Meyburg, B.-U. & R. D. Chancellor eds. 1989
Raptors in the Modern World
WWGBP: Berlin, London & Paris

Factors Limiting European Kestrel *Falco tinnunculus* Numbers in Different Habitats

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ABSTRACT

The factors limiting European Kestrel numbers in winter and summer were investigated during 1975-79 in South Scotland and during 1981-86 in two English farmland areas.

Differences in numbers within and between winters were largely related to food supply, though migration out of the Scottish area complicated the seasonal relationship between Kestrel and vole numbers. Winter density in English farmland seeemed to be mainly determined by the numbers that settled in autumn, and could have fallen below the food resource-level in late winter.

Breeding density was also limited mainly by the food supply. In the better vole area (Scotland), Kestrels held larger territories in a poor vole year than good ones, and this reduced the availability of nest-sites to other Kestrel pairs. In farmland, however, nest-sites were not in short supply, and food supply had a more direct effect on Kestrel breeding numbers, probably by limiting the number of males that were able to catch enough food to feed a mate.

INTRODUCTION

Raptor populations, like any others, may be limited either by a scarcity of resources (such as food, nest-sites or mates) or because numbers are held below the resource levels by excessive mortality or poor productivity. In the absence of human intervention, the factors limiting most raptor populations are, in winter, food supply and, in summer, food supply or nest-sites, whichever is scarcest (Newton 1979). At any given moment a population will usually be held in check by a single factor, and will, by definition, increase if that 'key' limiting factor is removed. Theoretically, the increase should continue until the population reaches the new limit set by the same, or another, factor. This does not mean that population size will correlate with only one factor, as some factors may be 'proximate' and merely mediate the effects of other 'ultimate' limiting factors. An example might be territorial behaviour, which could act proximately to regulate a population that is ultimately limited by food supply.

This paper examines the various factors that limit European Kestrel (*Falco tinnunculus*) numbers in three different localities where Kestrels were relatively free from the effects of pesticides or persecution. Kestrels are fairly common and have adapted well to man-made environments. They feed mainly on small mammals, especially microtine voles, but will also take a variety of other prey, including small birds, insects and earthworms (Village 1982a).

Data from the first study, on rough grassland in Scotland during 1975-79, have been published elsewhere (Village 1982a & b, 1983, 1985, 1986 and references therein). Since 1980, I have worked in England in two separate farmland areas. Although this latter study is not yet completed, the results analysed so far are summarised here. The aim is to identify the ultimate limiting factor in each area and to examine how any proximate factors interact to regulate Kestrel numbers.

STUDY AREAS

The grassland study area was some 100km^2 of young conifer plantation at Eskdalemuir in the southern uplands of Scotland (55 19' N 3 14' W, altitude 200-500m). Most of the trees were less than five years old and the predominant habitat was dense grassland, highly suited to Short-tailed Voles (*Microtus agrestis*). Kestrels nested mainly in old Crow (*Corvus corone*) nests, which were in the few mature trees present. The latter were mainly conifers planted in small shelter belts ($<$ 2 ha) along the valleys or, less often, on the hillsides. Winters were fairly harsh, with a mean January temperature (1975-86) of 1.2°C and an average of 14 days of snow cover in January (Meteorological Office).

The two farmland areas, some 330km to the south-east, differed in character, despite being only 25km apart. The mixed farmland area covered 108km^2 in Rutland (52 37'N 0 37'W, altitude 30-100m). The main crops were wheat and barley, with small patches of grass ley and permanent pasture in the valley bottoms. Kestrels nested mainly in holes in deciduous trees, the latter occurring in small woods or scattered among the numerous hedgerows. The arable area was intensively cropped farmland near Ramsey in Cambridgeshire (52 29'N 0 7'W, altitude 0-10m). It initially covered about 80km^2, but was enlarged to 250km^2 by 1984 in order to increase the sample of nests. The main crops were wheat and roots, such as sugar beet, potatoes and carrots. Kestrels nested mainly in tree-holes, though there were few trees, so other sites, such as buildings or straw-stacks, were also used. In both farmland areas, rough grass was confined to small patches or strips along hedgerows, ditches and roads. For much of the year the crops provided no cover for small-mammals, which were able to exploit crops only for a few weeks prior to harvest. Winters were milder than in Scotland, with a mean January temperature of 2.9°C and snow cover for five days in January, on average.

