The ecology of the Kestrel (Falco tinnunculus) in
relation to vole abundance at Eskdalemuir, south Scotland.

by

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DECLARATION

This thesis has been composed by myself. The data presented are my own, apart from the small mammal trapping data, which were provided by Mr. Nigel Charles, and meterological data, which were provided by Eskdalemuir Observatory.

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ABSTRACT.

Kestrels (Falco tinnunculus) were studied in an upland area of young conifer plantation in southern Scotland from 1976 to 1978. Voles were the main prey; other items such as shrews, birds and invertebrates were taken according to their abundance relative to voles. Energy demands on Kestrels were highest in the breeding season and lowest in winter, and this may have explained seasonal changes in body weight and hunting method.

Kestrel numbers within years varied roughly in parallel with vole density, being highest in the breeding season and lowest in winter. There were more yearlings in the breeding population when voles were plentiful than when they were scarce. Home range was measured using observations of wing-tagged birds and by radio-telemetry. Range-size varied with vole density and was smallest when voles were most numerous. Outside the breeding season, ranges were used by individuals and were largely exclusive. During the breeding season, ranges were held by pairs that defended only a 'core area' around the nest, and shared the rest of the range with other pairs.

Kestrels bred mainly in disused crow nests. Breeding

performance and density were better following warm, dry springs than cold, wet ones. Adults had a better average breeding performance than yearlings. Successful breeders were more likely to breed in the study area the following year than were unsuccesful ones. There was no firm evidence that birds preferred certain nesting areas to others, but performance was highest at those that were most often occupied. This was associated with a higher proportion of adults at such nesting areas. Nesting areas used only once were close to, or inbetween, those used in all three years.

Removal and other experiments suggested that nest availability limited breeding numbers 1978. The shortage of disused nests seemed to be caused by the territoriality of some Kestrels preventing other Kestrels occupying otherwise useable nests within the exclusive area of their range.

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CHAPTER 1

INTRODUCTION.

This thesis examines the relationships between a predator, the Kestrel (Falco tinnunculus), and its main prey, the Short-tailed vole (Microtus agrestis), at Eskdalemuir in south Scotland. It is generally accepted that most animal populations are affected by changes in the abundance of their food (for example see Lack 1954, Wynne-Edwards 1962, Watson and Moss 1970). That this is so for Kestrels was demonstrated by the vole plagues which occurred in the southern uplands of Scotland from 1890 to 1892. When these plagues reached their peak, Kestrels (and other vole predators such as Short-eared Owls, Asio flammeus) were extremely numerous and many pairs bred successfully. When vole numbers crashed, however, Kestrel numbers declined and many apparently emaciated and dying birds were found (Adair 1891 and 1893). Analysis of ringing returns has shown that Kestrels also respond to the less extreme variation in vole numbers between years, by breeding in greater numbers, and more successfully, when voles are plentiful than when they are scarce (Snow 1968). The main aim of my study was to examine the ways in which Kestrels are affected by changes in food supply which occur both between and within years, in order to find what factors, if any, limit their numbers.

The Kestrel is a small, diurnal raptor found throughout most of Europe, Asia and Africa (Brown and Amadon 1968). It is the most widespread and numerous raptor in Britain, being absent as a

breeding bird only from Shetland and parts of the Outer Hebrides (Sharrock 1976). Although only slightly different in size, adult males and females can be separated by their plumage. Males have a grey head, rump and tail and a rufous, spotted back, whereas females are brown with dark bars on the back, rump and tail. Juveniles resemble adult females, but in addition have buff tips to their primaries (D. Cook unpubl.). First year males are usually distinguishable from females in the hand, but full adult plumage is not attained until the second year.

Previous studies on Kestrels have concentrated on the breeding season, recording behaviour (Tinbergen 1940, Petersen 1956), population density and performance (Griffiths 1967, Montier 1967, Taylor 1967, Parr 1969, Shrubb 1970 and Riddle 1979 in Britain; Haas 1936, Piechocki 1959, Ortlieb 1963, Cave´ 1968 and Rockenbauch 1968 on the continent). Comparatively little work has been done at other times of year, mostly the analysis of pellets to determine diet (see Chapter 2) and the analysis of ringing data (Schifferli 1964 and 1965, Snow 1968). I examined a number of aspects of Kestrel ecology including diet, energetics and hunting behaviour, population density and turnover, dispersion and breeding performance. I tried to collect data in as many months as possible, though fieldwork was limited in winter because snow often made the study area inaccessible. I did no fieldwork in August or September, partly because the (presumed) high turnover of birds following the breeding season would have made home ranges difficult to determine.

The study started in October 1975 and ended in July 1978.

The Study Area.

This was an area of about 10x10 km to the north of Eskdalemuir village, in the southern uplands of Scotland. It was drained in the north by the Tima Water (a tributary of the River Tweed) and in the south by the White Esk. The altitude varied from about 205 m in the Esk Valley to between 400-540 m along the Tweed-Esk watershed. Until 1965, most of the area was hill farmland, but thereafter it was extensively planted for commercial forestry so that, during the study, over 60% of the area was young conifer plantation. The ground vegetation of both hill farmland and young plantations was predominately grassland, comprising associations of species such as Festuca ovina, F. rubra, Agrostis canina, A. tenuis, Molinia caerulea, Deschampsia cespitosa and D. flexuosa, that are typical of the region (Burnett 1964, McVean and Lockie 1969). As well as these, there were also a few scattered areas of heather (Calluna vulgaris and Erica spp.) and bracken (Pteridium aquilinum). Mature woodland was confined to small planted woods in the valley bottoms and shelter belts on the hillsides. These woods were mainly of spruce (Picea spp.), larch (Larix spp.) or Scots pine (Pinus sylvestris), though a few contained broad-leafed trees such as birch (Betula spp.) or ash (Fraxinus excelsior).

For the purposes of my study, I recognised three main habitat types (see Fig. 1.1 for their distribution in the area):

Figure 1.1 Distribution of habitat types within the study
area at Eskdalemuir.
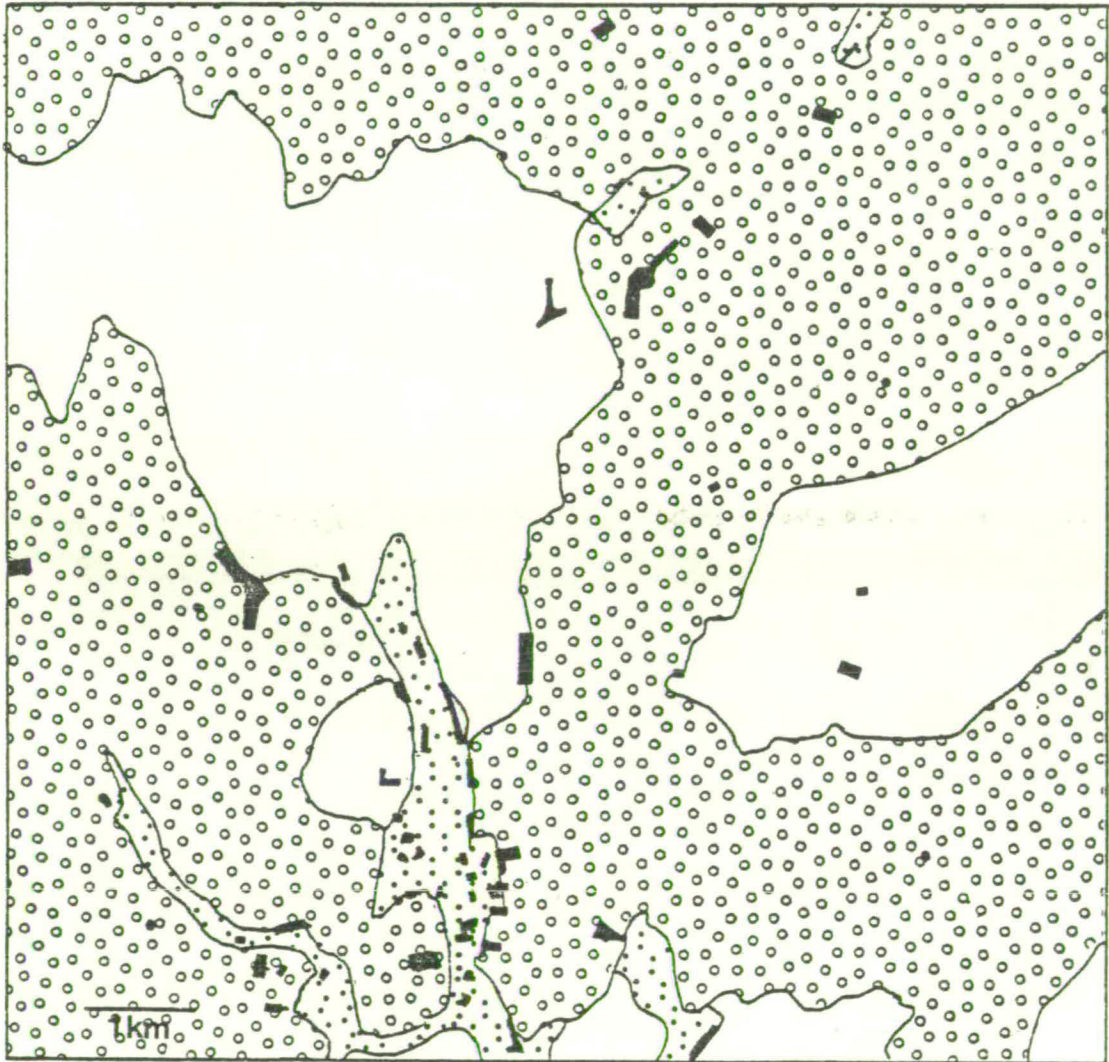
For description of habitat types see text page 5..

▨ = young-plantation, ▭ = sheepwalk, ▣ = farmland.
◼ = older woodland, capable of holding crow nests.

