within the study area were noticed only after hearing the grouse call (see chapter 4), though both of these were initially hidden in gullies from the observer. Some interactions probably did occur out of earshot

TABLE 5.2. Time spent observing harriers on intensive study areas on moor R and moor B from 1986 to 1988. Table also shows size of study area, numbers of harriers and numbers of grouse present and killed by harriers.

	MOOR R		MOOR B
	1986	1987	1988
SIZE OF STUDY AREA (ACRES).	1500	1500	1000
HOURS OBSERVATIONS AFTER GROUSE HATCH.	139.45	114.5	137.4
NO. HARRIER PRS. HUNTING AREA.	3	2	5-3
NO. GROUSE CHICKS PRESENT IN JUNE.	57	139	278
NO. GROUSE CHICKS SEEN TAKEN FROM STUDY AREA.	3	4	10

(>500m away) and out of view, though as the majority of the study area was visible, the number is likely to have been small. A second possibility is that interactions occurred whilst another harrier was being watched, though as the number of observations per hour is small (chapter 4) and one observation of a hunting bird followed directly on from another only four times in three years, the number is again likely to be minimal. Either way this technique provides a minimum estimate.

Chick losses were then calculated using the following equation:

$$\text{CHICKS TAKEN KM}^{-2} = H / (R * SA)$$

Where H = Amount of hunting time available (630 hours).
R = Rate at which chicks caught :
Observation time / No. seen taken from study area.
SA = Size of study area (km^{-2}).

The results obtained by this method were used as a comparison with estimates derived from the counts alone (Table 5.3) and show that estimates of losses to harriers were similar to observed losses. On the study areas during the three years of this study, harrier predation could account for grouse chick losses in the six week period. In other words, harriers could have accounted for the bulk of chick losses over that period.

5.3.3 The Impact of Harriers.

So far, predation by harriers has been estimated in the six weeks between counts. Mortality, however, will continue up to the shooting season (mid-August) and beyond. Beske (1981) showed that harriers tend to stay within their home range for 21 days after fledging (similar to sparrowhawks, Newton 1986), supported by observations in 1988, so predation can be expected to continue for at least two more weeks after the counts have taken place. In eight weeks, actual losses may be up to 30% higher. Observations of hunting harriers in June and July on moor B showed that harriers removed approximately 11.4 grouse chicks km^{-2} in six weeks. In eight weeks therefore, this could have risen to 15.2 grouse chicks, or 22% of the grouse chicks. In 1986 and 1987, 32% and 21% of the chicks were estimated to have been removed in eight weeks. On moor B, two pairs of harriers were suspected to have

TABLE 5.3. Comparison of expected (from observations of hunting harriers) and observed grouse chick losses (from counts) in six weeks on the intensive study areas from 1986-1988. The expected number of chicks lost km-2 are given with s.e.

	1986		1987		1988	
	EXP	OBS	EXP	OBS	EXP	OBS
NO. BROODS KM^{-2}		2		4		14.5
JUNE YOUNG PER FEMALE	----	4.75	----	5.78	----	4.80
JULY YOUNG PER FEMALE	3.62	4.08	4.86	4.26	4.01	3.99
NO. CHICKS LOST KM^{-2}	2.26±1.0	1.34	3.67±1.8	6.08	11.46±6.6	11.74

been killed two weeks after the first count. If these had been allowed to survive, harriers would have taken 30% of the available chicks.

5.3.4 Effect of grouse density on harrier diet.

Data from these three years and those from other studies were brought together to examine harrier diet in relation to grouse density (Fig.5.5). Data show that there was a large increase in the percentage of grouse in the diet at low densities but this quickly levelled off at about 33%.

To derive a functional response curve from Figure 5.5, it is necessary to understand what influences rate of prey capture. In this study harriers brought between 0.59 - 0.82 items per hour to the nests. This is lower than the rate observed by Picozzi (1978), though generally higher than other rates (Table 5.4) reviewed in Picozzi (1980). Regression analysis showed that differences in grouse density could account for 61% of the variation in rate (Fig. 5.6a) and the number of harrier chicks in the nest accounted for a further 17% (Fig. 5.6b). Another factor which seems to be important is alternative prey availability. Picozzi showed that the number of food items per chick was inversely related to the proportion of lagomorphs in the diet and the pattern was continued from the data in this study (Fig. 5.7). There was no relationship between feeding rate and the proportion of passerines, grouse or small mammals in the diet or between harrier brood size and grouse density. However, the density of hares and other alternatives was not measured on the moors (apart from this study), so the relationship between feeding rate and the percentage of lagomorphs in the diet may not have reflected alternative prey densities, but just individual harrier preferences. Knowing the relationship of rate of prey capture (Fig. 5.6) and the percentage of grouse in the diet (Fig. 5.5) to grouse density, it is possible to derive a functional response curve for the number of grouse chicks killed per pair of harriers in the six week period between counts (Fig. 5.8).

Harrier diet responded to changes in grouse density according to a 'Type II' functional response (Holling 1959). The finding that there was no evidence of a switch to predation on grouse chicks suggests that they were the preferred prey at all densities. This is supported by Table 5.5, which shows that grouse were of a greater proportion in the diet than on the moor.

FIGURE 5.5 Relationship between grouse density and the percentage of grouse in the diet of harriers. Equation - $Y = 34.07 - (35.42/X)$; $p<0.001$. References : 1 - Linfoot (pers. comm.); 2 - Picozzi (1980); 3-6 - This study; 7 - Picozzi (1978).

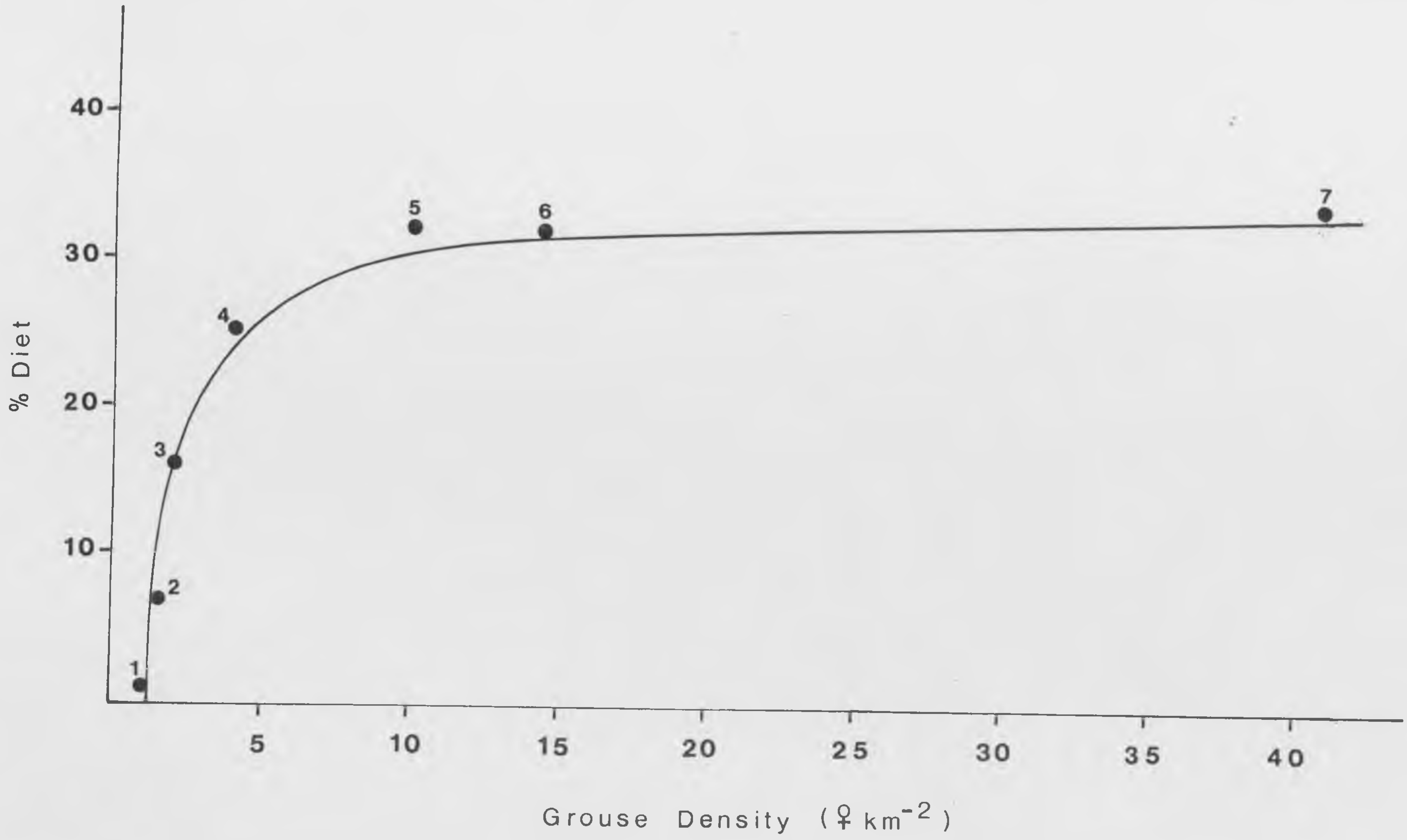

40
30
20
10
% Diet
1
2
3
4
5
6
7
5
10
15
20
25
30
35
40
Grouse Density (♀ km^{-2})

TABLE 5.4. Feeding rates and % prey types (GR - grouse chicks, SM - small mammals, LAGS - lagomorphs, PASS - passerines) in harrier diet. (based on table 4; Picozzi 1980).

REF.	NO. CHICKS	ITEMS HR^{-1}	% GR	% SM	% LAGS	% PASS
1.	4	0.44	---	4	13	56
	2	0.32	---	7	29	50
	3	0.42	---	?	?	?
	2	0.36	---	?	?	?
2.	4	0.80	---	37	10	37
3.	4-5	1.12	29	1	10	53
	4	1.04	32	1	5	54
	3	0.78	27	5	5	61
4.	1.5	0.47	15	0	0	67
	-	0.23*	35	3	0	46
5.	-	0.21*	---	5	18	53
6.	2	0.82	29	21	1	47
	2	0.59	62	8	2	21
	3	0.60	26	9	12	50

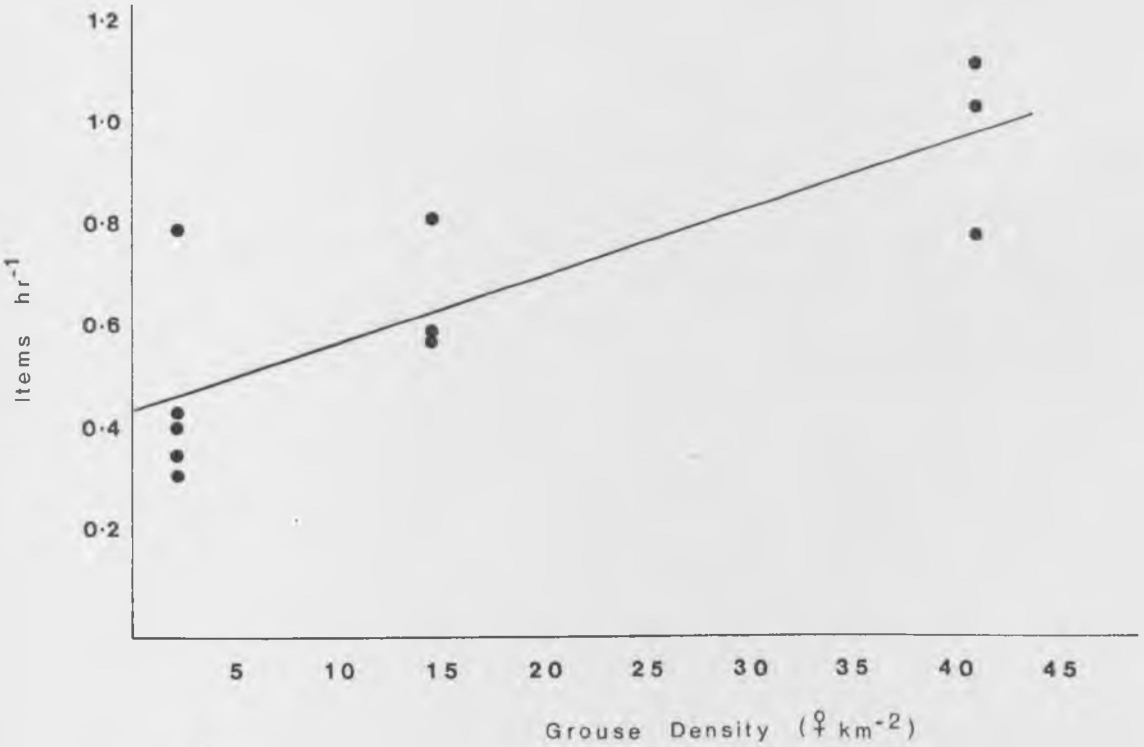
* - items chick^{-1} hour^{-1}

REFERENCES:

1. Picozzi 1980
2. Balfour and Macdonald 1970
3. Picozzi 1978
4. Watson 1977
5. Schipper 1973 - appendix 5
6. This study

FIGURE 5.6 Relationship between the number of prey items brought to harrier nests per hour and (a) grouse density (line equation: $Y = 0.45 + 0.013X$; $r=0.8$; $p= 0.002$); (b) number of harrier chicks per brood (line equation: $Y = 0.18 + 0.16X$; $r=0.61$; $p<0.05$).

a


1·2
1·0
0·8
0·6
0·4
0·2
Items hr^{-1}
5
10
15
20
25
30
35
40
45
Grouse Density (♀ km^{-2})

b

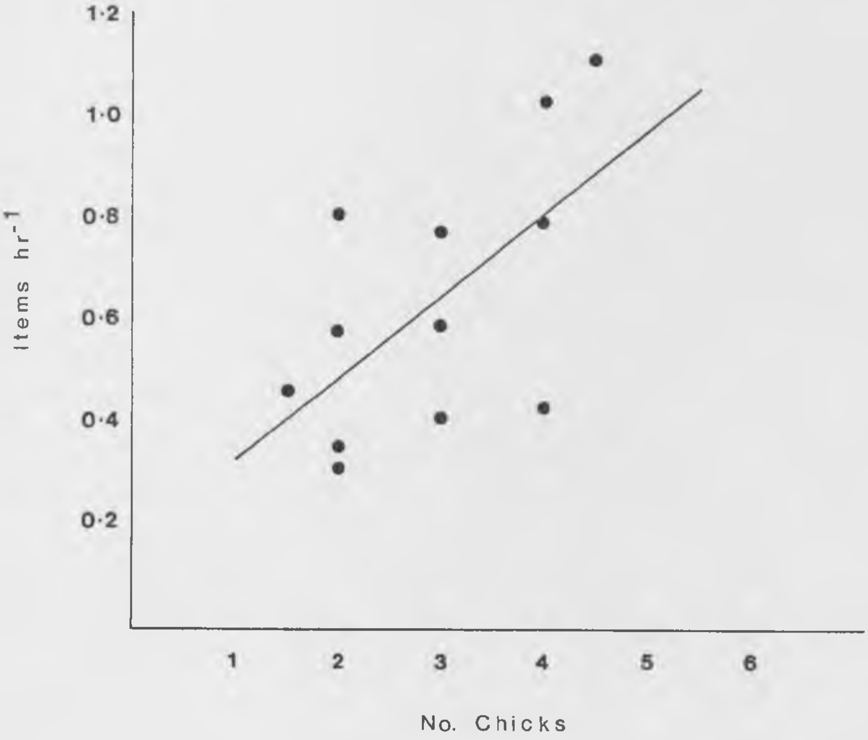

1·2
1·0
0·8
0·6
0·4
0·2
Items hr^{-1}
1
2
3
4
5
6
No. Chicks

FIGURE 5.7 Relationship between the number of prey items brought to harrier nests per chick per hour and the percentage of lagomorphs in the diet. Line equation: $Y = 0.29 - 0.006X$; $r=0.68$; $p=0.014$.

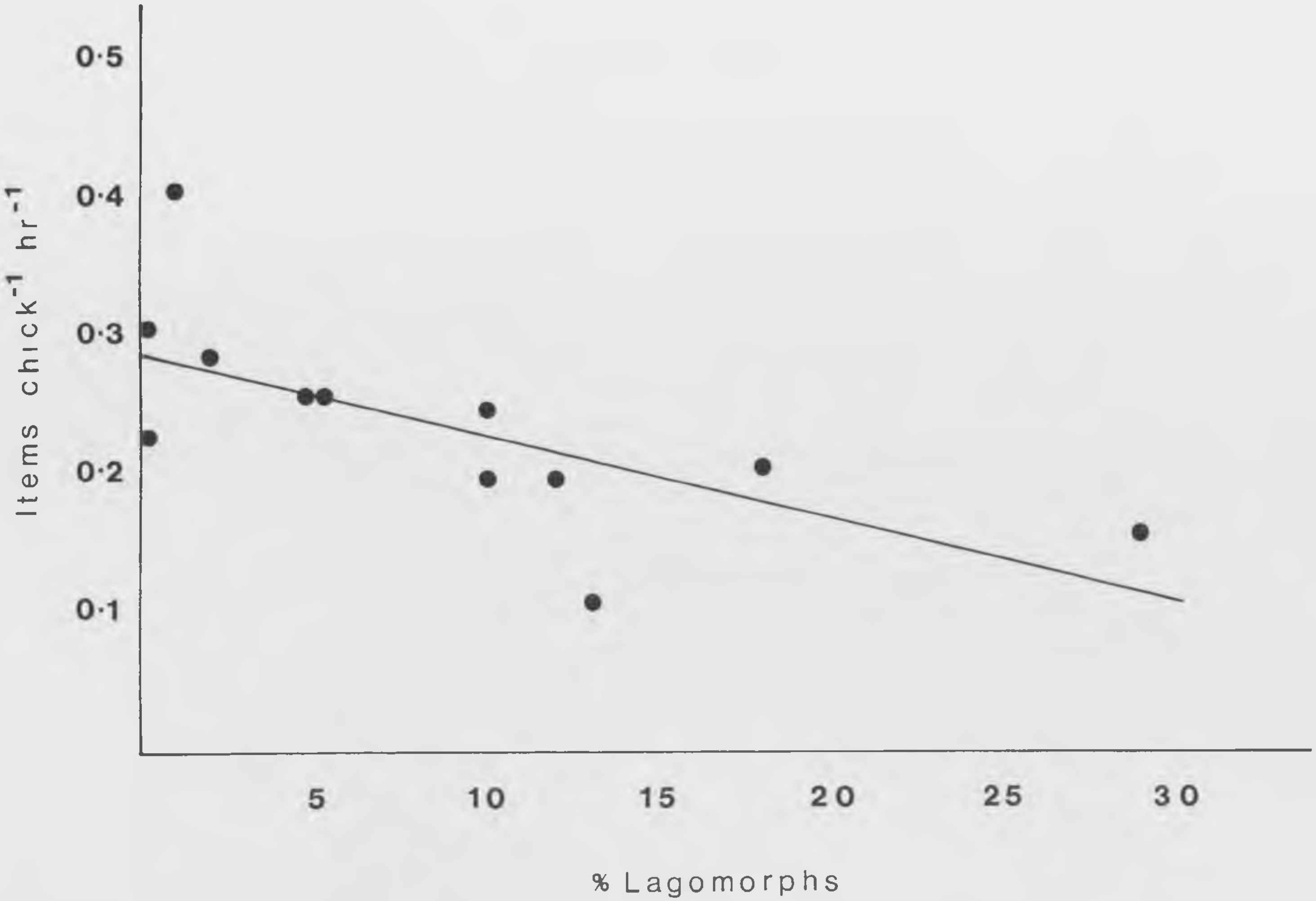

0·5
0·4
0·3
0·2
0·1
Items chick^{-1} hr^{-1}
5
10
15
20
25
30
% Lagomorphs

FIGURE 5.8 Functional response curve showing the number of grouse chicks killed per pair of harriers in relation to grouse density. Derived from Figs. 5.5 and 5.6a (see text).

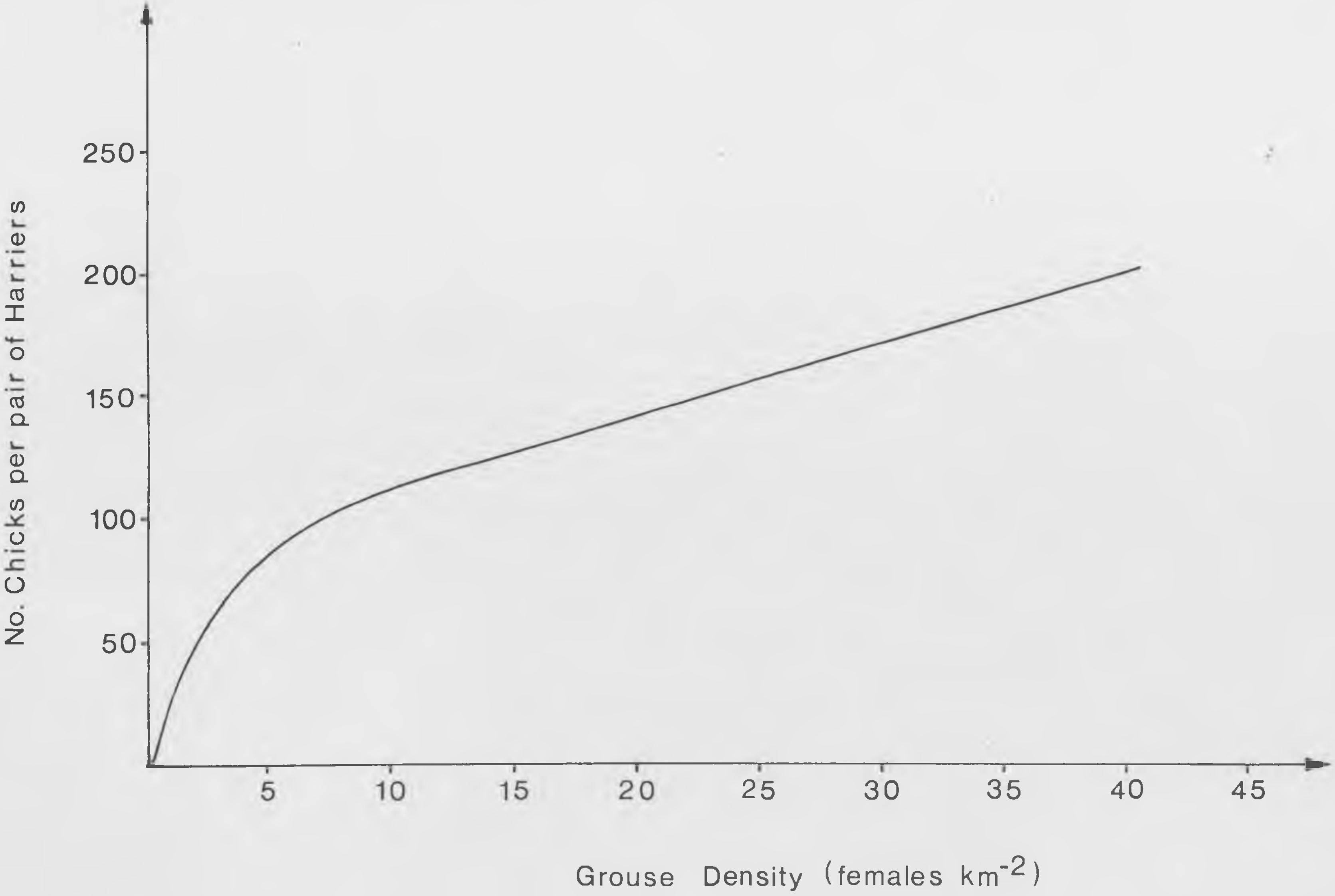

No. Chicks per pair of Harriers
250
200
150
100
50
5
10
15
20
25
30
35
40
45
Grouse Density (females km^{-2})

TABLE 5.5 Table of the percentage of the main prey types in the environment by number and their percentage as prey at nests in 1988, and seen caught in 1986 and 1987.