METHODS

Limiting factors were investigated by correlation analysis and, where possible, by testing with field experiments. It was difficult to alter food supply experimentally on a scale large enough to affect Kestrel population density, so I relied on correlations between small-mammal numbers, Kestrel diet and Kestrel numbers. The methods used in Scotland are described in greater detail elsewhere (Village 1982a, 1982b, 1986).

Small-mammal numbers

Unbaited snap-traps were set in vole runs at 17 sites in the grassland area and 6-9 sites in each of the farmland areas. Traps were set in 24 random positions for five successive nights in Scotland, whereas in England they were set in three rows of ten traps for two nights. In Scotland, voles were trapped twice a year, in April and October (during the seasonal low and high respectively), but in England traps were also set in July and January. Indices of abundance were not comparable between areas, though vole habitat was more extensive in the grassland than in the farmland areas.

Kestrel numbers in winter

Roadside counts from vehicles were used in all three areas. In Scotland counts were made throughout the year with no regular routes (Village 1982b). In England I drove an 80km route in each area up to three times a month from September to May each year 1980-85. To compare results between areas, it was necessary to convert the index of numbers into actual population densities. This was possible for those periods when I could accurately estimate the number of Kestrels in a given area using other means such as wing-tagging and radio-telemetry. Roadside counts were significantly correlated with actual densities in grassland ($r=0.94$ $df=7$, $P < 0.001$) and mixed farmland (r=0.63 df=12, P < 0.02), though less well in arable farmland where I had fewer accurate estimates (r=0.52 df=7, P < 0.15). The regressions were, nonetheless, sufficient to show that low counts in mixed farmland were largely due to poor visibility and that the actual winter densities were similar in the two farmland areas.

Experimental techniques

Three types of experiment were used to investigate the role of nest-sites and territorial behaviour in limiting density. *Removal experiments* involved trapping and removing one member of a pair, after 1 May, when all pairs had established themselves on their territories and were starting to breed. Replacement of the removed birds indicated the presence of non-breeders in the area that were unable to breed due to lack of a nest-site, suitable territory or partner (or any combination of these). Winter experiments involved removing a territorial individual after marking all its neighbours and finding their range boundaries. Replacement by new birds, settling on the vacated territory, would suggest that territorial behaviour limited density by preventing others from settling. Removed birds were released when any replacements had been caught and marked, or after two weeks if none was present.

Late-nest experiments in the breeding season tested specifically whether non-breeders were unable to breed for lack of a nest (rather than lack of a partner or territory). Nestboxes, or artificial stick-nests, were erected away from existing Kestrel nests (and therefore outside any defended areas) during the same period as removal experiments. A third experiment entailed the *provision of extra nest-sites* early in the season, to see if shortage of nest-sites prevented Kestrels from breeding in certain areas. Care was taken to monitor adjacent control areas to ensure that any increase in density in the experimental area was not caused solely by birds moving into artificial sites from inferior natural ones.

RESULTS

Small-mammal abundance

Species differed in relative abundance between areas. In grassland, Microtus was by far the most numerous species, followed by the Common Shrew (*Sorex araneus*), with Bank Vole (*Clethrionomys glareolus*) and Woodmouse (*Apodemus sylvaticus*) absent altogether. All four species were caught in mixed farmland where Short-tailed Voles were always more frequent than either Bank Voles or Woodmice. This was not always so in arable farmland, however, where Woodmice were sometimes more abundant than voles in October and January (Table 1). The seasonal decline in Woodmice from autumn to spring was steeper than in voles, so the latter were the most abundant small-mammals in both farmland areas in spring.