(a) Young-plantation. The majority of the trees planted were Sitka spruce (P. sitchensis), with some Norway spruce (P. abies), larch and pine (Pinus spp.). In nearly all the plantations the canopy had not closed and the ground vegetation provided almost continuous cover for voles.

(b) Sheepwalk. This comprised some 30% of the study area and was permanent rough pasture, grazed by sheep and, in some places, by cattle. Ground cover was more variable than in young-plantation, some areas being more heavily grazed than others.

(c) Farmland. This term was reserved for the more intensively grazed pastures and arable land, which made up less than 5% of the area. Such farmland was confined to the larger valley bottoms and consisted mainly of grass leys with small areas of cereal and root crops.

Marking Individuals.

Many aspects of the study relied on the identification of individuals by ringing, with numbered leg rings issued by the British Trust for Ornithology (BTO), and by marking with coloured patagial (wing) tags. Kestrels were caught either in baited traps such as bal-chatris (Berger and Mueller 1959), or by using an unbaited carpet of nylon nooses placed over dummy eggs on the nest, to catch incubating females. Apart from a few cases, I had no evidence that the trapping methods affected birds adversely, or

caused females to desert their clutches.

Wing tags measured 2x5 cm and were made of flexible nylon cloth ('SAFLAG'), which was available in nine colours (pink, red, orange, light-blue, dark-blue, green, white, black and purple). One tag was attached to each wing using monofilament nylon rod, which was sealed by melting the ends. Birds were identified by their sex (for adults only) and the colour of tags on each wing, which allowed about 100 birds of each sex to be individually marked. The few first-year birds which could not be sexed when trapped were given a tag colour combination that had not been used on either sex before. When no more unique combinations remained, I reused those of Kestrels which had not been seen for 18 months. I assumed such individuals were unlikely to return to the area but, in case this happened, repeat combinations were distinguished by a stripe across each tag.

I avoided using dark tags on both wings as these were hard to see when the bird was flying. Most individuals had at least one bright tag, which could been seen in flight from about 300 m with the aid of binoculars or a telescope. This was often sufficient for identification, and dark tags could be checked when the bird perched. Of 209 Kestrels tagged, 22 (11%) were known to have lost tags and, whenever possible, I retrapped them and replaced their tags (individuals that lost tags could still be identified, in the hand, by their BTO ring number). Judged by retrapped birds, tag loss was generally confined to one wing, and only two Kestrels were

caught that had lost both tags. Thus, unless trapping subsequently showed otherwise, untagged birds were assumed to have been previously uncaught.

CHAPTER 2.

PREY DENSITY AND KESTREL DIET.

PREY DENSITY.

Most studies on the food of Kestrels in Europe have shown that small mammals, particularly voles (<u>Microtus</u> spp.), form the bulk of the diet. Mitchell et al. (1974), on the basis of 25 pellets, concluded that Short-tailed voles (<u>M</u>. <u>agrestis</u>), and to a much lesser extent shrews (<u>Sorex</u> spp.), were the main prey items in Eskdalemuir; a result I confirmed by a more detailed examination of pellet remains (see later). The density of small mammals in the area was monitored as part of a larger, independent study (N. Charles) and the relevant data were kindly made available for me to use here. This data comprised the number of animals caught per trapping site in each period and the regression equation used to convert the trapping index into vole densities (see below).

Methods.

From 1975 to 1978, small mammal numbers were measured at 20 randomly chosen sites (3 on sheepwalk and 17 in young-plantation) using unbaited, break-back traps placed on vole runs. After spring 1978, censusing was continued at only 8 of the sites, 2 on sheepwalk and 6 in young-plantation. Trapping was done twice a

year, in spring (April to May) and autumn (September to October), when vole numbers were at their annual low and high, respectively. Densities at other times of the year were calculated by extrapolation, assuming linear changes between trapping months. This assumption may have been incorrect, but the available data did not permit a better estimation of vole numbers between trapping sessions. Although estimates for some months were only approximations, they were considered sufficiently accurate for my purposes.

Trapping sessions at a site lasted five nights. Two traps were set at each of 24 randomly chosen points within the site. Nearly all the captures were Short-tailed voles or Common shrews (Sorex araneus); species less often caught included Bank voles (Clethrionomys glareolus), which occurred only locally, and Pygmy shrews (S. minutus), which were widespread but scarce. The latter two species were excluded from the totals as they were generally unimportant as Kestrel prey. I used the number of captures of each species over the whole five nights as an index of abundance at that time. The trapping-out of voles at similar sites in other areas had shown that this index was not linearly related to vole density because it was less sensitive to changes in abundance when vole densities were high (N. Charles unpubl.). Using a regression based on the comparison of index scores and the total number of voles trapped-out at 15 sites (N. Charles), I converted the mean index scores for each period into an estimated vole density. The

relationship of the index to density for shrews was unknown, and their abundance had to be expressed as the original index. An analysis of variance was used to test for differences in both the vole and shrew index scores between habitats, years and seasons.

Results.

The changes in vole and shrew numbers from 1975 to 1978 are shown in Fig. 2.1a (vole densities), Fig. 2.1b (shrew index scores) and Fig. 2.2 (vole and shrew index scores). The results of the analyses of variance of index scores are shown in in Tables 2.1 (voles) and 2.2 (shrews).

(a) Voles. The seasonal changes were similar each year, but the peaks and troughs might not always have coincided exactly with the times of trapping, so the apparently regular nature of the annual cycle was possibly an artifact. To examine long-term changes in vole abundance, I used the interpolated values for summer (July) and winter (January) only (broken line Fig. 2.1a). The line joining these estimates reduced the short-term, seasonal fluctuations in vole numbers and revealed a general decline from 1975 to spring 1977, followed by a slight increase in 1978. Vole numbers in spring 1977 were extremely low for young coniferous plantations, judging from experience in Eskdalemuir and elsewhere (N. Charles pers. comm.).

Vole densities in sheepwalk were consistently low, the average

Table 2.1 Analysis of variance of vole numbers using autumn and
spring trapping index scores, 1975 to 1978.

Test of differences between:	df	Sum of squares	Mean square	Variance ratio
Sheepwalk and young-plantation.	1	15769	15769	69.538***
Years within habitats.	3	14896	4965	21.896***
Seasons within years.	1	11166	11166	49.240***
Residual	138(16)	31294	227	
Total	143	73126	103	

Table 2.2 Analysis of variance of shrew numbers using autumn and
spring trapping index scores, 1975 to 1978.

Test of differences between:	df	Sum of squares	Mean square	Variance ratio
Sheepwalk and young-plantation.	1	676	676	27.258***
Years within habitats.	3	508	169	6.836***
Seasons within years.	1	424	424	17.110***
Residual	138(16)	3420	25	
Total	143	5028	35	

Figures in parentheses are the number of missing values.
***= P<0.001.

Figure 2.1 Estimated abundance of voles and shrews on young-plantation
           and sheepwalk, 1975-78.

       Each point is the mean of all the trapping sites in each habitat
in spring (S) and autumn (A). The left-hand scale refers to vole
density per hectare, the right-hand scale is the trapping index (i.e.
the mean number of individuals caught per trapping site.)

       The broken line gives vole densities estimated from the
interpolated values for summer (July) and winter (January), see text
page 10.

(a) Voles

Young-plantation.
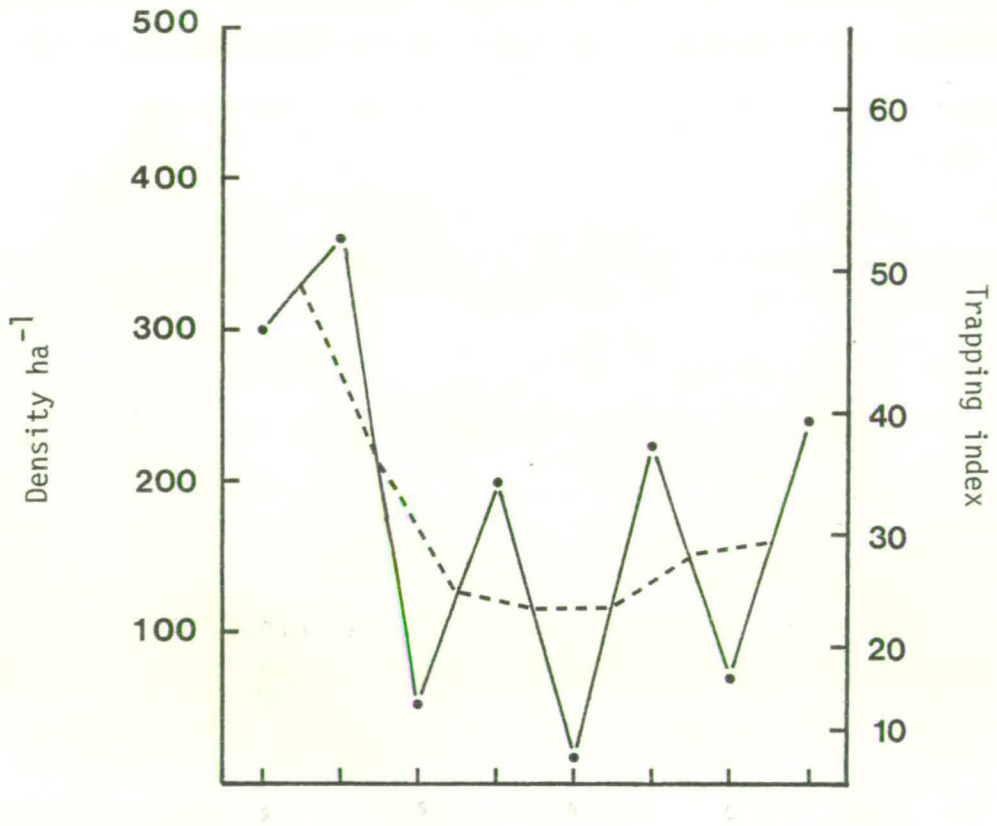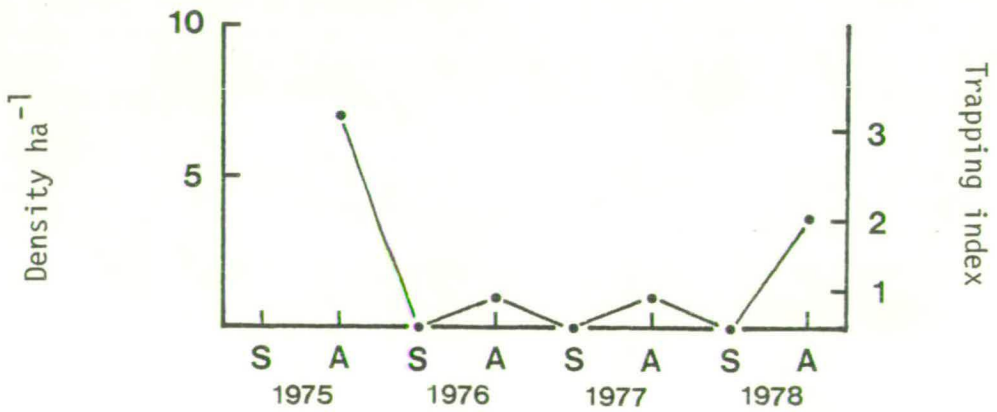
Sheepwalk.