	MEADOW PIPITS		GROUSE CHICKS		HARES	
	Env^n	Prey	Env^n	Prey	Env^n	Prey
1986	97%	---	2%	16%	1%	0%
1987	93%	---	6%	25%	1%	0%
1988 (R)	92%	---	7%	---	1%	---
1988 (B)	72%	29%	19%	32%	9%	6%

5.4 Discussion

5.4.1 Harriers and Grouse Production

Moors with breeding hen harriers produced on average 17% fewer young grouse per female in July than moors without. However, within these moors the cause of loss was not determined and may not have been due to harriers. The existence of breeding harriers may simply have been a reflection of overall management; where harriers were allowed to breed, heather management and the control of other predators may have been less rigorous and this may have led to poorer breeding.

The argument that harriers were the cause of much of these losses was supported by the data from one pair of moors where grouse breeding success between the two varied with harrier density. This indicated that on some of the moors harriers may have been responsible for the poorer grouse breeding. Overall, data suggested that chick losses were additive to other chick losses, at least to the end of July.

Chick losses were examined in more detail on the intensive study areas and their 'controls'. In June, brood sizes were not significantly different, but six weeks later, broods were smaller on the moors with harriers. Observations of harrier predation indicated that this loss could largely be accounted for by harriers. In each year, harriers were estimated to have removed between 20% and 32% of the grouse chicks between June and late July.

Harriers exhibited a type II functional response to grouse density. Similar relationships have been found for goshawks feeding on pheasants (Kenward 1986) and woodland grouse (Wikman & Linden 1981) in Scandinavia and for other raptors in North America (Keith et al. 1977). The shape of the response indicates that grouse chick are preferred prey by harriers at all densities, though the degree of preference varies between individuals (chapter 4). At low density harriers preyed disproportionately more on grouse chicks.

5.4.2 Factors influencing predation on grouse

Whilst the above relationships suggest how harrier predation responds to grouse availability, at any one density the number of grouse chicks killed will depend on:

1). Grouse brood size. Harriers responded to the density of female grouse, or in other words to the density of broods on the moorland. They did not appear to select the larger broods, and probably preyed randomly on all brood sizes. The fact that they did not return immediately to a brood once located suggests that it may have been the vigilance behaviour of the adult grouse (i.e. the ability to warn the brood), not brood size, which determined whether or not a brood was attacked. However, the success rate of hunting harriers will probably be greater on larger broods than smaller ones, as the greater the number of chicks in a brood, the greater the probability of one being located by a harrier and the decreased ability of the adult grouse to defend their young. This could partly explain why harriers did not take more of their preferred prey (ie. grouse chicks) at high density. In Picozzi's study (1978), grouse brood size was small (average of 3 young). Had brood size been larger, a greater proportion of grouse may have been taken.

2). Alternative prey availability. At any one density, alternative prey availability may vary considerably. Reed (1985) has indicated that alternative prey (in this case wader species) increase as management for grouse improves and there may therefore be a trend of increasing alternative prey with increasing grouse density, as suggested from moors R and B in this study (chapter 4). Where there is more alternative prey, predation on grouse chicks could be reduced. However, this is not always the case, as indicated by Kenward (1986). He showed that goshawk predation on pheasants increased in the presence of rabbits, as the increase in prey availability attracted more goshawks. Kenward went on to suggest that this response depends on the relative vulnerabilities of the two prey types. If alternative prey are easily caught, then the percentage of main prey in the diet will be reduced, though this will also depend on the relative profitability of the two species. The more profitable the alternative, the greater the reduction of the main prey in the predators diet.

In Wisconsin (USA), Hamerstrom (1979) found no apparent relationship between harrier brood size and the density of their main prey, which were voles (though see Barnard _et al._ 1987). Similarly in this study harrier brood size was not related to grouse density. This is not surprising, as male harriers set up their territory and the females layed their eggs in spring, before grouse chicks were available. However, female harriers are able to kill adult grouse and may therefore select areas to breed where there are high densities of grouse. Harrier brood size will therefore probably be dependent on other prey species. This is another way in which alternative prey can influence predation on grouse. If these species are common at the start of the year, harriers may have large broods, which could increase predation pressure on grouse once the grouse had hatched.

3). Harrier density. Hamerstrom (1979) found that harriers showed a clear numerical response (variation in the number of breeding birds with prey density) to vole abundance and a similar response has been found for other birds of prey (Keith _et al._ 1977, Phelan & Robertson 1978, Kenward 1986). Were harriers allowed to survive on grouse moors, it is likely that their numbers would also vary with overall prey density, with the maximum density determined by food supply, as shown for sparrowhawks (Newton 1986). If densities increase up to levels seen in Orkney (0.66 pairs km^{-2}, Cramp & Simmons 1980), then their impact could potentially be severe.

4). Behavioural response. Individual differences in hunting behaviour may play a part in determining the response to prey (see Begon _et al._ 1986). If hunting harriers had little experience of grouse chicks, they may have been less successful at locating and catching them. As an individual becomes more successful, it may concentrate on grouse, as one male did in 1988 (see chapter 4). Males seldom return to the same nesting area each year (Picozzi 1978) and therefore the number of chicks they kill may depend upon their experience in previous years.

5). Possible costs of feeding on grouse. Optimal foraging theory (see Stephens & Krebs 1986) suggests that as densities of profitable prey increase, alternative prey (ie. passerines and small mammals) should be ignored, though this may depend upon length of hunt time, with predators only being selective after a critical time (Orians & Pearson 1979). There is, however, a cost to catching grouse and hares, not only in increased handling time, which is small for the male, but in terms of injury risk. All grouse chicks and leverets that were attacked, were strongly defended by the adults, even to the extent of knocking a harrier out of the air (see chapter 4). Interestingly, the strength of aggressive behaviour by grouse to humans and dogs varies. Hudson (1989) shows that variation between districts is correlated with fox density. If grouse also vary their response to harriers, then the risk of catching grouse chicks may be greater on some moors than others. However, no variation in behaviour was noted in this study.

All of these factors are important if we are to predict accurately the impact of harriers on grouse chicks in any one area, and they highlight aspects of research that need further investigation. In particular the effects of alternative prey and grouse brood size on the preference of grouse chicks in the harrier diet need to be examined. Also the factors influencing individual behaviour need to be discovered as they could determine whether harriers seriously reduce grouse chick numbers or have little effect.

5.5 **Summary**

Grouse moors with breeding harriers produced fewer young grouse per hen than nearby moors without harriers. On those moors where harrier predation was examined for in June and July, it could account for the bulk of chick losses in that period. These intensive studies revealed that up to 32% of grouse chicks present in June were killed by harriers within eight weeks.

Data from this study and other similar work indicated that harriers exhibit a type II functional response to grouse chicks and these were the preferred prey, with harriers killing disproportionately more at low and medium density.

On any one grouse moor, the impact of harriers will depend on a variety of factors. These are briefly discussed and show that the effects of alternative prey, grouse brood size and the factors influencing individual harrier predation need further investigation before we can accurately predict the effect of harrier predation.

CHAPTER 6

EFFECT OF HARRIERS ON GROUSE BAG SIZE AND BREEDING DENSITY

6.1 Introduction

Grouse chick losses to harriers are potentially high (see chapter 5). These losses are only important to landowners, however, if they affect the number of grouse shot in autumn or the density of breeding birds the next year, thereby influencing revenue for an estate. In this chapter a deterministic model is presented which examines the impact of harrier predation on grouse bag size and the possible consequences, in financial terms, to an estate. Overwinter losses are then incorporated to discover the potential impact on breeding density in the following year. The model examines changes in mean population values and does not deal with cycles.

6.2 Methods

The impact of harrier predation on the bag was examined using the models summarised in Fig.6.1. Model I was run without stochastic variation for spring grouse densities of 1 pair to 50 pairs km^{-2}. At each density the average bag was obtained for harrier densities ranging from 0 to 0.2 pairs km^{-2} (density observed in 1988). Various assumptions, based on published data and discussions in previous chapters, were made in the model and these are outlined below.

6.2.1 Inputs and parameters of the model.

1). Sex ratio. Hudson (unpub.) has shown that the ratio of males to female grouse in spring is biased towards males and this falls with increasing density according to the equation: Sexratio = 1.98 - (0.46 * LOG(Spring grouse)) ($N = 79$, $r = 0.48$, $p<0.001$). This equation was used to determine the number of breeding females.

2). Grouse breeding. Clutch size was regarded as constant and taken as

FIGURE 6.1. Schematic representation of the grouse / harrier models. Model I (left of dotted line) was run for grouse spring densities of 1 to 50 pairs and for harrier densities up to 0.2 pairs km^{-2}. Model II incorporated overwinter losses and was run from spring densities of 1 pair until equilibrium levels reached.

VARIABLES (see text) :

1). Y = 1.98 - (0.46 * LOG (SPRING GROUSE))