Table 1. Occurrence of Woodmice in Kestrel diets (% of pellets containing mouse remains) and traps (% of total vole and mouse captures) in mixed and arable farmland, 1980-85.

		Arable				Mixed			
		%Pellets	n	%Traps	n	%Pellets	n	% Traps	n
1981	Winter	-	0	-	0	8	90	0	42
	Spring	21	28	0	94	2	60	0	107
	Autumn	19	37	27	115	8	69	4	68
1982	Winter	18	45	3	39	10	93	0	41
	Spring	13	52	8	24	3	78	0	22
	Autumn	35	46	57	72	12	50	8	72
1983	Winter	35	110	46	35	6	144	15	54
	Spring	33	49	33	6	5	55	7	30
	Autumn	51	65	30	43	20	60	9	137
1984	Winter	46	160	60	67	7	165	4	48
	Spring	12	65	0	10	2	65	0	34
	Autumn	48	62	31	85	18	85	8	119
1985	Winter	35	165	11	36	11	166	19	31
	Spring	10	125	0	11	4	111	5	19

Kestrel diet

Microtus was the main prey in grassland, occurring in at least 80% of pellets, even in the poor vole year of 1977 (Village 1982a). Other items were important when voles were scarce (e.g. shrews), or at times of seasonal abundance (e.g. birds in summer and earthworms in spring). Kestrels in farmland were also dependent on voles, though other items were much more frequently found in pellets there than in grassland. Birds, for example, were again more often taken in summer, but they also occurred in 30-70% of pellets in winter, compared with less than 10% in grassland. The greater variability of Kestrel diets in farmland was reflected in the proportion of pellets that contained solely vole remains (Fig. 1). The proportion was low in all years in farmland because items other than voles were taken so frequently, whereas in grassland nearly half the pellets had only vole remains in some years.

The main difference between the two farmland areas was the greater frequency of pellets containing Woodmice in the arable area. This was especially so in autumn, when mice were also most abundant in trap samples (Table 1).

Kestrel populations in winter

In the grassland area in Scotland, Kestrel numbers declined from October to January and increased thereafter until May (Village 1982b). This contrasted with the English farmland areas, where numbers declined slowly from October to May and were therefore higher than in grassland in mid-winter (Fig. 2). Kestrels in grassland were partial migrants, most of the breeding population leaving in autumn and all paired birds separating between breeding seasons (Village 1985). In English farmland, however, I had no evidence of regular summer migrants, and some pairs remained together on the same territory throughout the year. A few marked Kestrels that occupied the same winter territory in successive years were not present in the intervening summer, and these were probably winter migrants.

Figure 1. Proportions of pellets containing solely vole remains in grassland (▲), 1976-79, and farmland (●), 1980-85. Farmland data were for mixed and arable areas combined. Each point refers to at least 100 pellets collected in two-monthly periods. The decline in the proportion of solely vole pellets in grassland coincided with the poor vole year of 1976/77, when other prey were taken more frequently.

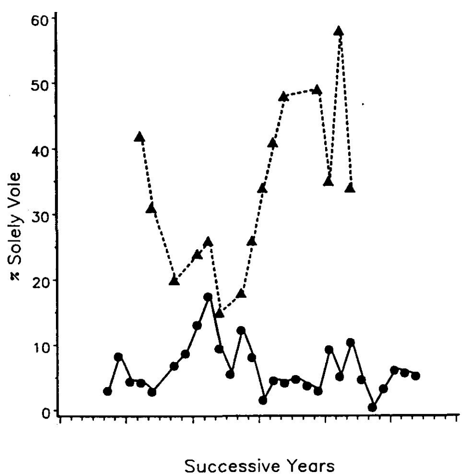


Figure 2. Mean Kestrel densities in winter in grassland (■), 1975-77 and mixed (▲) and arable (●) farmland, 1980-85. Standard errors (vertical bars) were similar in size between the two farmland areas, so they are not given for mixed farmland to avoid confusion.