(b)   Shrews

Young-plantation.
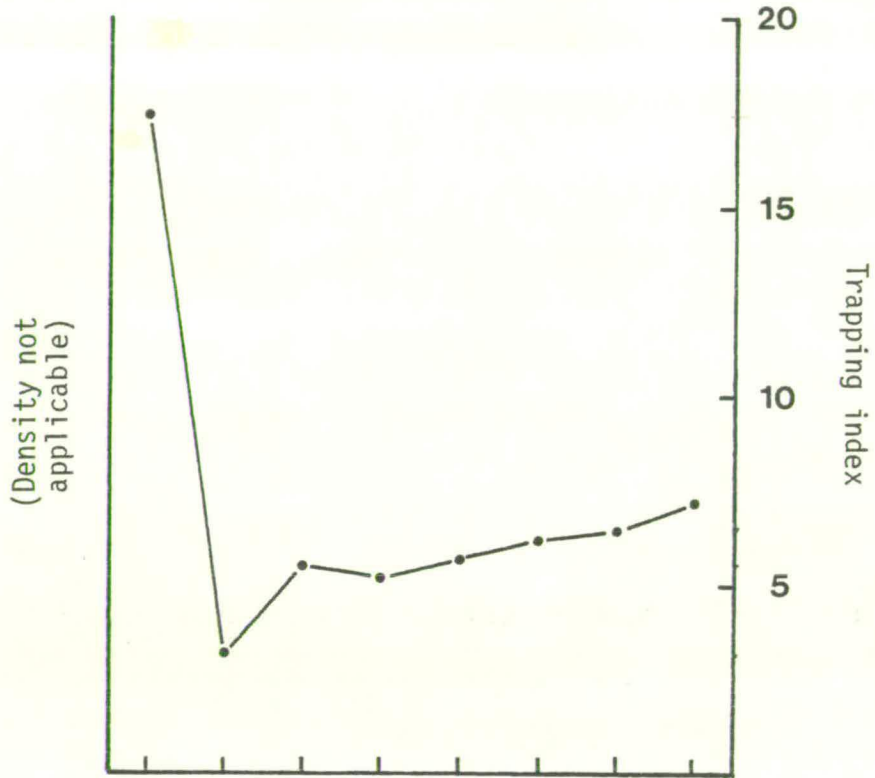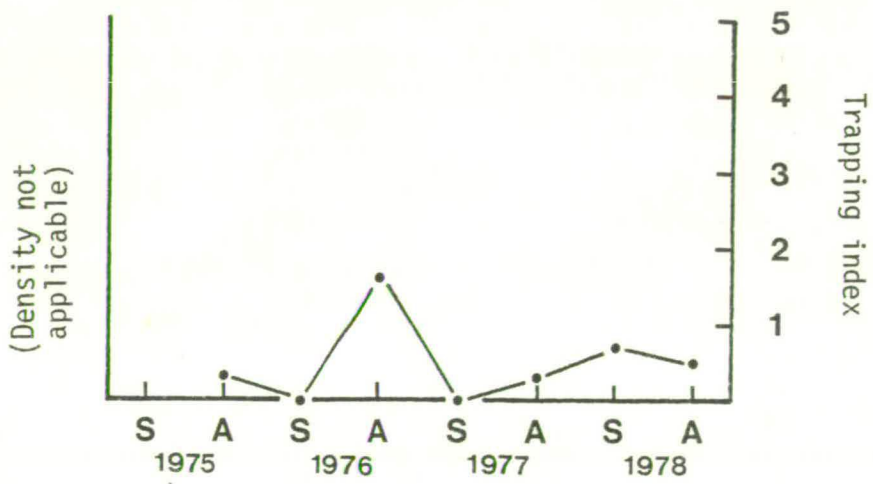
Sheepwalk.

of around 1-2 voles/ha was less than 2% of that in young-plantation (average= 151 voles/ha). Grazing and trampling by stock meant that there was much less cover than in young-plantation, particularly in spring when no voles were caught on sheepwalk.

(b) Shrews. In contrast to voles, shrews showed little variation in numbers (Fig. 2.1b); the index was high in spring 1975, but had fallen sharply by the autumn and remained fairly constant thereafter. Numbers in grazed areas were again consistently lower than in ungrazed, planted areas, though the difference was not as great as for voles (mean young-plantation index= 5.65, mean sheepwalk index= 0.50).

Judged by index scores (Fig. 2.2a-b), shrews seemed much less abundant than voles. I assumed that shrews were as easily caught as voles and used the index scores as a rough estimate of changes in their relative abundance during the study. As vole numbers fluctuated more than shrew numbers, the relative abundance of the two species depended mainly on the population level of voles. In young-plantation, vole captures always outnumbered those of shrews, except in spring 1977, when there were few voles and both species had similar index scores. Results from sheepwalk were harder to interpret because captures were so few. However, they did suggest that vole and shrew numbers were more similar than in young-plantation.

Figure 2.2 Comparison of vole and shrew trapping index scores for
young-plantation and sheepwalk.

(a) Young-plantation.
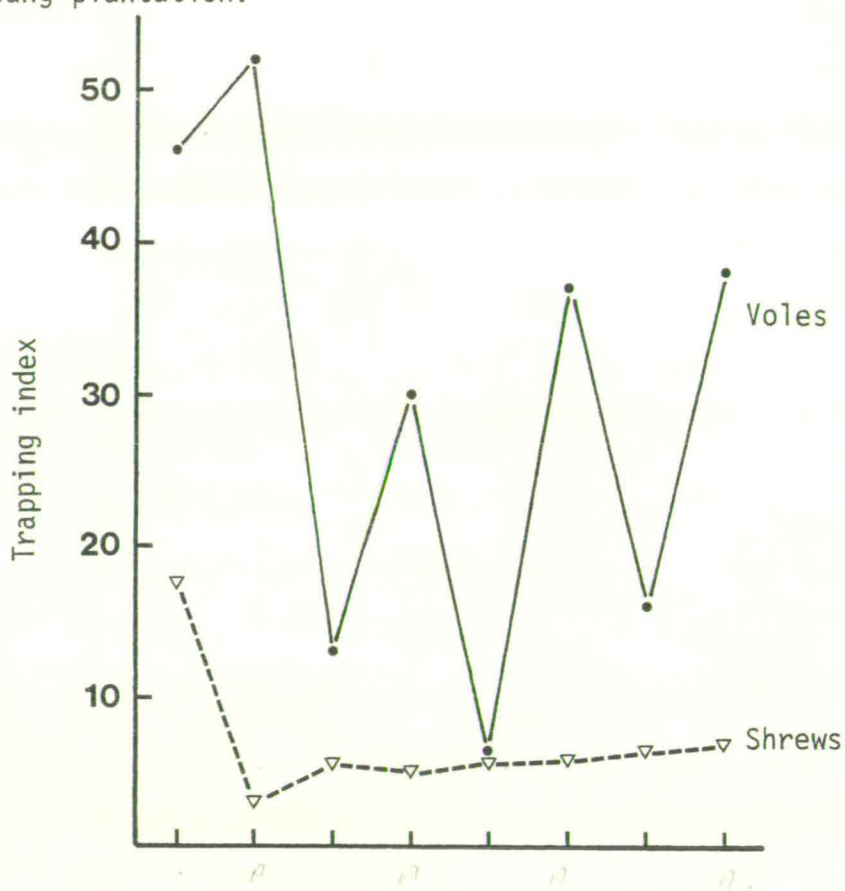
(b) Sheepwalk.
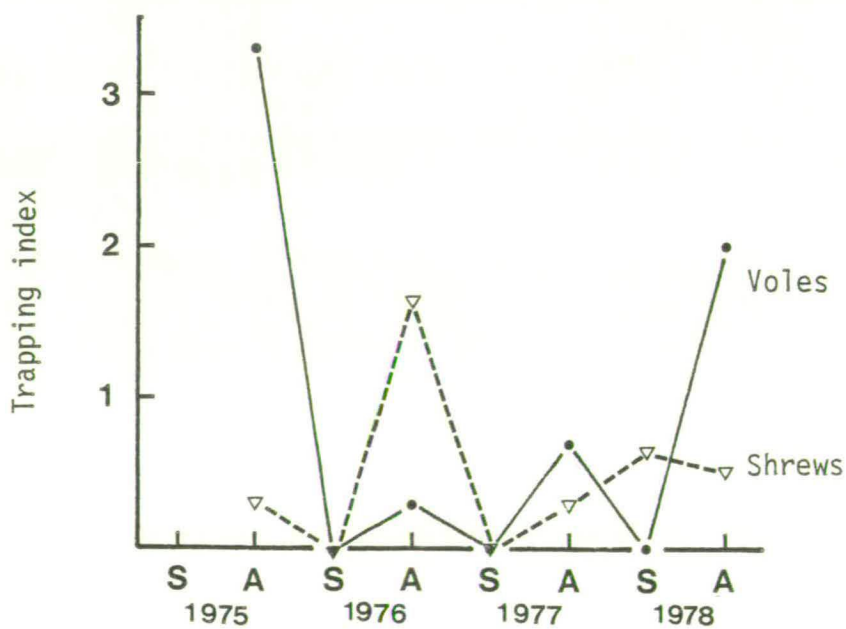
Discussion.