2). 8.03

3). 85%

4). 56%

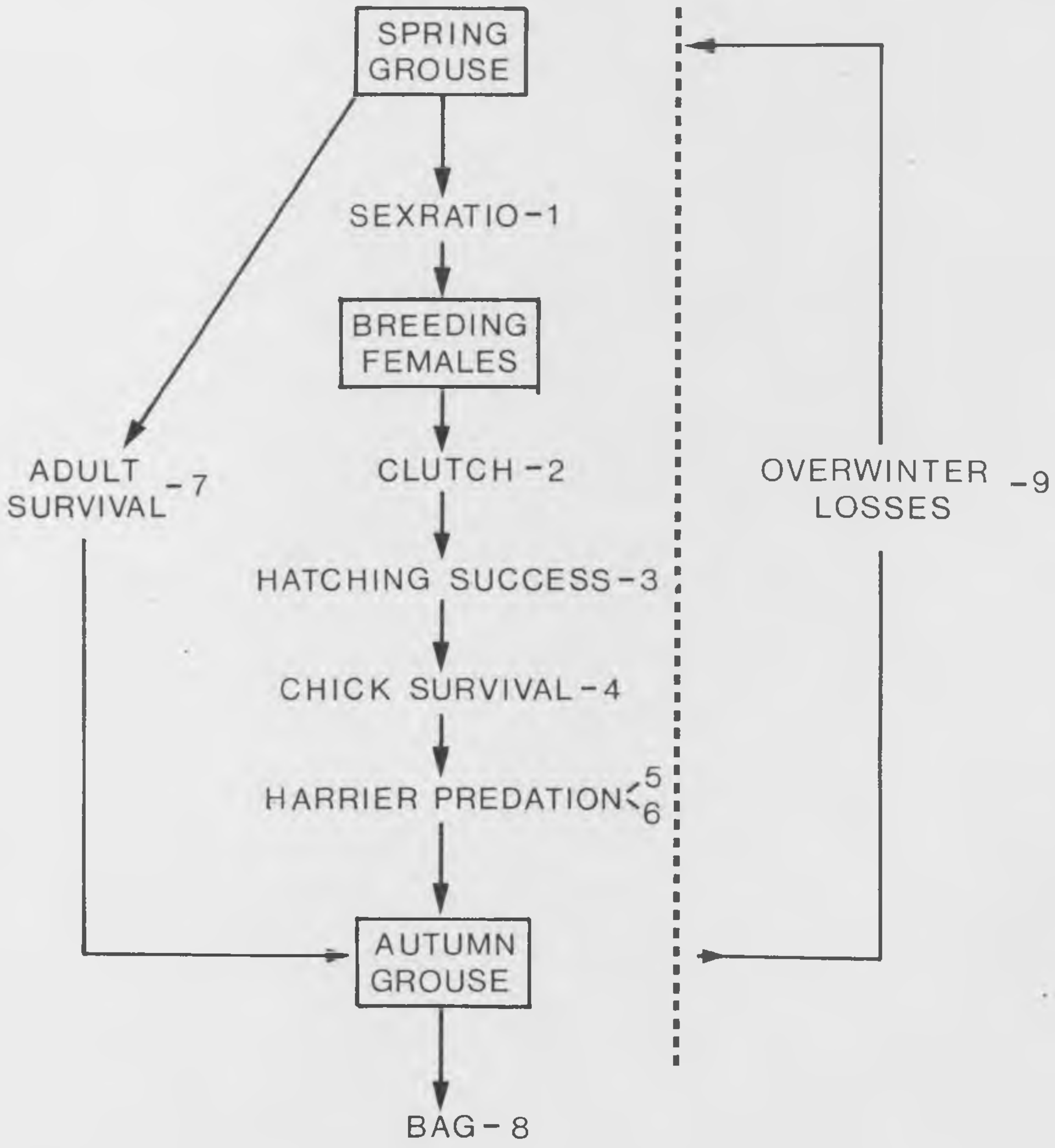
5). Y = 34.07 - (35.42 / X)

6). Y = 0.45 + (0.013 * X)

7). 81%

8). Y = 0.43 * X

9). Y = (0.73 * X) - 18.8


SPRING GROUSE
SEXRATIO-1
BREEDING FEMALES
ADULT SURVIVAL -7
CLUTCH -2
OVERWINTER LOSSES -9
HATCHING SUCCESS-3
CHICK SURVIVAL-4
HARRIER PREDATION 5 6
AUTUMN GROUSE
BAG-8

8.03 eggs per female, with hatching success at 85% (Hudson 1986). Chick losses, not due to harriers, were assumed to be additive to harrier predation (see chapter 5) and the model was run with values from 20% to 90% lost. This gave an average brood size (young per hen) ranging from 1.69 to 7.58, figures similar to those reviewed in Potts et al. (1984) and Hudson (1986b). The young to old ratio measured in July was 2.18±0.1 (1979 to 1986 data). For the model, chick survival (before harriers) was set at 56%, which gave a young:old ratio of 2.19 and the effects of harriers then imposed. There was no relationship between young:old ratio and density ($r=0.05$, $p=0.95$).

3). Harrier predation. Predation rates varied with grouse density (Figs. 5.5 + 5.6a) and these regression equations were used in the model. This gave the total number of grouse taken by each pair in eight weeks. The product of this figure and the density of harriers gave the average number of grouse lost km^{-2}. For any given area, harrier densities were assumed to be equal both inside and outside its boundaries. Home ranges were assumed to overlap (chapter 5) and the effects of harriers to be additive to each other. In this study harrier densities ranged from approximately 0.04 pairs km^{-2} (based on 100 km^2 on moor R and surrounding moorland) to 0.2 pairs km^{-2} (50 km^2 on moor B and surrounds).

4). Adult summer survival. Jenkins et al. (1963) showed that 19% of adult grouse were lost from March to August and adult survival was therefore set at 0.81.

5). Dispersal. The extent of late summer dispersal in August / September is largely unknown. Watson et al. (1984) indicated that the degree of movement may be large, but these studies covered a small area and may therefore be slightly biased. The bag equation examines the relationship between autumn counts and the number shot and therefore incorporates any dispersal which took place between these two events.

6). Grouse bags. The dynamics of grouse shooting are described in detail in Hudson (1986). Briefly, above densities of about 80 grouse km^{-2} (Potts et al. 1984), birds are driven by beaters over guns, which are placed in butts across the moor. At lower densities grouse are shot by groups of guns walking over the moor with dogs (rough shooting). This is less important financially, as fewer birds are shot and these are worth less. Bags are counted in brace, where one brace equals two grouse.

To determine the relationship between the number of grouse counted in August and the number shot, data were obtained from all moors covered by S.G.R.P. and N.E.G.R.P. in all years (N= 188). These gave a regression line ($Y=0.37X + 10.52$, $r=0.54$, $p<0.001$) which did not pass through the origin (Fig. 6.2). To make the line biologically meaningful, the line was forced through the origin (Steel & Torrie 1960) and this line was also significant ($Y=0.43X$, $p<0.001$). Overall, 43% of the populations were shot, similar to the 46% estimated by Hudson (1986a).

7). Loss of revenue. Based on 1988 figures, each bird lost from the bag, for driven grouse, was assumed to cost the estate £30.00. This is an overall figure, as birds are worth more early in the season. In contrast, grouse shot by rough shooting are worth approximately £12.50 (Hudson pers. comm.)

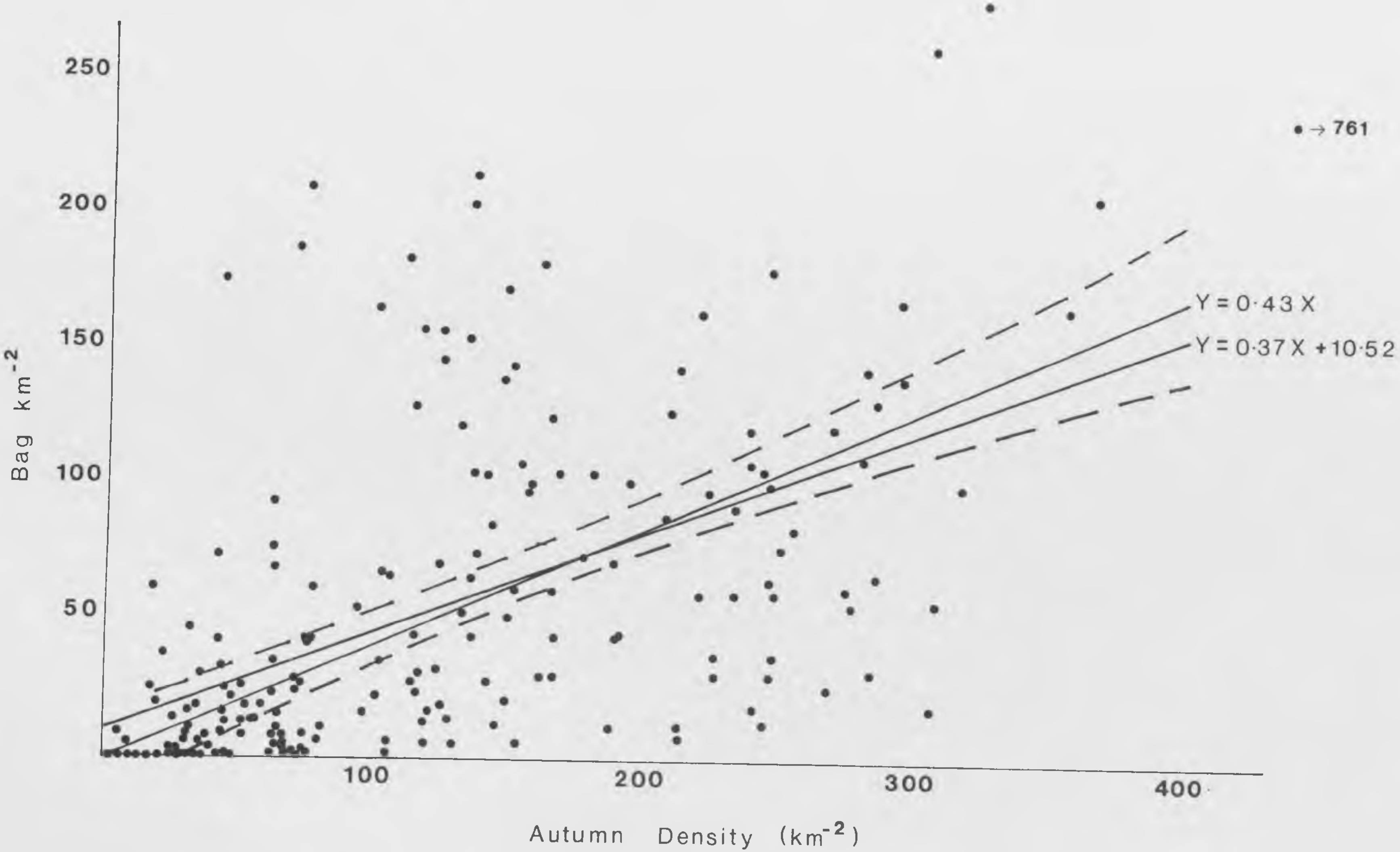
Using this model (displayed in appendix 1), some idea of bag losses and loss in revenue were obtained.

6.3 Results

The slope of the relationship between bag size and spring density was dependent on overall chick survival (ie. brood size) with bags km^{-2} ranging from 0 at low density to 83 ± 12 brace km^{-2} at high density and good breeding success (Fig. 6.3). For an average young:old of 2.19, bags ranged from 0 to 62.5 ± 8 brace and onto this relationship harrier predation was imposed (Fig.6.4.).

When the effects of harriers on the number of grouse shot was examined (Fig.6.5) it was apparent that the effects of harriers increased with density but, as a proportion, the impact was highest at low density. Harrier predation was assumed to be independent of grouse breeding success and therefore the shapes of these relationships did not

FIGURE 6.2. Variation in the number shot (km^{-2}) with increasing grouse densities. Two lines are shown : the normal regression line ($Y=0.37x-10.52$) and one forced through the origin ±95% confidence zone ($Y=0.43X$).



Bag km^{-2}
250
200
150
100
50
100
200
300
400
Autumn Density (km^{-2})
• → 761
Y = 0·43 X
Y = 0·37 X + 10·52

FIGURE 6.3. Model I run without harriers to show the variation in the number of grouse shot at grouse spring densities of 1 to 50 pairs and increasing breeding success (young : female from 1.69 to 7.58).