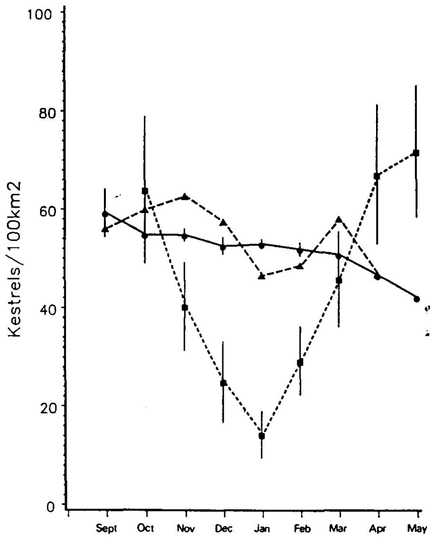
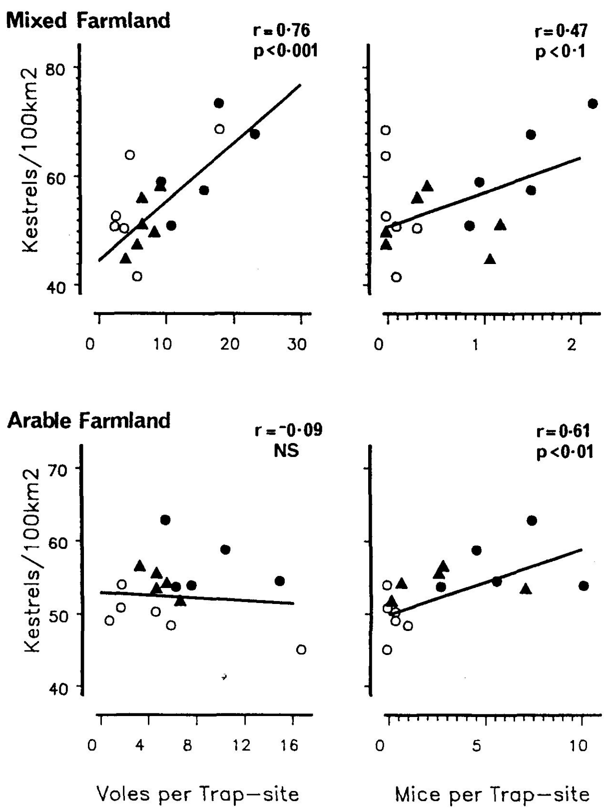


Figure 3. Relationships between Kestrel densities and vole or Woodmouse numbers in mixed and arable farmland. The apparent trend between Kestrel density and mice numbers in mixed farmland disappeared when the covariation of voles and mice was allowed for by partial correlation. ● = autumn; ▲ = winter; ○ = spring.



The decline in numbers from October to January in grassland was expected from the seasonal decline in voles, and there was a significant correlation between vole and Kestrel numbers in autumn and winter of three successive years (Village 1982b). The increase in Kestrel numbers from February to April was not, however, related to any increase in voles, as the latter continued to decline until they started breeding in April or May. The immigration of Kestrels prior to breeding meant that Kestrel densities in spring were similar to those in autumn, even though voles were less abundant. In spring, Kestrel numbers and territory-size were nonetheless correlated with vole numbers between years (Village 1982b, 1983), so voles were still important in affecting Kestrel densities at that time of year.

In the farmland areas, the decline in numbers from autumn to spring followed that of the main prey in each case. Thus Kestrel numbers were better correlated with vole than mouse numbers in mixed farmland, and the reverse was true in arable farmland (Fig. 3). These trends generally held within seasons in both areas in autumn and winter, but not in spring, when there were few voles or mice in either area.

The age composition of the winter population also differed between areas, with a higher proportion of adult males in grassland than in the two farmland areas (Table 2). The majority of 'brown' (i.e. non-adult male) Kestrels were juvenile males in mixed farmland and juveniles of both sexes in arable farmland.

Table 2. Age and sex of Kestrels trapped during October-March in each study area.