Vole populations in northern Europe undergo periodic fluctuations with peaks every 3-5 years (Elton 1942, Middleton 1930 and 1931). Such '4-year' cycles have been recorded in the Scottish Borders (Snow 1968) and seemed to occur in Eskdalemuir (as well as elsewhere in Dumfries and Galloway) because numbers were high in 1971 (Mitchell et al. 1974) and again in 1975. The number of voles caught in different trapping sites within Eskdalemuir usually varied in parallel (N. Charles), suggesting that there was a general synchrony in the vole cycle within the study area. This was probably true even between sheepwalk and young-plantation, despite the difference in vole densities between the two habitats. My study thus seemed to coincide with a decline in vole numbers following a peak in 1975.

The size of the autumn peaks depended mainly on the rate of population increase through the summer. The latter depended on the breeding of voles, high rates being associated with an early start to breeding, more young produced per litter and breeding at an earlier age (N. Charles). Thus, in spring and early summer, there was a higher proportion of young animals in populations that were increasing rapidly and a lower proportion in those that were increasing slowly or declining. The age structure of the vole population might have affected Kestrel food supply because younger animals seem to be more easily predated than older ones (Lockie 1955).

VEGETATION COVER.

Although voles were scarce on sheepwalk, they may have been more easily caught by Kestrels (i.e. more available) than in young-plantation because of the reduction in ground cover caused by livestock. To assess the amount of cover in different habitats in each season, I measured vegetation structure in both sheepwalk and young-plantation in one complete year from May 1977.

Methods.

Two aspects of structure were measured, the height of grass stems and the depth of the mat created by mosses and dead vegetation, under which voles were assumed to spend most of their time. Ranging poles, marked into 10 cm sections, were pushed into the ground a fixed distance and I recorded the height of the uppermost section obscured, or partly obscured, by ground vegetation when viewed from a distance of 15 m. The depth of the vegetation mat was recorded at the base of the pole, by pushing a ruler through the vegetation until it touched soil.

Measurements were taken once every two months at 8 sites; 2 in each of 4 habitat types (sheepwalk, recently planted ground, establishment plantation and thicket plantation- for a description of these see Table 2.3), which all had grass as the dominant ground vegetation (I avoided areas of heather or bracken as these

Table 2.3 Description of plots used in vegetation analysis.

Habitat Type	Plot No.	Grid Ref.	Plantation Age	Main Grasses Present
Sheepwalk	1	240060	-	Ac, Fr, Mc
	2	270040	-	Mc, At, Ac
Recently Planted*	1	218035	2	Dc, Ac, Hl, Df, Mc
	2	242093	4	Dc, Ac, Hm, Hl, At, Fr
Establishment Plantation*	1	250044	8	Ac, Mc, At, Df, Hl
	2	263050	7	Df, Mc, Ac
Thicket Plantation*	1	259032	9	Mc, Df, Ac
	2	254010	10	At, Ac, Hm, Mc

* Habitat types within young-plantation.

All grid references refer to sheet O. S. NT20, and give the approximate centre of the plot. Grasses are listed in the approximate order of their abundance in the plots. Ac= Agrostis canina, At= A. tenuis, Dc= Deschampsia cespitosa, Df= D. flexuosa, Fr= Festuca rubra, Hl= Holcus lanatus, Hm= H. mollis, Mc= Molinia caerulea. Plantation age is given in years.

had a different structure and were rarely used by Kestrels). Within each habitat type, the locations of the two sites were chosen at random but those which would have been on a steep slope were rejected as this may have made the assessment of vegetation height inaccurate. The same sites were sampled on each occasion by taking 20 readings of both height and depth in the rows between trees (or, on sheepwalk, in parallel rows 2 m apart).

Results.

Tables 2.4a-b give the results of an analysis of variance of depth and height respectively. In general there were no differences between sites of the same habitat, although vegetation height did vary significantly between some sites in the same plantation habitats. This seemed to confirm my impression that height was more dependent on the species present than was depth. Species composition varied between sites and the presence of some grasses (especially tall species such as Deschampsia cespitosa) had a marked effect on height at certain times of year.

Vegetation mat depth and height were both significantly smaller on sheepwalk than in the plantation habitats (Fig. 2.3). The latter were fairly similar to one another, but differed consistently in vegetation height, possibly because of variation in the grass species between different plots.

Seasonal changes in vegetation were similar in all habitats

Table 2.4 Analysis of variance of vegetation cover, using data
collected every two months from May 1977 to July 1978.

(a) Vegetation-mat Depth.

Test of differences between:	df	Sum of squares	Mean square	Variance ratio
Sites within habitats.	1	16	16	0.709(NS)
Replicates within habitats.	38	741	20	0.858(NS)
Replicates between habitats.	3	6207	2069	90.998***
Replicates between months.	6	1935	322	14.180***
Residual	1011	22988	23	
Total	1020	31130	31	

(b) Vegetation Height.

Test of differences between:	df	Sum of squares	Mean square	Variance ratio
Sites within habitats.	1	31	31	9.368***
Replicates within habitats.	38	115	3	0.906(NS)
Replicates between habitats.	3	885	295	88.043***
Replicates between months.	6	2329	388	115.811***
Residual	1011	3389	3	
Total	1020	6603	7	

***= P<0.001, NS= Not Significant.

Figure 2.3   Changes in vegetation mat depth and height in different
             habitats, May 1977-July 1978.

(a)   Vegetation mat depth.

(b)   Vegetation height.

KEY: •——•   =   sheepwalk (unplanted).
                  ■——■   =   recently planted (1-4 years old).
                  ▽---▽   =   establishment plantation (5-8 years old).
                  ○·····○ =   thicket plantation (9-10 years old).

      For a description of these habitat types see Table 2.3.

(a)
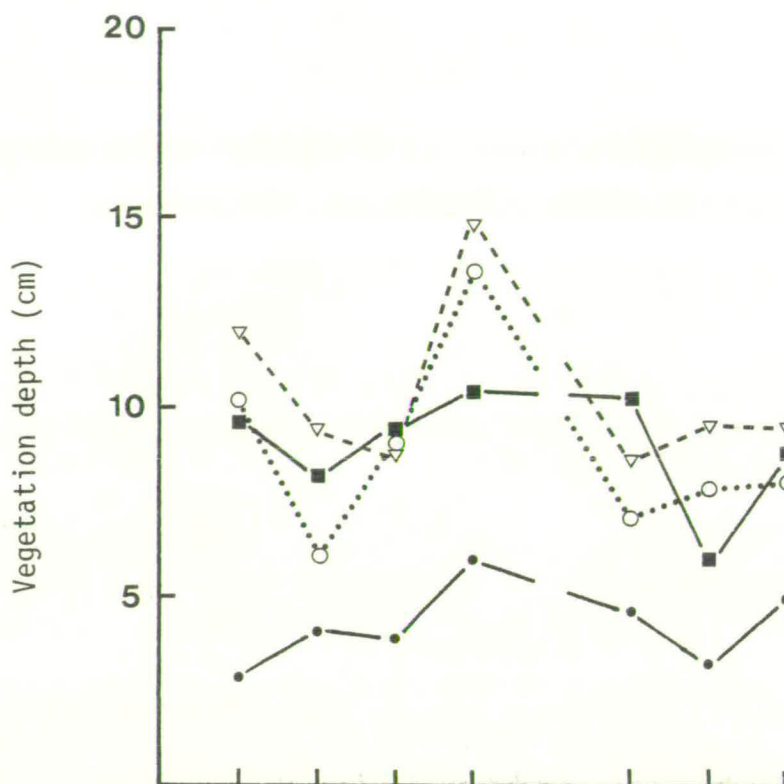
(b)
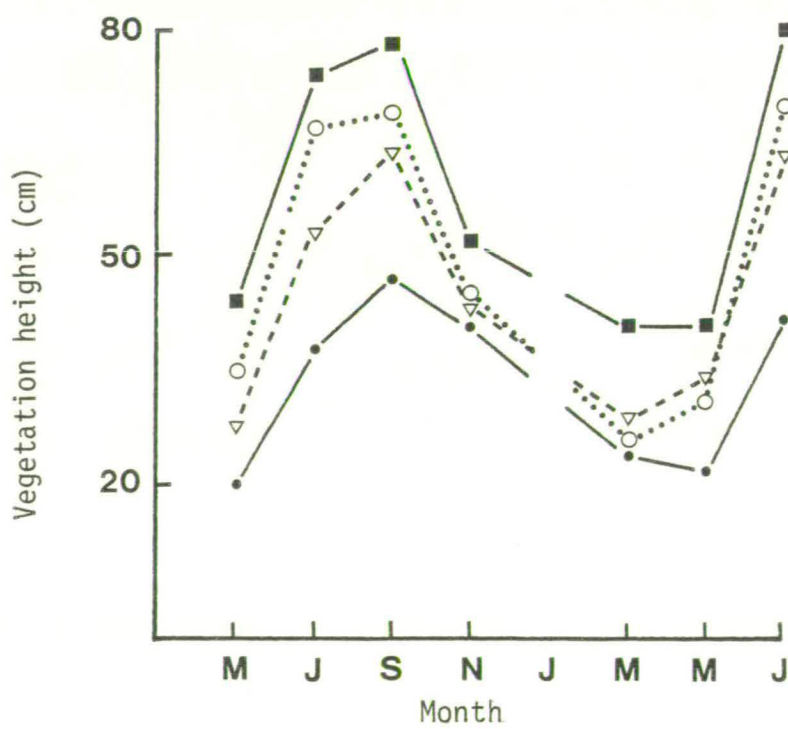
(Fig. 2.3). Stem height increased rapidly between May and July and reached a peak in August or September. As the vegetation died in late autumn, stem height decreased and a deep mat was formed. After November, cover was gradually diminished by rain, snow and decomposition of the vegetation, so that depth and height were lowest between March and May.