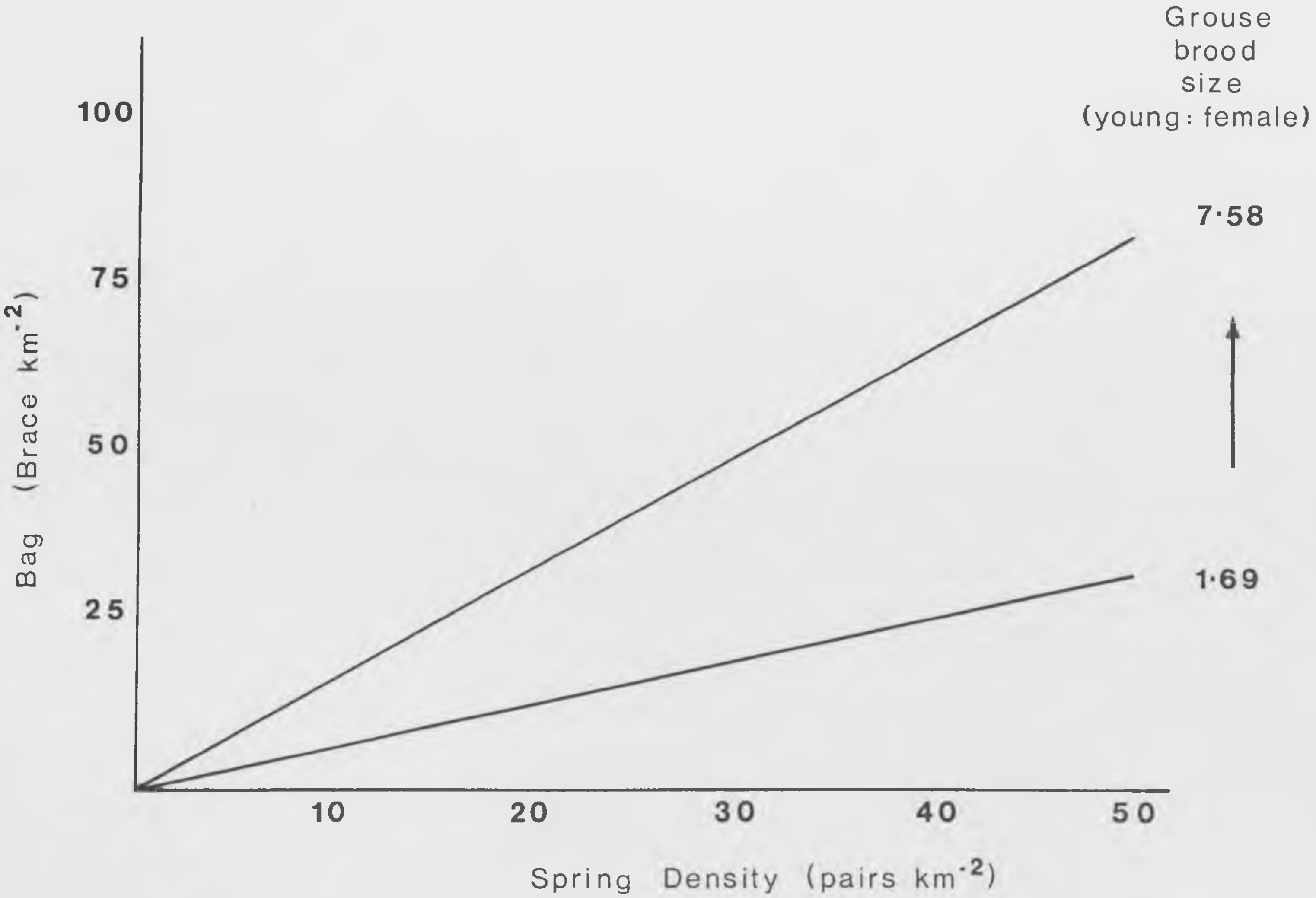

Grouse brood size (young: female)
7·58
1·69
100
75
50
25
Bag (Brace km⁻²)
10
20
30
40
50
Spring Density (pairs km⁻²)

FIGURE 6.4. Model I run with breeding success set at 56% and harrier densities ranging from 0 to 0.2 pairs km^{-2}. Dashed lines represent the 95% confidence zone for the no harrier line.

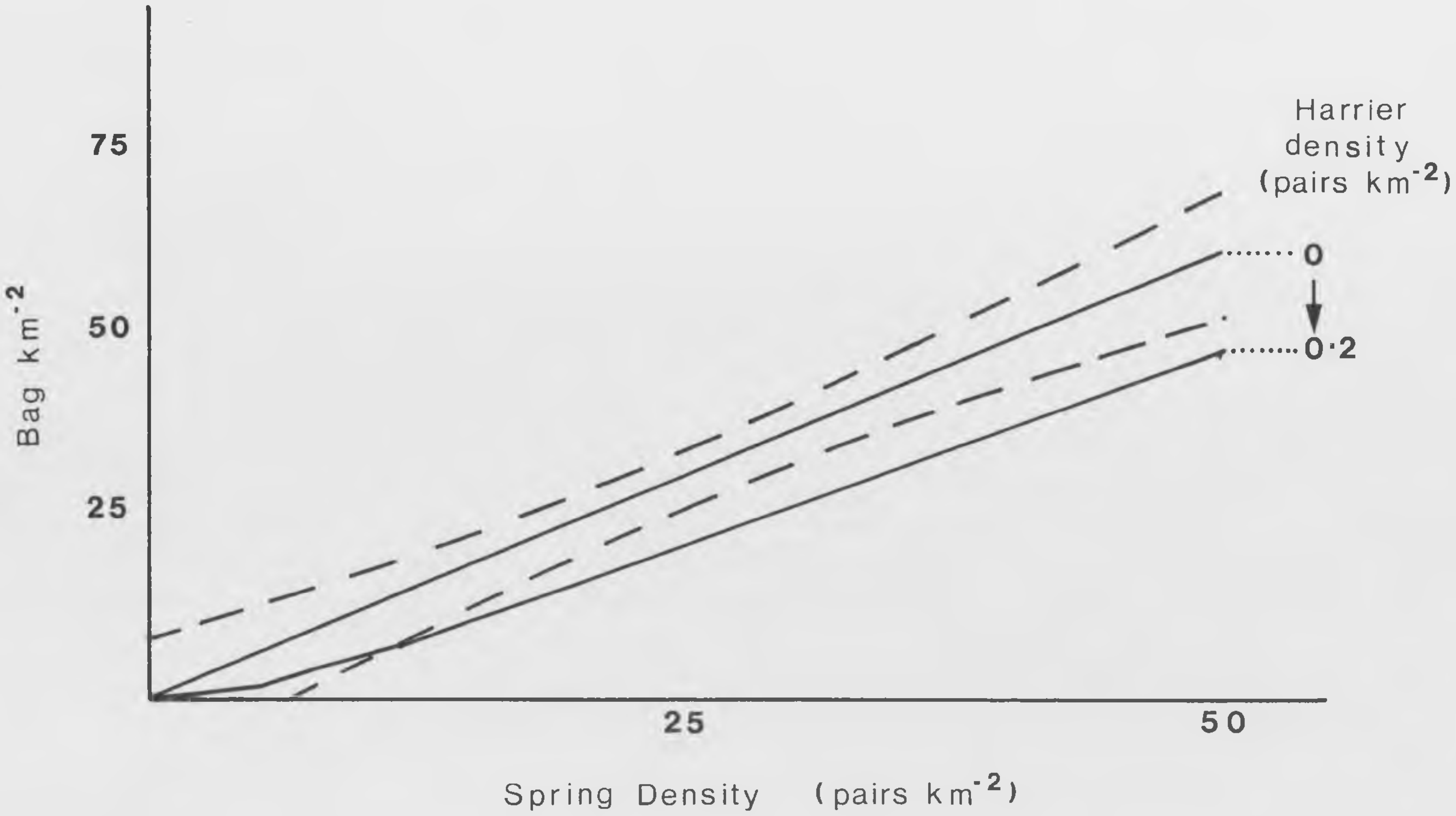
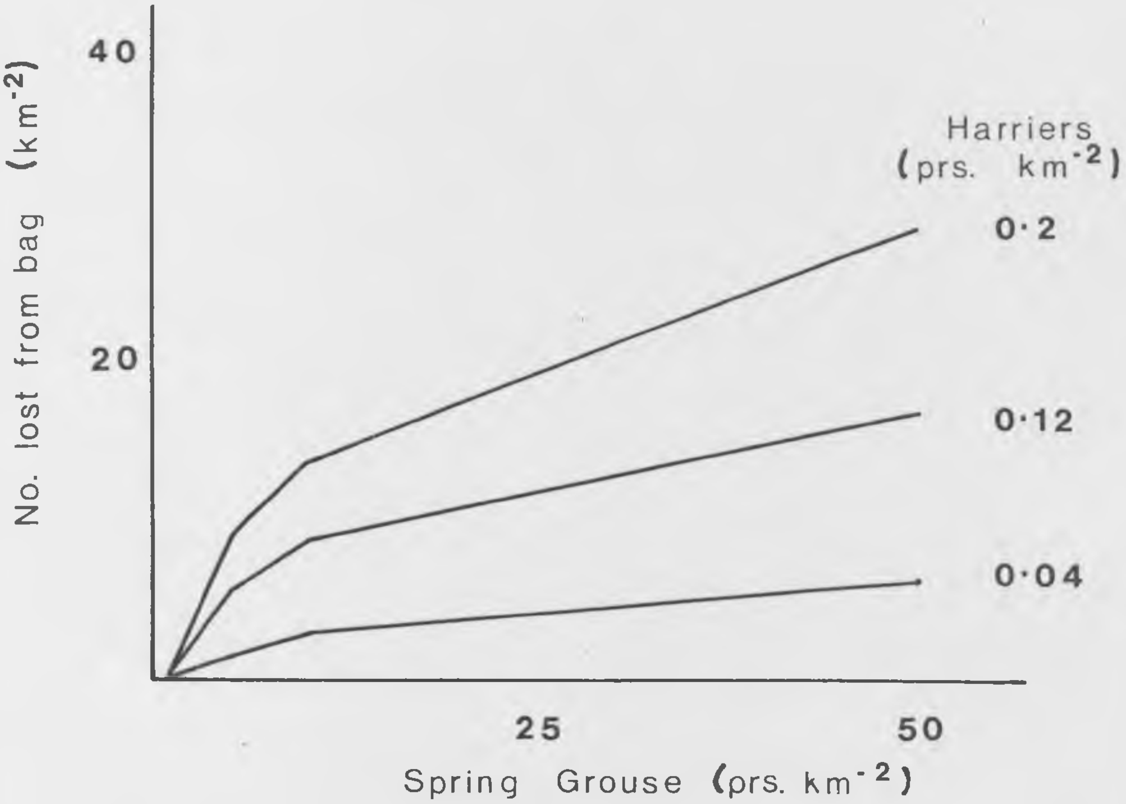

Harrier
density
(pairs km^{-2})
0
0·2
Bag km^{-2}
75
50
25
25
50
Spring Density (pairs km^{-2})

FIGURE 6.5 Output from model I showing the effect of harriers on the number of grouse lost from the bag for grouse densities from 1 to 50 pairs km^{-2}.


40
20
No. lost from bag (km^{-2})
Harriers (prs. km^{-2})
0·2
0·12
0·04
25
50
Spring Grouse (prs. km^{-2})

change, though the percentage of the bag lost was dependent on breeding. Harriers, at high density, decreased bag size by up to 14.5 brace km^{-2}, or 23% of the number shot. If this is related into financial terms, a high density of harriers could cost an estate up to £870 km^{-2} in lost revenue. At low density, although harriers have a greater impact on bag size, fewer grouse are shot and these are financially less important.

6.3.1 Overwinter losses

The number of birds lost overwinter was examined from the losses between counts carried out in autumn and the following spring. This included losses to predators, shooting and dispersal. The relationship between autumn density and number lost (Fig. 6.6) was highly significant ($N=101$, $r=0.97$, $p<0.001$). The graph shows a small spread around the line and at autumn densities below 26 birds, the number lost overwinter is negative, i.e. populations are sustained by dispersal into the areas. This regression was introduced into the model, without stochastic elements and run for 50 years. The equilibrium levels were then calculated and compared to field data from Potts _et al._ 1984 and from SGRP and NEGRP data from 1986 to 1988 (Table 6.1). The model successfully measured mean levels for published data, although spring density was a little lower and bags higher.