AREA	Total captures	%First-year males	%Adult males	%First-year females	%Adult females
Grassland	54	24	35	22	19
Mixed farmland	100	37	28	17	18
Arable farmland	80	29	18	34	20

Winter removal experiments

In the grassland areas, Kestrels expanded their territories into areas vacated by their neighbours that died or moved away in winter (Village 1982b). The expansions were sudden and often within a day or two of the neighbour disappearing, so it appeared that territory size was determined by density and not vice versa.

To see if this was so in farmland, I removed ten Kestrels from their territories in mixed farmland in autumn and winter of 1983 and 1984. Ideally this should have been done in the post-breeding settling period (September), but it was necessary to have full knowledge of all neighbouring ranges before removing a bird and this was not possible until October, when the range system had stabilised. Only three of the ten removed birds were replaced, and none of the incomers stayed more than a few days. Two of the three replacements were trapped and radio-tagged. One moved to a new territory 7km away after three days and was there until it died two years later. The other moved after ten days and was found dead some 13km away within a few days. Four of the vacated ranges were used occasionally by neighbours that expanded their ranges, though none was seen to defend the newly-acquired area. I was able to release seven of the ten birds later in the same winter, and all but one remained on their original territories.

Breeding density and performance

The density of breeding pairs was highest in grassland, intermediate in mixed farmland and lowest in arable farmland (Table 3). Breeding density was correlated with vole numbers in grassland, Kestrel nests being closer together, on average, in good vole years than in poor ones (Village 1983). There was no strong correlation between breeding density and vole numbers in either farmland area, though in mixed farmland the highest Kestrel numbers were in the year with highest spring vole numbers (Table 3).

Table 3. **Breeding density, mean laying date and vole numbers in each study area by year. The vole index was not directly comparable between grassland and farmland.**

Area	Year	Pairs per $200km^2$: Territorial	Breeding	Mean laying date (SE days)		Voles per trap-site
Grassland	1976	30	22	28 April	(1.9)	13.6
	77	28	27	11 May	(1.9)	5.8
	78	38	37	28 April	(1.6)	16.1
	79	36	36	1 May	(1.6)	20.1
	Overall	33	31	2 May		
Mixed farmland	1981	29	27	13 May	(2.0)	17.8
	82	22	19	17 May	(1.8)	2.8
	83	28	23	12 May	(1.0)	4.0
	84	21	20	11 May	(2.2)	4.9
	85	17	13	13 May	(2.7)	2.6
	86	9	9	16 May	(2.6)	5.9
	Overall	21	19	13 May	(0.8)	
Arable farmland	1981	12	11	4 May	(8.4)	15.7
	82	12	12	17 May	(2.7)	4.4
	83	22	19	14 May	(1.7)	0.8
	84	14	13	7 May	(2.0)	1.7
	85	15	11	12 May	(3.0)	1.8
	86	13	12	12 May	(1.9)	5.6
	Overall	12	13	11 May	(1.1)	

In all years, and in all areas, there was a surplus of unoccupied nest-sites. In grassland, vacant sites were usually other old Crow nests in the same woods as nests already occupied by Kestrels. Over 80% of unused sites were within 0.5km of occupied Kestrel nests, and therefore likely to be within the defended territory of the occupying pair. In farmland, however, nest-sites were more evenly spaced, and a good proportion was further from occupied sites than the mean separation of pairs; they were therefore likely to have been outside defended Kestrel territories (Table 4).