Discussion.

Several studies have shown that vegetation cover may affect the ease with which raptors capture food. Prey may be more vulnerable in reduced or patchy vegetation, than where they have sufficient cover to remain hidden at all times (Craighead and Craighead 1956). Southern and Lowe (1968) found that cover density was important in affecting the predation of Tawny Owls (Strix aluco) on woodmice (Apodemus sylvaticus), while Wakeley (1978) showed that Ferruginous Hawks (Buteo regalis) preferred to hunt over areas of bare ground or grazed vegetation, even though prey density there may have been lower than in areas of thicker cover. Unfortunately the effects of vegetation cover on vole availability in Eskdalemuir were unknown and they may have varied between habitats and at different vole densities. Nonetheless, two points arose from the above results.

(a) Vegetation cover was at its maximum in autumn and its minimum in spring. This was the opposite of seasonal changes in vole density and may have made voles harder to catch when they were

numerous and vice versa. Thus the availability of voles to Kestrels may not have varied by as much as was suggested by the seasonal changes in vole density. Lack of cover may have been particularly important early in the breeding season, when Kestrels required increasing amounts of food and vole densities were still comparatively low. Vegetation cover did not increase substantially until late June, when most young had nearly fledged, and it is possible that Kestrels timed their breeding so that young were in the nest when voles were most available, even if not most abundant.

(b) The differences in cover between sheepwalk and young-plantation probably reduced the effects of differences in vole densities between the two habitats, making sheepwalk more suitable to Kestrels than expected from the low vole numbers (especially in summer when alternative prey were also available).

I tried to allow for the effects of ground cover by producing an 'availability index', defined as the vole density per hectare divided by the product of vegetation depth and height. However, this made a number of untested assumptions about vole availability and did not improve any of the relationships of vole density to diet, home range or breeding performance (see below and chapters 5 and 6). For this reason, I used vole densities as an index of food supply, even though they may not have accurately reflected the ease of capturing prey at all times of year.

KESTREL DIET.

The diet of Kestrels has been studied in several areas of
Britain and Europe, encompassing a variety of habitats (Table 2.5).
The most prominent items were usually small mammals, especially the
Short-tailed vole or, on the continent, its counterpart the Common
vole (M. arvalis). Few of these studies measured prey abundance, so
my purpose in monitoring diet was to check whether voles were the
main prey item in Eskdalemuir and to examine changes in Kestrel
diet in relation to vole numbers.

Methods.

Like other raptors, Kestrels regurgitate pellets of undigested
prey remains, such as fur, feathers and bones. The frequencies of
prey items in the pellets may reflect differences in diet between
habitats or years, but they do not necessarily give the relative
frequency with which items were eaten because some prey leave fewer
remains than others. As a comparison with pellet analysis, I also
assessed diet by recording prey remains found on or near the nest.

1. Pellet Analysis.

Pellets were collected from nests or roosts from spring 1976
onwards. Each collection place was classed by habitat as either
grazed areas (which included farmland and sheepwalk) or
young-plantation. To ensure that pellets came from Kestrels hunting

Table 2.5 Comparison of previous studies that used pellet analysis to determine Kestrel diet.

Area	Habitat	Time of year	no. of pellets	Main prey item	Other common items	Infrequent items	Source
Yorkshire (W. Riding)	Arable Farmland	July-March	206	stv	cs,wm,bd, be	ws,fg	Ellis (1946)
Yorkshire (Clevland)	Rough pasture heather moor	Throughout year	438	stv,ps	cs,bv	be,mt,hm, bd	Simms (1961)
Ireland	?	Summer	420*	wm	bd	hm,br,ps, ra,be	Fairley and McLean (1965)
Holland	Reed-beds+ pasture	Spring+ Summer	7000	cv	bd,ham,cs, br	wm,be,ml ps	Cave´ (1968)
Ireland (Galloway)	Farmland scrub, marsh	Winter	200*	wm,bd	lz	cs,ps	Fairley (1973)
Scotland (Dumfries)	Grassland+ young plant.	May-Sept.	25	stv	cs	?	Mitchell et al. (1974)
Wales (Pembroke.)	Farmland salt marsh	October-April	379	stv	cs,ps,bd, be	ew	Davis (1975)
Scotland (Edinburgh)	Urban woods	April	50	stv,bd	be,bv,wm	?	Crichton (1977)
Cumbria	Salt marsh hill farms	Throughout year	400	stv	cs,bv,be, ew	bd,wm,gh	Yalden and Warburton (1979)

Key to prey items: bd=birds, be=beetles, br=brown rat, bv=bank vole, cs=common shrew, cv=common vole, ew=earthworms, fg=frogs, gh=grasshoppers, ham=harvest mouse, hm=house mouse, lz=lizards, ml=mole, mt=moths, ps=pygmy shrew, ra= rabbit, stv= short-tailed vole, wm= wood mouse, ws= water shrew.

* These studies used 10g batches of material as basic unit, number is pellet equivalent.

on mainly one habitat, I either used only pellets from places that had predominately one habitat within 1-2 km, or used home range data to exclude those individuals that hunted both habitats. Apart from a few individuals at certain seasons (see chapter 5), birds hunted mainly within 2 km of their nest or roost. Results were grouped into two-monthly periods and, as far as possible, 50 pellets from a variety of sites in each habitat were examined in each period. In most cases the same roosts or nesting areas were sampled over the three years, but pellet collection was not systematic because not all the sites were permanently in use.

Pellets were oven-dried at 20-30 °C for at least a week, by which time they could be stored for long periods and were assumed to be at constant weight. Analysis was confined to whole pellets or to fragments which obviously originated from the same pellet. Each pellet was weighed to the nearest 0.1 g, measured to the nearest 1 mm and dissected dry, noting the presence or absence of the following groups: voles, shrews, birds, beetles, earthworms and others. Voles were separated from shrews by reference to bones, jaws or fur (examined microscopically, Day 1966). The powder from each pellet was scanned for earthworm chaetea using a stereoscopic microscope. Items were then scored on the following scale: 0= absent; 1= comprising a small part of the pellet; 2= comprising a major part of the pellet; 3= comprising the whole pellet. The definition of categories 1 and 2 varied from item to item (Table 2.6). No attempt was made to estimate the number of items per

Table 2.6 Criteria used in assessing the abundance of prey items
in Kestrel pellets.

Item	Score	
	1	2
Voles	Small amounts of fur, no bones	Large amounts of fur and several bones
Shrews	Small amounts of fur, no bones	Large amounts of fur and several bones
Birds	Feather powder or barbacules only	Whole feathers and/or bones
Beetles	A few small fragments	Large fragments throughout the pellet
Earthworms	<3 cheatea in field of microscope at X20	>3 cheatea in field of microscope at X20
Moths	Less than 10% of pellet	More than 10% of pellet
Frogs	Flakes of skin only	Pieces of skin plus claws or bones

pellet, and the relationship of frequency in pellets to frequency in the diet was not known. However, Crichton (1977), after a detailed study of pellet formation in captive Kestrels, concluded that recording the frequency of presence in pellets was preferable to using percentages calculated from the number of items identified per pellet (e.g. Davis 1975).

The percentage of pellets containing each item was calculated for each period, and standard errors were calculated assuming a binomial-like distribution. Strictly, the scores for pellets were not entirely independent, because pellets from the same site may have been more similar to one another than to those from elsewhere. The confidence limits were thus only approximate, but this was unlikely to affect the validity of my conclusions.

2. Prey remains at nests.

Males began bringing food to females at least a week before the first egg was laid, and continued to do so until after the young had hatched. Females plucked and ate kills near the nest, usually at regular places such as fence posts or earth-piles. I recorded prey items at these 'plucking posts' whenever I found them during visits to nests. During the nestling period, prey were brought direct to the young and I counted items found on the nest.

The conspicuousness and rate of disintegration of signs may have varied between the different prey types. Invertebrates left

few remains, but it is also likely that they were less often brought to the nest than were larger, vertebrate prey. When plucked away from the nest, piles of vole and shrew fur and of feathers seemed as equally detectable and persistent as one another, so that even kills up to a week old could be counted. On the nest, however, the young trampled prey remains, making individual voles and shrews more difficult to separate than birds because fur was more easily mixed than feathers. For this reason, only fresh prey remains which were still distinct could be used at this stage.

Results.

1. Pellet analysis.

The 1014 pellets analysed showed that the frequency of prey items varied within and between years (Fig. 2.4).

(a) Voles were the most frequent prey throughout the study, being present in at least 85% of pellets in every 2-month period. Changes in frequency were hard to assess with such a constantly high level, but the proportion was lowest in summer (June and July) and rose to a peak between February and May in both 1977 and 1978.

(b) Shrews were common at times, but even at their highest occurrence (in 55% of pellets), they were still less frequent than voles. There was no obvious seasonal trend, though the frequency

Figure 2.4 Frequency of prey items in pellets collected in 2-monthly
periods from April 1976 to July 1978.

Each point is the percentage of pellets per period that contained
the prey item. Limits to means are approximately $\pm$ 2 S.E.%, and were
calculated assuming a binomial-like distribution:

$$S.E.\% = \sqrt{pq/n}$$

Where   p = % pellets containing item.

q = % pellets not containing item.

n = number of pellets.

The number of pellets in each period is given at the head of the
opposite page.

KEY TO PERIODS:

AM = April/May

JJ = June/July

ON = October/November

DJ = December/January

FM = February/March

(This key also applies to Figures 2.5, 2.6 and 2.7).