6.3.2 Sensitivity Analysis

The model has two main parameters: breeding success and overwinter losses. These were separately altered and their influence on the model compared. The values of young : old were altered by 1 s.e. and simulated by the model. Similarly the equation for overwinter losses was varied by running the equation firstly with the slope at each of the 95% confidence limits and then with the mean Y values at the 95% confidence limits. (Table 6.2). Lastly the model was run for 20 years, then spring populations taken to maximum (100 pairs) and minimum (1 pair) to check that populations returned to the same equilibrium, which was the case.

6.3.3 Impact of Harriers

Onto this model, the effects of increasing harrier densities (from 0.04 to 0.2 pairs km^{-2} were imposed (Table 6.3). At high densities, the young:old ratio was reduced to 0.7, which in turn brought spring

FIGURE 6.6 Relationship between autumn densities and overwinter losses (km^{-2}). $Y = 0.73X - 18.8$, $r = 0.97$, $p<0.001$.

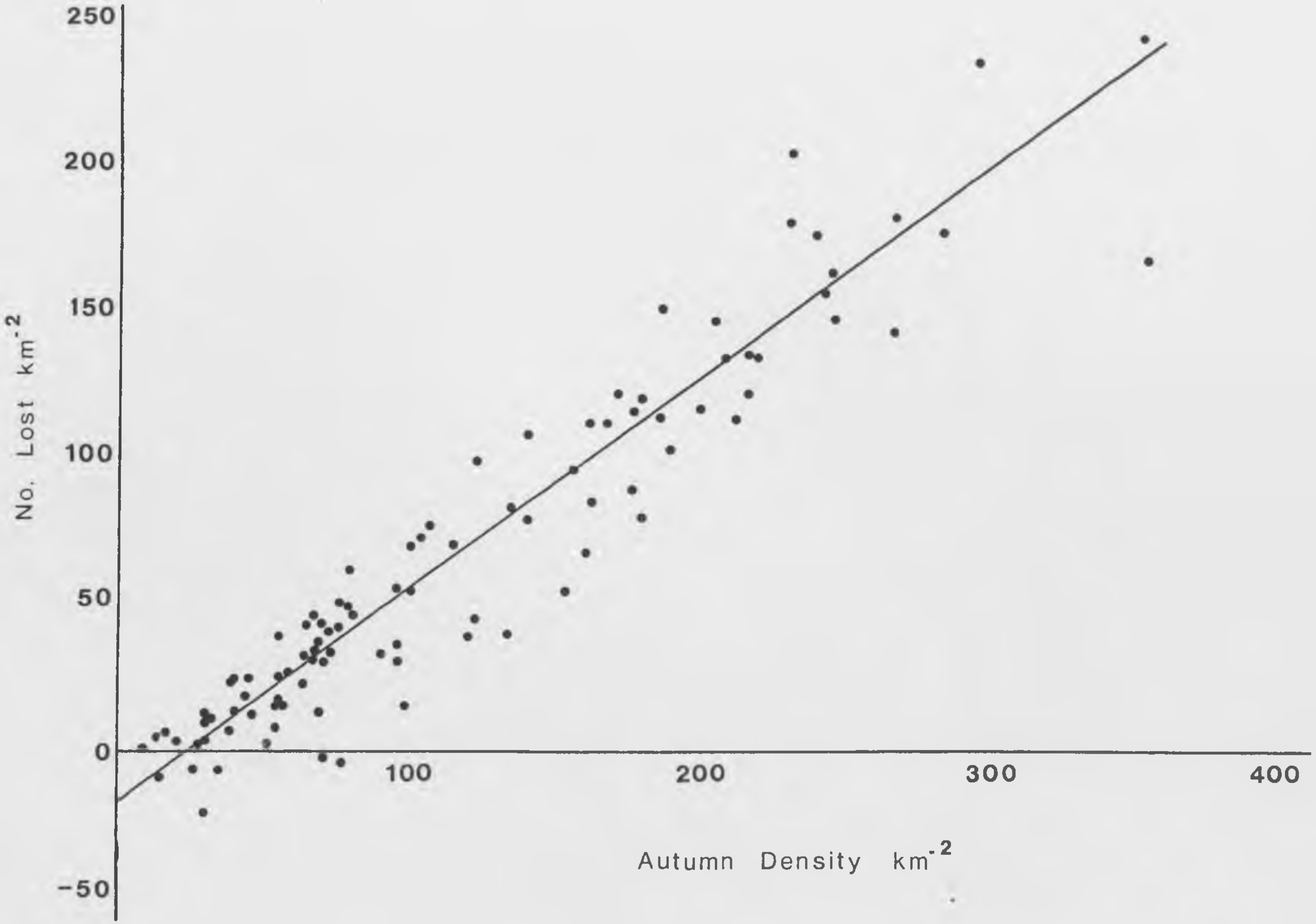

250
200
150
100
50
0
-50
No. Lost km^{-2}
100
200
300
400
Autumn Density km^{-2}

TABLE 6.1 Comparison of population statistics for red grouse from the model run without harriers with data from Potts *et al.* (1984) and S.G.R.P. data 1986 - 1988 (unpub). Data presented as means ± 1 s.d.

	POTTS *et al.*		SGRP	MODEL
	Moorhouse	Others		
APRIL DENSITY (pairs km^{-2})	35.6 ± 5.2	36.7 ± 4.9	20.9 ± 17.0	31.2
YOUNG : OLD (in August)	2.0 ± 0.9	2.3 ± 0.9	2.4 ± 0.9	2.2
AUGUST DENSITY (km^{-2})	169	140	117 ± 86	161
BAG (km^{-2})	55	50	60	69

TABLE 6.2. Sensitivity analysis. Variations in average grouse population levels through altering one variable at a time: a) chicklosses ± 1 s.e., b) overwinter losses, ± slope 95% c.l., c) overwinter losses, Y values ± 95% c.l. Values given as range, with MODEL column giving mean values from model without change.

	a	b	c	MODEL
APRIL DENSITY (pairs km^{-2})	28.7 - 33.3	23.7 - 38.8	22.5 - 56.5	31.2
YOUNG : OLD (August)	2.1 - 2.3	2.1 - 2.2	2.1 - 2.3	2.2
AUTUMN DENSITY (km^{-2})	143 - 177	121 - 204	114 - 303	161
BAG (km^{-2})	61 - 76	52 - 88	49 - 130	69

TABLE 6.3. Impact of harrier densities on grouse population values, derived from the model, run until equilibria reached.

	HARRIER DENSITY (PAIRS KM^{-2})			
	0	0.04	0.12	0.2
APRIL DENSITY (pairs km^{-2})	31.2	26.7	20.0	15.0
YOUNG : OLD (August)	2.2	2.0	1.4	0.7
AUTUMN DENSITY (km^{-2})	161	129	79	42
BAG (km^{-2})	69	55	34	18

density down by 32 birds. Harrier predation can vary considerably (chapter 4), so the relationship which governed the rate at which harriers caught prey was altered by 30% to encompass over 90% of the values in Fig. 5.6a. The model was then run for medium harrier densities (0.12 km^{-2}) to examine the effects of altering predation rate (Table 6.4). This had little impact on either spring density or bag size in the model.

6.4 Discussion

The impact of harriers on the grouse bag was dependent on grouse and harrier densities and on grouse breeding success prior to predation. At average breeding levels, harriers could potentially decrease the bag by up to 29 ± 16 birds km^{-2}, at a cost of £870 ± £480 in lost revenue. Altering the rate with which harriers caught prey by up to 30% had little overall impact on the outcome of the model. These figures are based on predation on grouse chicks. However, harriers could also influence the size of the bag, by altering grouse behaviour, in two other ways. Firstly, they could force birds into larger packs as a protection against predation (chapter 3) and Hudson (1985) showed that fewer grouse were shot from larger packs. However, it could equally be argued that by reducing brood size, harriers decrease covey size and thereby increase the chances of birds being shot. The other way they can reduce the bag is by flying over the moor when shooting is taking place, as this can disrupt a whole drive (Watson & Miller 1970) and make the grouse flighty and hard to shoot.

There was a high degree of variation in the number of grouse shot at any one autumn density (29% of the variation could be accounted for by density), making it difficult to determine the precise impact of harriers on the bag in any one year. However, above densities of approximately 0.1 km^{-2} harriers decreased the bag to a level that lay outside the 95% confidence limits for the no-harrier line. Above these densities therefore, the impact of harriers will be more noticeable. There are various possible reasons for the variations in the number shot:

1). Sampling error. Autumn populations were estimated from 1km^2 sample counts which may have misrepresented overall density. However, some

TABLE 6.4. Impact of harrier predation rate (variable 7 in Fig. 6.1) on grouse population values, derived from the model, run with harrier densities set at 0.12 km^{-2} until equilibria reached.

	RATE OF PREY INTAKE		
	NORMAL	+30%	-30%
APRIL DENSITY (Pairs km^{-2})	17.8	21.0	16.0
YOUNG : OLD (August)	1.4	1.7	1.2
AUTUMN DENSITY (km^{-2})	79	102	65
BAG (km^{-2})	34	44	28

large scale counts have been carried out by the S.G.R.P., which indicated that the counts were representative (Hudson unpub.).

2). Grouse behaviour. Dispersal rates after the count and before shooting could vary with, for example varying breeding success and this could influence the number shot.

3). Shooting pressure. Differences between moors in the number of days shooting and the number and quality of the guns will obviously influence the number shot.

It is important to discover the main cause for variations in bag levels, because if there is control over bag levels then harrier predation could be compensated for, although this will depend on whether mortality from shooting is compensatory. Hudson (1985) suggested that hunting mortality was partially compensated for, up to a certain level, after which it becomes additive. He stressed that this threshold needs to be discovered before optimal harvesting strategies can be developed and this is particularly important in the case of harrier predation. If losses due to harriers can be compensated for by increasing shooting pressure then these raptors will have little overall effect. However, as Hudson (1986) states : "In reality this is not so simple since shooting harder results in days of 20 or 30 brace; daily bags which are unacceptable on commercial estates." Also this could only be done up to the threshold density where grouse populations tend to be undershot (Hudson 1985).

The first model examined the impact of harriers on the bag in any one year. When the regression line for overwinter losses was introduced, their potential effect over a number of years could be assessed. At high harrier densities spring grouse were reduced by over 30 birds and the subsequent bags by 20 brace. Indeed the populations were only sustained by immigration into the areas over winter. Realistically, this is unlikely over a long period for two reasons: firstly, dispersal from surrounding areas will only occur if breeding there is good. If harrier densities are high on these areas also, then the populations will probably not be sustained. Also, Hudson (1986a) indicates that young females may be the birds that dispersed. When harrier predation is high, the number of young, and therefore dispersion, will be reduced. Secondly, harrier densities will fluctuate with prey availability and would be unlikely to remain at high densities continuously.

As the model draws data from a number of populations, it is difficult to detect the density dependence that has previously been detected in chick and overwinter losses (see chapter 1) and such density dependence may alter the outcome of the model. As more data are collected from various populations, the effects of density and the inter-relationship of variables can be modelled for each. This will provide a more specific assessment of the effects of harriers, as opposed to the more general picture obtained from this model.

In the model, harrier predation may be slightly overestimated as it assumes that predation is equally successful on small broods as well as large. As discussed in chapter 5, the probability that a harrier will successfully locate a chick may depend on grouse brood size, so the effects of harriers may be less severe when breeding is poor.