Table 4. **Spacing and occupancy of Kestrel nest-sites in each study area. An unoccupied site was considered to be outside a territory if it was more than the mean nearest-neighbour distance (NND) + 2S.E. from an occupied Kestrel nest.**

	Mean number of usable sites/year	Mean % not occupied	Mean (SE) NND of occupied sites (km)	% Unoccupied sites outside territories
Grassland (1976-79)	70	51	0.7 (0.09)	2
Mixed farmland (1981-86)	87	72	1.4 (0.06)	10
Arable farmland (1981-86)	57	59	1.6 (0.09)	20

The distribution of nest-sites suggested that they may have been in short supply in grassland but not in farmland. This was supported by the results of experiments in the breeding season:
i) *Provision of extra nests:* Nest-sites erected in winter 1977-78 in previously vacant areas of grassland were occupied in 1978 and 1979, and this increased local density over the previous level and

compared with control areas (Village 1983). Nestboxes were erected in 7x7km sections of each farmland area in early 1985, but these have so far failed to increase breeding density compared with the rest of the study areas. This implies that nest-sites were limiting in grassland but not in farmland.

ii) *Breeding season removals:* Removals in grassland showed that both males and females were replaced and bred successfully (Village 1983). Eleven females and ten males were removed from farmland sites during 1984-86. Females were more likely than males to be replaced (7 vs 3), more likely to breed (7 vs 2) and to rear young (6 vs 0), though only in the last two cases was the difference between the sexes statistically significant.

iii) *Late nest experiments:* In the grassland area, 82% of late nest-sites were occupied in 1978, suggesting that substantial numbers of non-breeders were present which were unable to breed for lack of a nest (Village 1983). Every year during 1983-86, about 25 late sites were made available in each farmland area, but none was ever occupied.

Breeding performance: Mean laying date was used as a measure of breeding performance because it proved to be a good indication, within years, of clutch size or the likelihood of fledging young (Village 1986). It was also an indicator of food supply as evidenced by the earlier laying of wild Kestrels given extra food (Dijkstra *et al.* 1982). Mean laying date in grassland was some two weeks later in the poor vole year of 1977 than in other years (Village 1986). Laying dates in all years in farmland were as late, or later than, those in the poor vole year in grassland (Table 3). Average annual production of young in farmland was 1.9 young per territorial pair compared with 2.3 in grassland.

DISCUSSION

Winter density

The upland grassland in the north was characterised by large areas of good vole habitat but fairly severe winters. Kestrels were heavily dependent on voles, especially in mid-winter when there was little alternative prey (Village 1982a). Winter food supply would therefore have varied because of: (a) year to year differences due to the cycle of vole numbers, (b) the seasonal decline in vole numbers and (c) variation in weather, especially snow cover, during and between winters. Most breeding birds left the area by October, and newcomers (mainly juveniles) settled from July to September. It was the loss of these newcomers that caused the decline in numbers in early winter. The decline was about 80%, on average, which was more than could be easily explained by mortality and was probably due largely to birds leaving the area. It was not clear if birds left as a direct result of declining food supply, or if they anticipated such a decline and left before the weather deteriorated enough to reduce food supply. Mid-winter population levels were apparently lower than the area could sustain during mild weather, because Kestrels were able to immigrate into the area in February and March, before vole numbers had increased. An alternative explanation is that food supply increased in late winter, despite the declining vole numbers, because other factors such as low ground cover, changes in vole behaviour or increasing daylength improved the availability of voles to Kestrels.

The farmland areas, in contrast, had little vole habitat, had a wider variety of other prey and were less likely to have snow cover in winter. The steady decline in Kestrel numbers from autumn to spring mirrored the seasonal decline in voles and mice. Mice were able to colonise root crops in autumn, and their marked decline probably reflected the loss of habitat as crops were harvested. The large proportion of juvenile Kestrels in arable farmland in winter suggested that part of the population consisted of immigrants concentrating in areas of temporary food abundance caused by the high *Apodemus* numbers. The over-winter decline of Kestrel numbers in farmland areas was about 30% on average, which was roughly what might be expected from mortality alone, though recoveries of birds which had moved elsewhere showed that some emigration was involved.