(a) Vole
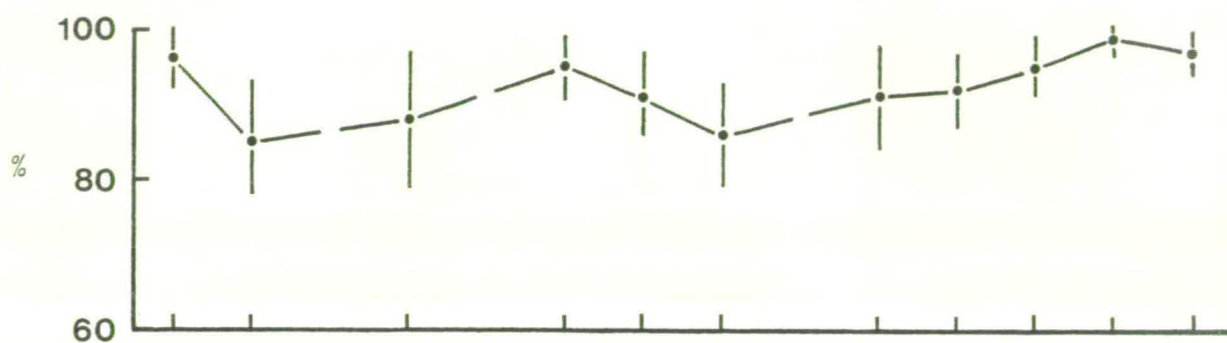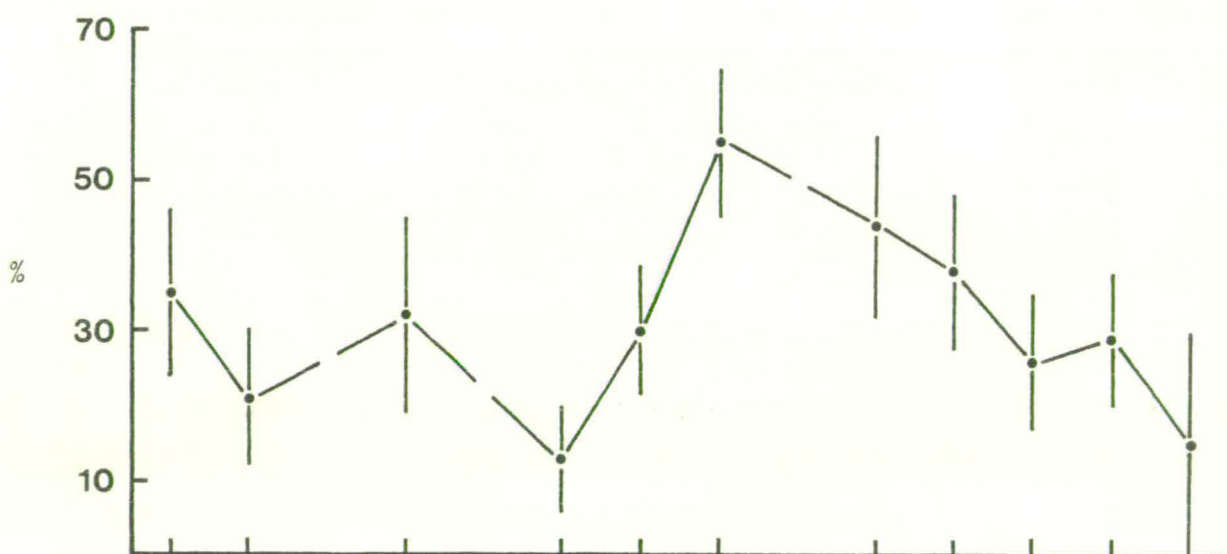
(b) Shrew

(c) Bird
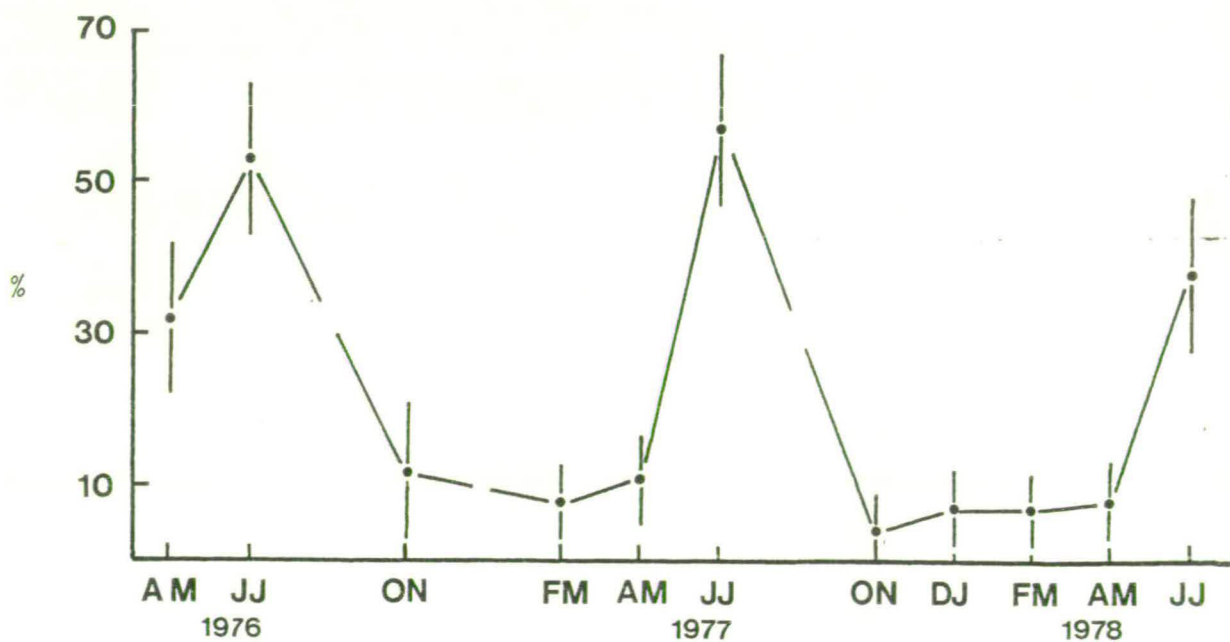
(d) Beetle
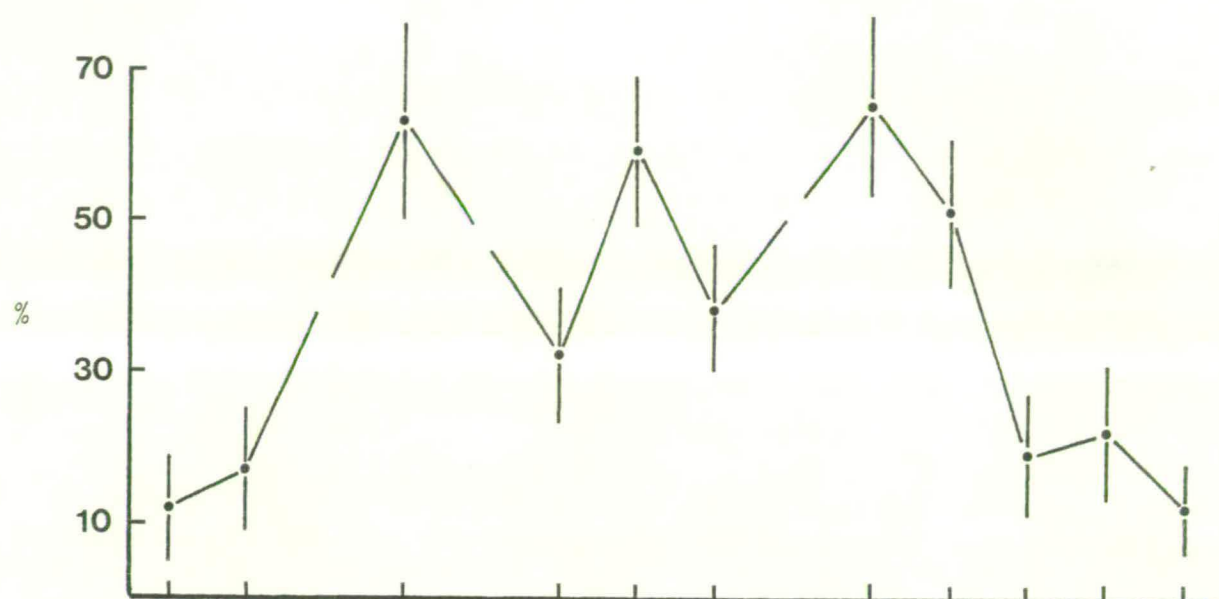
(e) Earthworm
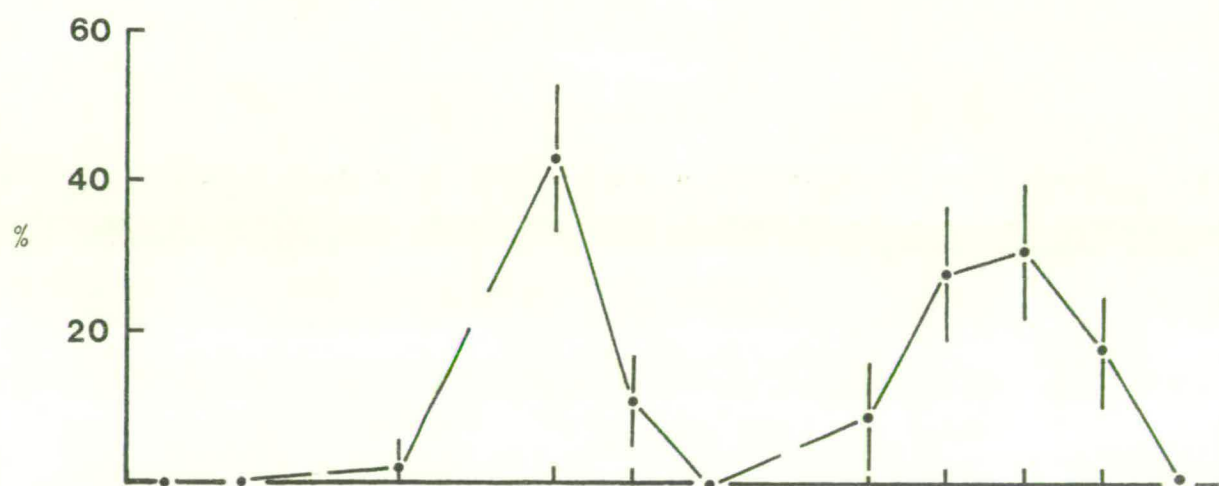
(f) 'Others'
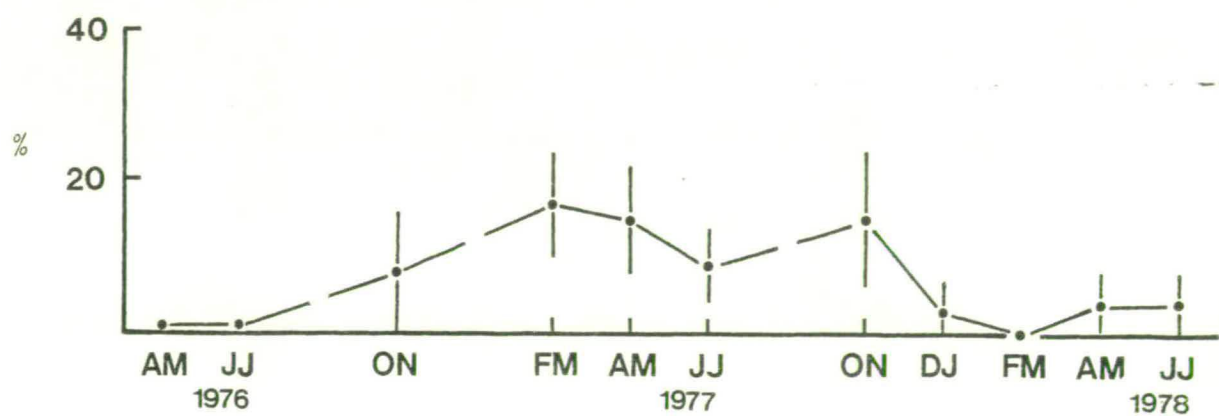
increased from winter 1976/77 to a peak in summer 1977, when over half the pellets contained shrew remains. The rise corresponded with a slight decline in the number of pellets containing voles, and the frequencies of the two items were inversely correlated ($r = -0.6774$, $P < 0.05 > 0.01$).