It is interesting that although there is a high degree of variation in the number of grouse shot at various densities, this variation is reduced when examining overwinter losses, supporting the view that there is some compensation to shooting mortality. In this study overwinter mortality appeared to be inversely density dependent, indicating that the compensation comes from variation in dispersal.

6.5 **Summary**

Harriers reduce grouse breeding success and thereby reduce the number of grouse available for shooting. This predation can decrease bag size, though the high degree of variation in the bag makes it difficult to determine the precise impact on the bag in any one year. It has been suggested that shooting mortality is partially compensated for. If this is the case, then the impact of harriers could be lessened by increasing shooting pressure. Sensitivity analysis showed that slight changes in the level of overwinter losses could have a dramatic effect on the model and it is therefore important to determine to what extent dispersal and predation influence these losses. If the population parameters used in the model are sustained in the field, over a number of years, then harriers could seriously reduce a grouse population, though this would be dependent on how harrier and alternative prey densities vary.

CHAPTER 7

GENERAL DISCUSSION

In order to assess the impact of predation on a prey population it is necessary to know, not only the number, time and selectivity of deaths caused by the predators, but also the strength of this relationship in relation to other demographic processes. As Begon et al. (1986), and other ecological texts have stated:

$$N_{t+1} = N_t + B - D + I - E$$

Where N_{t+1} is the number of animals in the generation after N_t and B=births, D=deaths, I=immigration and E=emigration. This study, outlined in the previous six chapters, has focused on the mortality in red grouse populations, but in order to understand its importance it is necessary to consider it in relation to dispersal and fecundity.

Throughout the three years, overwinter losses to predators were high relative to other losses, and appeared to be inversely related to density, though the causes of this relationship and whether it is a local or widespread pattern need examining. Such a relationship is destabilising in terms of population dynamics, as it will tend to drive a population to extinction. However, grouse populations did not decline, apparently because of dispersal. At low densities there was net immigration which compensated for the high mortality. These populations were therefore sustained by dispersal. Red grouse are known to be relatively sedentary animals (Jenkins et al. 1963) and dispersal here is used in the sense of small scale movement between neighbouring moors.

This situation is different to that previously studied by Jenkins et al. (1963 and subsequent papers) in north-east Scotland and by Hudson in northern England. They examined high density cyclic populations and consequently were more concerned with factors that decreased the population from high density, be it territorial behaviour or parasitism. One exception to this was the work carried out by Watson & O'Hare (1973 & 1979) in Ireland. Here densities ranged from 0-12 km^{-2} and Watson and O'Hare (1979) suggested that dispersal was important in maintaining very low density populations, and the reason the populations did not increase was due to poor breeding. In my study dispersal was important in maintaining low density populations, but populations increased because of the good breeding that occurred in all years.

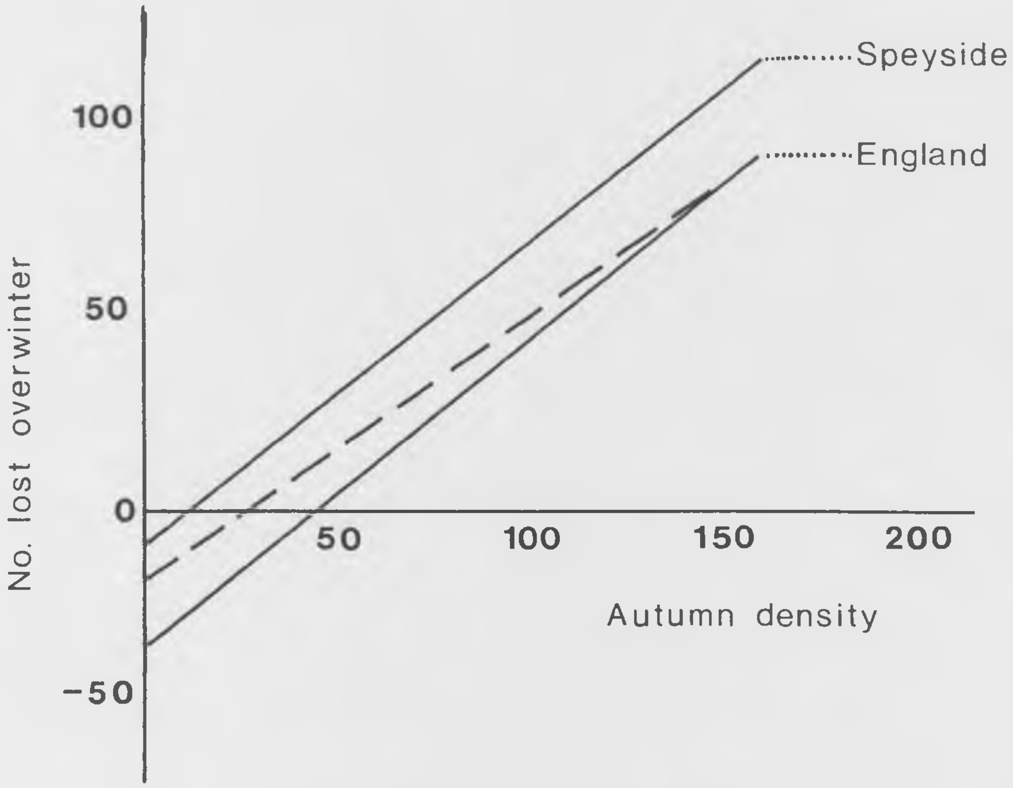
The traditional approach to managing red grouse populations has been primarily to control predators. It is therefore important to know whether the control of predators overwinter in this study would have improved subsequent breeding densities. There has been much argument over this issue (chapter 1) but it seems likely that overwinter losses at low density will be largely additive, as there will be enough space for all individuals to breed.

When the overwinter losses data from my study sites were compared to those from England, where losses to predators are low, there was a noticeable difference. To see whether the observed increase in mortality could account for this difference, the study site losses were reduced by the number of grouse found dead (Fig. 7.1). This indicated that predator and fence mortality could account for a large part of the difference between the two lines, especially as it is unlikely that all kills (especially mammal kills) were found. Kills accounted for less of the loss at low densities indicating that dispersal levels themselves may be different between study areas, possibly due to variations in grouse density on moorland adjacent to the study areas, or variations in shooting mortality between regions. The model (chapter 6) suggests that grouse populations may be sensitive to small changes in overwinter losses, which indicates that management procedures aimed at reducing this loss could be beneficial.

A related issue is whether the birds killed are mainly those which are dispersing. For example, if one estate controls its predators, will the birds that they have saved from predation, simply move out into neighbouring 'predator-sink' areas? Whether or not this would occur depends on the timing of dispersal and mortality.

The main grouse dispersal is thought to occur in late-summer / early-winter, when family coveys split up and the young move away (Jenkins et al. 1963). In my study mortality to predators was associated with periods of territorial activity and dispersal, but the

FIGURE 7.1 Differences in the number of grouse lost overwinter through shooting, dispersal and mortality (August to March incl.) between Speyside ($Y=0.8X-9.1$, $r=0.99$, $p<0.0001$) and north England ($Y=0.77X-34.2$, $r=0.97$, $p<0.0001$). Dotted line represents Speyside losses minus the number of kills found ($Y=0.67X-16.2$, $r=0.94$, $p<0.001$).


Speyside
England
100
50
0
-50
No. lost overwinter
50
100
150
200
Autumn density

finding that few young birds were killed suggests that it was not only the dispersing birds that died. To return to management procedures, this indicates that any one estate could, through the control of predators decrease the number of birds lost. However, the estate would be unable to prevent losses from dispersal into neighbouring areas, so control would have to be over a large enough area to prevent net emigration. This agrees with Hudson's (1986a) finding that isolated moors were less productive than those surrounded by keepered areas. This is unlikely to be solely due to dispersal from the moor, but also to the movement of predators into the estate. The finding that fences killed large numbers of young birds suggests that the prevention of fence deaths (by making the fences more visible to the grouse) may have less effect on the following breeding population, as they may have been dispersing birds. However, mortality from fences occurred in mid-winter when dispersal is thought to be slight, so radio-telemetry work is necessary to determine the movement of such individuals.

As stated earlier, the high overwinter losses observed in this study were not sufficient to depress the populations, which increased due to high breeding success, thereby providing individuals for the lowest density areas. Any factor that can influence breeding success will therefore play a vital role in grouse population dynamics.

There is general agreement amongst grouse biologists that moorland should be managed to maximise breeding success (Watson & Miller 1971, Hudson 1986a). Such management includes the established methods of heather burning, the control of foxes and crows and more recently, the control of the parasite T. tenuis. In addition to these, gamekeepers have also been illegally killing the raptors which feed on grouse chicks, most notably the hen harrier. Data collected in this study and other similar ones suggest that harriers exhibit a type II functional response to grouse density. This in addition to observations of hunting birds, indicated that grouse were their preferred prey and constituted a disproportionately greater percentage of the prey at low and medium density. Quite why harriers do not eat more grouse at high density is unclear, though the relationship between grouse at high density and harrier diet was based on just one point, where grouse breeding prior to predation was poor. Further research is necessary to clarify the impact of grouse brood size on harrier diet.

Grouse density is not the only factor which influences the number of chicks killed by harriers. In many studies the role of alternative prey have been shown to have an influence on the survival of the main prey (Angelstam et al. 1984, 1985, Marcstrom et al. 1988). For example, Marcstrom et al. showed that grouse breeding success increased when voles were at high density. However, alternative prey may also have the effect of increasing the number of predators (especially more mobile avian predators) thereby increasing predation on the main prey (Kenward 1986). This is another area that needs further investigation, to see whether harriers respond numerically to prey density, either through increased density (Hamerstrom 1979) or increasing their brood size (Barnard et al. 1986), and whether harriers would increase their predation levels on grouse chicks.

Much individual variation in harrier diet has been noted, both in this study and others, and it is important to understand what influences these changes. Why does one pair of harriers, nesting <1km. from another pair, take twice as many grouse chicks? This is an important issue, for it could mean the difference between a drastic reduction in grouse density and a situation where harriers have little impact.

Although there are several factors that need further clarification, it is possible to infer, from the data already obtained, the potential impact of harriers on grouse populations. In this study harriers were estimated to have reduced grouse breeding success by up to 32% in eight weeks. Such a loss is only important if it reduces the number of grouse shot, either directly in that year, or indirectly through decreasing breeding density in subsequent years.

At any one grouse density there was a high degree of variation in the number of birds shot, making it difficult to determine the effect of harriers on the bag. However, above harrier densities of 0.12 (one pair every 8 km^2) it is likely that their impact will become more noticeable. The fact that there is much less variation in overwinter losses indicates that shooting mortality is at least partially compensated for, as suggested by Hudson (1985). It is important to find out how this compensation operates and where the threshold density lies between compensatory and additive losses, as this will determine whether moors with harriers could shoot their grouse populations harder to compensate for losses.

The issue of whether harriers can reduce subsequent breeding density is more complicated. Both hypotheses concerning population dynamics suggest that at low density in particular, poor breeding can reduce the subsequent spring population, although they propose different proximate factors behind this decrease. If harriers reduce breeding success over a large area, such that the grouse losses outweigh the gains, then the populations will be unable to increase. The threshold density for breeding success beyond which the population will decline will depend upon the level of overwinter losses. If overwinter losses are high then grouse have to produce more young in order to maintain or increase their density. However, if losses are low, populations could increase with lower breeding success. The impact of harriers will therefore depend on the number of chicks they take relative to grouse breeding success prior to predation, and the degree of overwinter predation and dispersal.