The winter removal experiments were not conclusive proof that territorial behaviour limited numbers in late autumn in farmland. It seemed that there were few transients available to fill any gaps after mid-October, and those that did settle were unable, or unwilling, to remain. The fact that the original occupants would survive there when released showed that the territories were still usable. The results further indicated that, as in grassland, winter numbers may have been at levels lower than the food supply could support, because any losses that were not directly or indirectly due to food shortage would not necessarily be made up by immigration. Winter density may be adjusted to food supply in autumn, but any correlations thereafter may arise because neither vole nor Kestrel populations can increase (due to low immigration), and both are likely to decline because some mortality is inevitable. More work is needed in early autumn to determine the role of territorial behaviour in limiting winter numbers.

Breeding density

The Kestrel population in summer consisted of both paired, territorial birds ('breeders') and unpaired birds which may or may not have defended territories ('non-breeders'). Breeding density is therefore determined partly by whichever factors affect the proportion of the summer poupulation that is able to breed. Male Kestrels fed their partners for several weeks prior to egg-laying, so their effectiveness in getting food would largely have determined whether they could keep a mate.

During early spring (March-April), Kestrels in all areas were largely dependent on voles to provide sufficient food to breed. The higher breeding density and generally earlier laying dates in grassland, compared with farmland, were in line with the greater amount of vole habitat in that area. In Scotland, low vole densities were associated with large Kestrel territories, low nesting density and late egg-laying (Village 1983, 1986). The shortage of nest-sites indicated by the experiments resulted from the territorial behaviour of pairs excluding others from nearby unused sites. Vole numbers may thus have ultimately limited the breeding population, but the effect was mediated by territorial behaviour affecting the availability of nesting sites. In large open areas devoid of trees, lack of nest-sites seemed to be the ultimate limiting factor which held breeding numbers below the limit of the food supply.

In mixed farmland there was some indication that vole numbers may have been related to Kestrel breeding density, but the relationship was weak and not significant in either farmland area. The nest-site experiments ruled out nest availability as a limiting factor and the removal experiments further indicated a shortage of competent breeding males as the most likely proximate factor limiting Kestrel breeding numbers in both farmland areas. This was also true of Sparrowhawks (*Accipiter nisus*) in south Scotland (Newton 1986), but not of Kestrels in the grassland area, nor of American Kestrels (*F. sparverius*) in Quebec, where both sexes were successfully replaced (Bowman & Bird 1986).

This begs the question of what limited the number of breeding males in farmland, and why there was no relationship between Kestrel and vole numbers. This may have been because most crops were unsuitable for voles in spring, and voles were found only in isolated patches of rough grass. Thus even major changes in vole density in these patches would not have had much effect on the numbers of voles in the area as a whole. Changes in the amount of vole habitat may have been more important in affecting Kestrel numbers than variation in vole numbers from year to year. A second reason could have been the low levels of immigration in spring, compared with the grassland area. In farmland, the breeding population was largely drawn from birds already present in the previous autumn, and therefore depended mainly on how many settled in autumn and how many survived the winter. Finally, the greater dependence of Kestrels in farmland on alternative prey to voles may have meant that small-mammal numbers were a poor measure of food supply, and other factors such as small-bird densities or weather were more important.

Food supply was an important limiting factor in both winter and summer in all areas. Although the vole-trapping index gave some indication of Kestrel food supply, other factors besides vole numbers were also important. Thus, although vole densities were probably higher in grassland than in farmland during winter, the risk of snow cover and lack of small birds (which can be caught even when there is deep snow cover) made it a less suitable wintering area for Kestrels than farmland in England. In spring, however, the better vole densities in grassland resulted in a higher breeding population than in farmland, with the availability of nest-sites becoming a proximate limiting factor due to territorial behaviour. In farmland, there was no lack of nest-sites, and the late laying and lack of male replacements implied that food supply was more directly limiting breeding numbers.

ACKNOWLEDGEMENTS

My thanks to the Economic Forestry Group and all the many farmers who allowed me access to their land. Nigel Charles collected and gave me free access to the vole data for Scotland. In England, David Myhill helped with the vole trapping, and he and Nigel Westwood analysed the Kestrel pellets. Ian Newton provided and clarified many ideas, as well as commenting on the manuscript.

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