(c) Birds were seldom identified to the species in pellets, but bird kills collected at nests were nearly all Meadow Pipits (Anthus pratensis), with the occasional Skylark (Alauda arrensis) and young Lapwing (Vanellus vanellus). They were present in appreciable numbers of pellets only when Kestrels were feeding young (June and July). This corresponded to the usual fledging period of these birds and most of the feathers found were from young birds rather than adults (the feathers of fledglings could be distinguished from those of adults as they were still growing). Cave' (1968) obtained a similar result, but the main species in his area was the Starling (Sturnus vulgaris).

(d) Beetles usually left visible remains in pellets because their hard parts resisted digestion. Some may have come from the gut of other prey items such as birds or shrews and the errors caused by this were unknown. However, as some pellets were almost entirely beetle, and beetles were often found solely in conjunction with herbivorous prey such as voles, I assumed that most were eaten directly by Kestrels. Beetles were found in over 60% of pellets in both autumn 1976 and 1977, most remains being of Ground beetles (Carabidae) and Dung beetles (Geotrupes spp.). Fewer pellets

contained beetles in winter and summer, though this was less so in 1977 than in the other two years.

(e) Earthworms were a rarer item, occurring mainly in late winter and early spring (March to May), only occasionally in autumn and never in June or July.

(f) 'Others'. This miscellaneous group included moths, frogs (Rana temporana) and lizards (Lacertia spp.), which were found in less than 10% of pellets. Moth remains were usually scales, egg cases (presumably from gravid females) and larval mandibles, which were common in autumn pellets. Numbers in this group were generally higher in 1977, than in equivalent periods the following year.

Seasonal changes in the frequency of prey items were similar between habitats, though the diet of Kestrels on grazed areas was more varied than those in young-plantation (Fig. 2.5, Tables 2.7a-f). The overall frequency of both voles and shrews did not differ significantly between the habitats, although Fig 2.7b suggests that more shrews were taken in grazed areas than in young-plantation during 1977. Birds, beetles and earthworms were more often recorded from grazed areas than from young-plantation. Earthworms in particular were five times more frequent in pellets from grazed areas.

To examine the relationship of Kestrel diet to vole numbers, I used the frequency of all-vole pellets as an index of diet variability because this was inversely related to the occurrence of

Figure 2.5   Frequency of prey items in pellets collected from grazed
             areas and young-plantation, April 1976 to July 1978.

        Each bar gives the percentage of pellets in each habitat per
period that contained the item.

        KEY:

                    Shaded areas   = young-plantation.
                    Unshaded areas = grazed areas (sheepwalk and
                                       farmland).

For key to 2-monthly periods see Figure 2.4.

(a) Voles
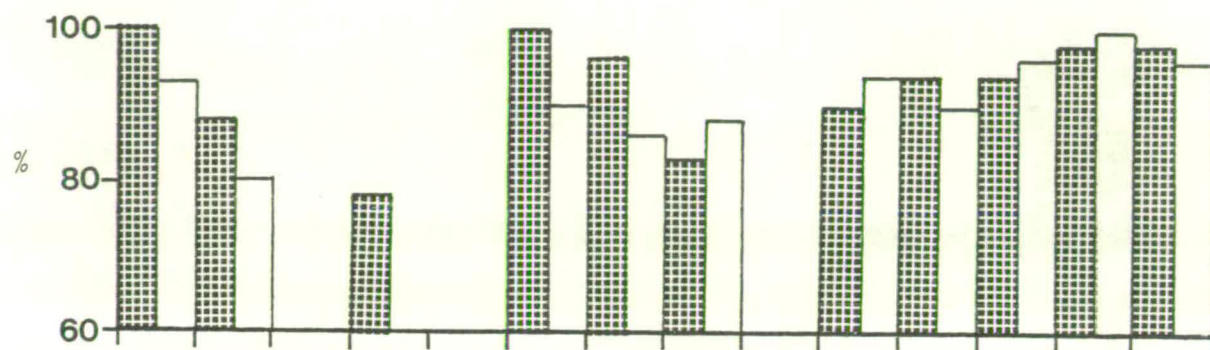
(b) Shrews
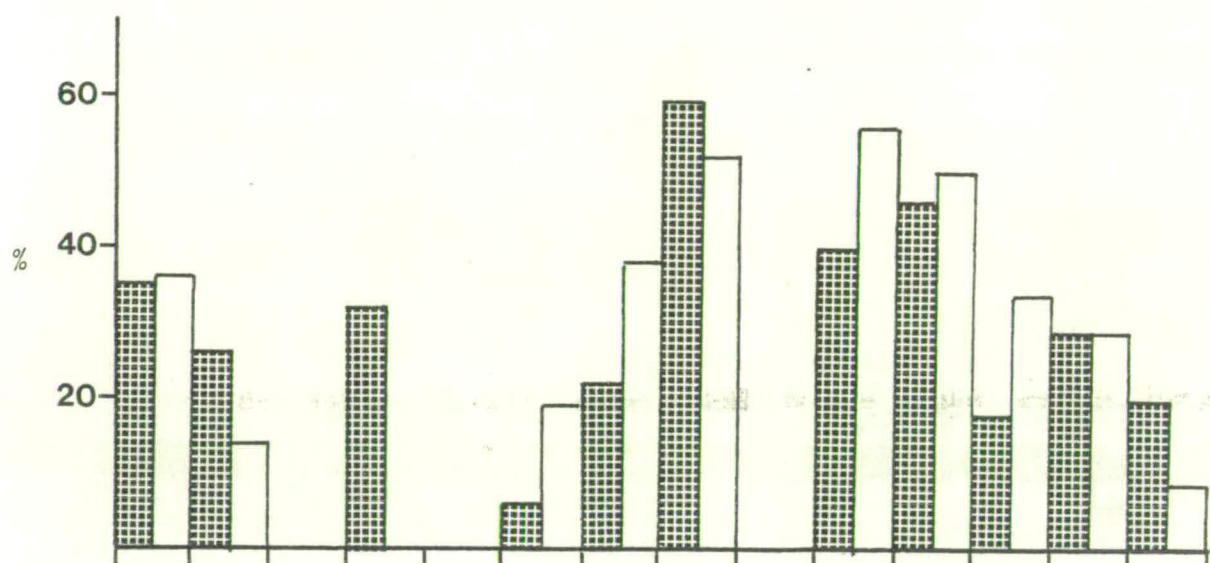
(c) Birds
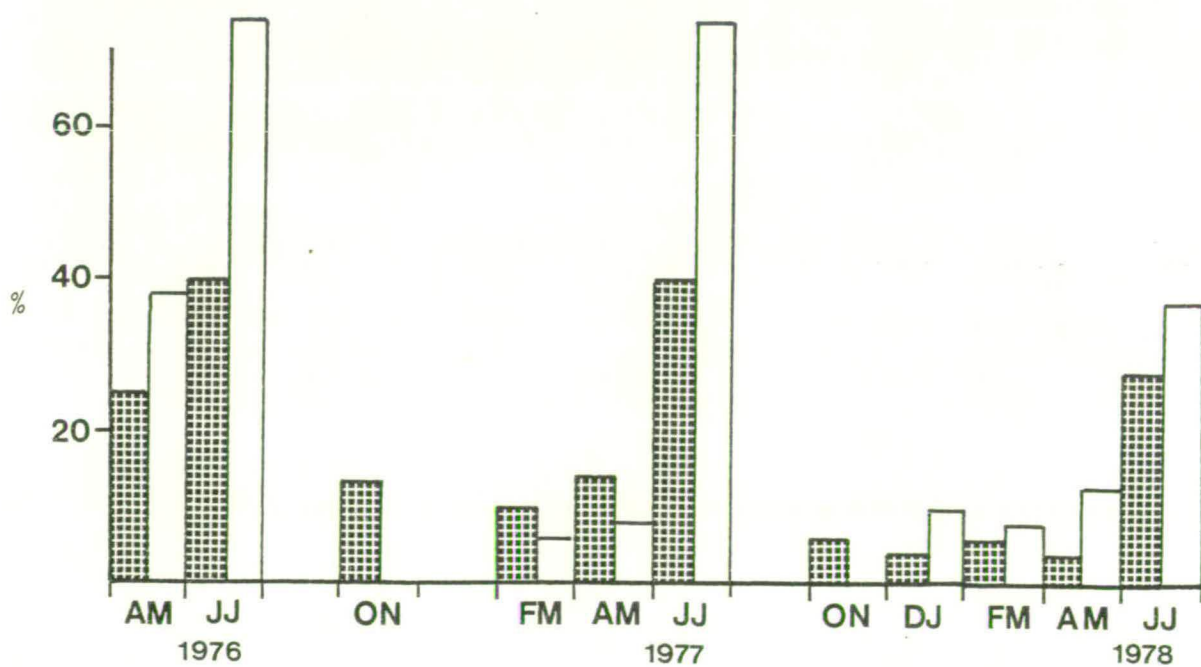
(d) Beetles
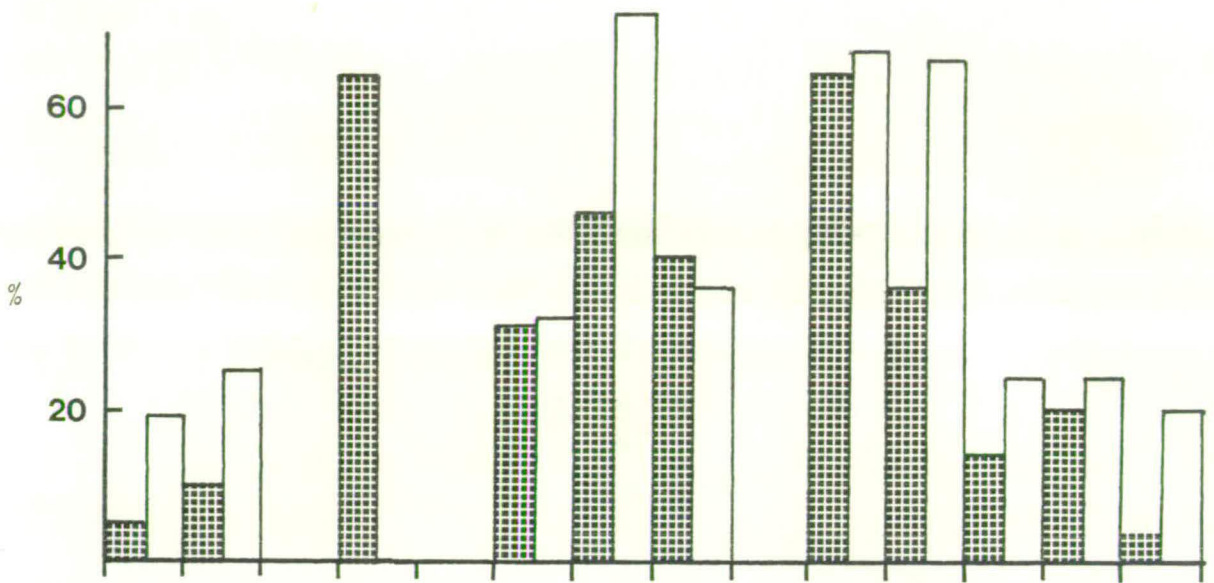
(e) Earthworms