As discussed in chapter 1, extrinsic factors are thought to be important in determining population change at low density. At high density there is controversy over their importance relative to intrinsic factors. The grouse-predator relationships described in this study (ie. the inverse density dependence of overwinter losses and the type II functional response of harriers) indicate that predation will be less important at high density, where parasitism and spacing behaviour become significant and predators take the more vulnerable diseased birds (Hudson 1986a) or 'surplus birds' (Jenkins et al. 1964). An important issue is whether predators can suppress a population at low density. This will depend on breeding success relative to overall losses. If breeding success is high (as observed in this study) then predators would, unless at very high density, be unable to prevent a rise in density, though their removal would amplify the rate of increase. For cyclic populations, this would mean that low densities would be extended in the presence of predators, thereby lengthening the fluctuations.

If harriers increased up to levels seen in Orkney (0.66 km^{-2}) then they would undoubtedly have a severe impact on grouse populations. However, whether or not this would occur remains to be seen. Such questions are hard to answer due to the difficulties of finding an estate where harriers are left to breed freely for a number of years. Such an estate would be necessary to discover the numerical response of harriers to grouse, a relationship which needs to be known if the long term impact of harriers on grouse populations can be determined.

Are gamekeepers justified in illegally persecuting birds of prey? This is a difficult question to answer because, as Newton (1979) mentions, it: "..depends on what value you place on these birds in the environment." However, from the available evidence a tentative answer can be found for the question of whether the killing of raptors increases the number of grouse available for an estate.

Predation by raptors can be considered in two parts: overwinter, when the peregrine takes adult grouse (the impact of harriers and eagles being negligible), and the summer when the harrier kills chicks. At high grouse densities it is unlikely that raptors will have any real impact on populations, although they can be expected to have a small effect on the number shot in autumn. It is when grouse are at low density that problems may arise. In such situations, the role of the peregrine is related to whether there is a surplus of non-breeding grouse available (an issue which is currently being investigated by the Game Conservancy, see Hudson & Renton 1988). Overwinter, peregrines may be harder to control as persecuted birds tend to be quickly replaced (Ratcliffe 1980). This suggests that even if peregrines do take potential breeding grouse, keepers should concentrate on fox control throughout the winter, in combination with decreasing mortality through fences, though other ways of alleviating peregrine predation at low densities, such as providing alternative prey, should be examined.

One problem which the control of foxes could create would be a compensatory increase in predation by raptors. Such compensation has been shown to occur with egg predators by Parker (1984). He removed crows from an island in Norway, in an attempt to increase the breeding success in willow and black grouse. This was unsuccessful, however, as there was an increase in predation by mustelids. Whether peregrines would kill more grouse in the absence of foxes remains to be seen.

Hen harriers may present a more serious problem for low density grouse populations. Whilst all estates should be able to support low numbers of harriers without any detrimental effect, at high numbers they could potentially prevent a grouse population from increasing, especially in combination with high overwinter losses. In such situations, the control of harrier predation could probably increase the number of grouse on an estate.

A subsequent question to the effect of harriers on grouse numbers is whether the increase in grouse outweighs the loss of harriers. The harrier is a schedule 1 bird and every effort must be made to maintain a viable population. However, if harriers can limit grouse numbers, then their protection could indirectly lead to further afforestation which in turn could reduce their populations. At present the persecution of harriers appears to be limiting their distribution, but a greater threat comes from the loss of habitat to forestry.

Heather moorland is an internationally important habitat (see Usher & Thompson 1988) and is largely maintained by managers of red grouse populations. On moors where grouse are economically important anything that threatens their viability may, in the present financial climate, lead to further afforestation which could have important consequences for raptor populations, many of which are susceptible to such a change in the environment (Thompson et al. 1988). As Newton (1979) points out: "The only permanent way to reduce a birds population is to reduce its habitat and food supply." The prime aim of conservationists should therefore be to protect the heather moorland.

Ironically, although persecution by keepers is at present a lesser threat, as plantations develop, the remaining grouse moorland will become progressively more important to many species. The continued persecution of harriers by game keepers on these areas may become an increasingly significant mortality factor for harrier populations.

It is hoped that a sensible conservation plan can be formulated for the uplands, which takes into account both the needs of raptors and grouse, by concentrating on the protection of the heather moorland.

Further Studies

This research has outlined the basic pattern of predation on red grouse populations in Speyside. If we are to accurately determine the impact of these predators then further research is necessary to uncover the following:

1. Variation in the bag. Grouse density can only account for 29% of the bag, if the source of much of the remaining variation can be found then it may be possible to develop a harvesting model to see whether harrier predation can be compensated for.

2. Overwinter losses. Evidence of surplus grouse overwinter is necessary to determine whether mortality is compensatory or additive, especially at low density. A related issue is that of determining the extent of dispersal and its selectivity in terms of age and sex. Such research is currently being undertaken by Hudson in Speyside and north England. Also, it would be useful to discover why raptors are inversely related to density overwinter and whether this is a general or site specific trend.

3. Harrier predation. The effects of grouse brood size, alternative prey and the factors influencing individual variation on harrier predation require further investigation. In addition, it is important to discover the numerical response of harriers. The most useful way of determining these relationships would be to carry out a study of several pairs of harriers on one large estate over a number of years, if such an estate could be found.

Such research, in combination with studies already performed would help provide a more detailed picture of the effects of harrier and other predators on red grouse populations, which could be used in a long term management plan for the uplands.

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APPENDIX 1

Dead grouse found on three estates, each containing two study sites of 1km^2. Mortality is divided into number of kills by raptors (R), mammals (M) fences (F) and others (O), for each month. Seasonal kills are listed below.

MONTH	MOOR R				MOOR C				MOOR D				TOTAL
	R	M	F	O	R	M	F	O	R	M	F	O	
1985													
OCT	-	-	-	-	-	-	-	-	2	1	-	-	3
1986													
FEB	1	-	-	-	10	-	-	-	-	-	-	-	11
MAR	1	-	-	-	-	2	-	-	3	5	-	-	11
APR	-	-	-	-	-	-	-	-	11	5	-	-	16
MAY	-	-	-	-	-	-	1	-	4	1	-	-	6
JUN	-	-	-	-	2	-	-	-	2	1	-	-	5
JUL	-	-	-	-	-	-	-	-	-	1	-	-	1
AUG	1	-	-	-	1	-	-	-	1	-	-	-	3
SEP	1	-	-	-	2	-	-	-	3	1	-	-	7
OCT	2	-	-	-	3	1	-	1	1	1	-	-	9
NOV	-	-	-	-	-	1	-	-	3	-	2	-	6
DEC	2	-	-	-	1	-	-	-	1	-	2	-	6
1987													
JAN	-	-	-	-	1	-	4	1	1	-	4.5	-	11.5
FEB	1	-	-	-	1	1	-	-	1	-	4	-	8
MAR	1	1	-	-	2	1	-	1	6	4	0.5	-	16.5
APR	1	-	-	-	1	1	-	-	2	3	-	-	8
MAY	-	-	-	-	1	-	-	1	-	1	-	-	3
JUN	-	-	-	-	1	-	-	-	1	-	-	-	2
JUL	-	-	-	-	-	1	-	-	-	2	-	-	3
AUG	-	-	-	-	2	-	-	-	-	1	-	1	4
SEP	-	-	-	-	3	-	-	-	-	2	0.5	-	5.5
OCT	1	-	-	-	-	1	-	-	3	-	1	-	6
NOV	1	-	-	-	2	-	-	-	2	-	-	-	5
DEC	1	1	1	-	-	-	-	-	-	-	-	-	3

	MOOR R				MOOR C				MOOR D				TOTAL
	R	M	F	O	R	M	F	O	R	M	F	O	
1988													
JAN	-	1	-	-	-	2	-	-	-	-	0.5	-	3.5
FEB	-	-	-	-	2	-	-	-	1	4	3.5	-	10.5
MAR	1	2	-	-	2	3	1	-	1	3	3	-	16
APR	3	-	1	-	1	-	-	-	2	1	0.5	-	8.5
MAY	1	-	-	-	1	-	-	-	-	2	0.5	-	4.5
JUN	-	-	-	-	-	-	-	-	-	-	-	-	0
JUL	-	-	-	-	-	-	0.5	-	-	-	0.5	-	1
85/86 WINTER	-	-	-	-	3	1	-	-	5	5	-	-	14
1986 SPRING	-	-	-	-	-	-	-	-	1	4	-	-	5
1986 SUMMER	-	-	-	-	1	-	-	-	-	-	-	-	1
86/87 WINTER	5	2	0.5	-	4	2	-	-	1	4	4	1	23.5
1987 SPRING	-	-	-	-	-	1	-	-	-	-	-	-	1
1987 UNKNOWN	-	-	-	-	-	-	1	-	-	-	-	-	1
87/88 WINTER	4	3	1	-	3	-	-	-	2	4	4	1	22
1988 UNKNOWN	-	-	-	-	1	-	-	-	-	-	-	-	1
TOT	28	10	3.5	-	51	18	7.5	4	60	56	31	3	272

APPENDIX 2

GROUSE POPULATION MODEL. Here the basic outline of the model and the main procedures are given. Input, output and graphical details of the model are omitted. The variables displayed in Fig. 6.1 are shown to the right in parentheses.

BASIC OUTLINE

```
10   REM GROUSE - HARRIER MODEL
20
30   VDU 19,0,4,0,0,0
40   PROCvariables
50   PROCinput
60   FOR N = 1 TO GEN
70     PROCbrood size
80     PROCchick losses
90     PROCharrier losses
100    PROCsummer adult losses
110    PROCbag losses
120    PROCoverwinter losses
130  NEXT N
140  IF N = GEN THEN END
150  PROCoutput
```

PROCvariables

```
700  DEF PROCvariables
710   CLUTCH = 8.03                                      (VARIABLE 2)
720   HATCH = 0.85                                       (VARIABLE 3)
730   CHICKSURV = 0.56                                   (VARIABLE 4)
740  ENDPROC
```

APPENDIX 2 - continued

PROCbrood size

```
2000 DEF PROCbrood size
2010  SEXRATIO = 1.981 - (0.461 * LOG (SPRING GR))     (VARIABLE 1)
2020  BREEDFEM = SPRING GR / (1 + SEXRATIO)
2030  EGGS = BREEDFEM * CLUTCH
2040  MAY YOUNG = EGGS * HATCH
2050 ENDPROC
```

PROCchick losses

```
2100 DEF PROCchick losses
2110  JUNY YOUNG = MAY YOUNG * CHICKSURV
2120 ENDPROC
```

PROCharrier losses

```
2200 DEF PROCharrier losses
2210  PROPDIET = (34.07 - (35.42 / BREEDFEM)) / 100    (VARIABLE 5)
2220  RATE = 0.45 + (0.013 * BREEFEM)                  (VARIABLE 6)
2230  GRPREY = RATE * PROPDIET * 8 * 7 * 15
2240  GROUSE TO HARRIER = GRPREY * DENSITY
2250  POST HARRIER = JUNE YOUNG - GROUSE TO HARRIER
2260 ENDPROC
```

APPENDIX 2 - continued

PROCsummer adult losses

```
2300 DEF PROCsummer adult losses
2310  JULY AD = SPRING GR * 0.81
2320  PRE SHOOTAD = JULY AD + POSTHARR
2330 ENDPROC
```

PROCbag losses

```
2400 DEF PROCbag losses
2410  BAG = PRE SHOOTAD * 0.43                        (VARIABLE 8)
2420 ENDPROC
```

PROCoverwinter losses

```
2500 DEF PROCoverwinter losses
2510  WINTERLOSSES = (PRE SHOOTAD * 0.73) - 18.8
2520  SPRING GR = PRE SHOOTAD - WINTERLOSSES
2530 ENDPROC
```