(f) 'Others'

36
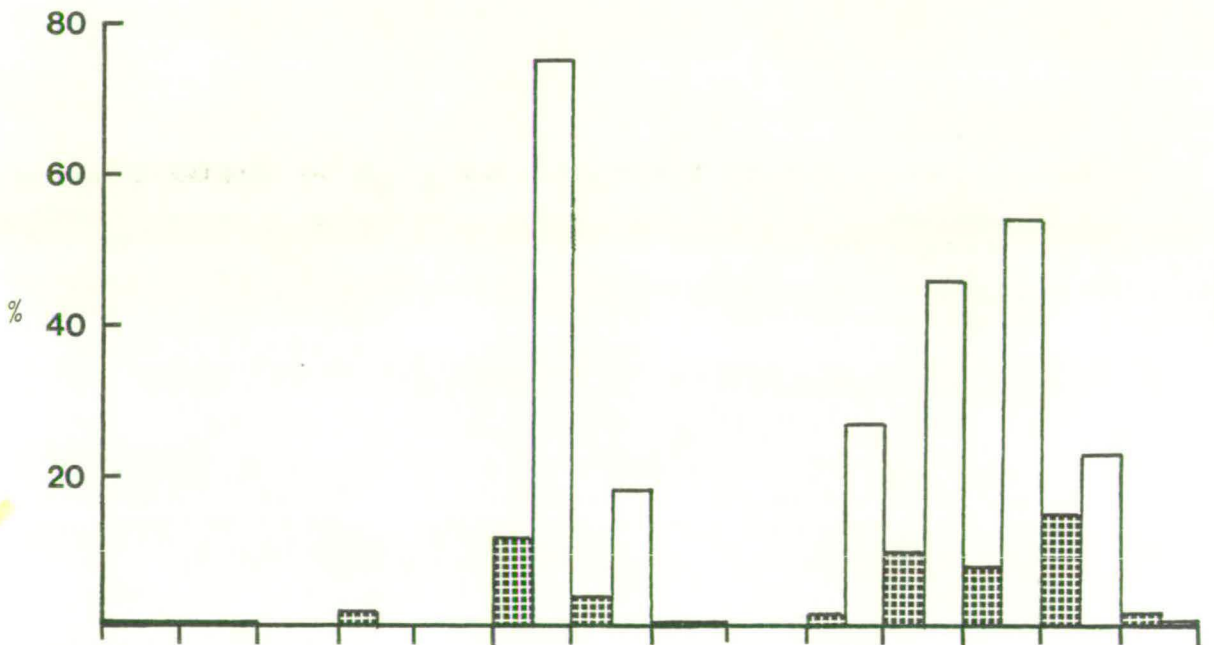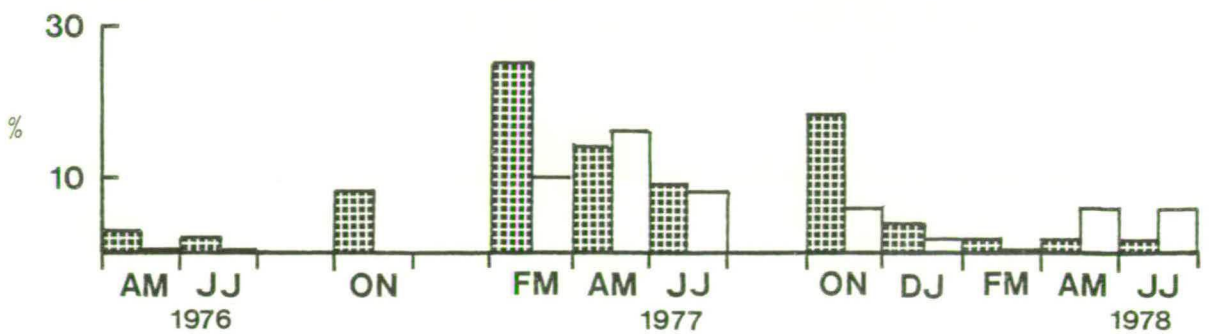
Table 2.7 Differences in the frequency of items in pellets

collected from young-plantation and grazed areas.

(a) Voles.

	A	P
YP	36	518
GA	38	422

Chi-squared= 1.153   P=NS

(b) Shrews.

	A	P
YP	392	162
GA	316	144

Chi-squared= 0.41   P=NS

(c) Birds.

	A	P
YP	460	94
GA	330	130

Chi-squared= 17.97   P<0.001

(d) Beetles.

	A	P
YP	385	169
GA	290	170

Chi-squared= 4.41   P<0.05>0.01

(e) Earthworms.

	A	P
YP	526	28
GA	345	115

Chi-squared= 80.90 P<0.0001

(f) Others.

	A	P
YP	509	45
GA	435	25

Chi-squared= 3.26   P<NS>0.05

Data refer to all pellets collected from 1976-1978.

A= no. pellets with item absent, P= no. pellets with item present.

YP= young-plantation, GA= grazed areas.

items other than voles in the diet. There was no significant relationship between the frequency of all-vole pellets and vole numbers on a seasonal basis (Fig 2.6), apparently because prey selection depended on the abundance of other items more than that of voles. Thus, even though the number of voles rose in summer, so did those of birds and beetles and these were taken in increasing numbers. Similarily, voles were at their lowest in spring but they made up most of the diet because there was little alternative food during that season.

Long term changes in vole numbers were, however, reflected in the diet. Vole densities calculated from summer and winter values (broken line Fig 2.6) reduced the effects of short-term, seasonal variation in vole numbers (see above) and were significantly correlated with the frequency of all-vole pellets in each period ($r= 0.8350$, $P<0.02>0.01$). Thus, for example, voles were scarcer in summer 1977 than in summer 1978, and alternative items were more frequently found in pellets. This was true of shrews, whose increase in pellets could not be attributed to any change in their density, and of seasonal items such as birds which still occurred mainly in pellets found in summer, but more often.

2. Prey remains.

Prey remains were collected from May to July in the first two years and from April to July in 1978. They were nearly all either

Figure 2.6   Frequency of all-vole pellets in 2-monthly samples, in
             relation to long- and short-term changes in vole density.

(a)   Vole density.

     Each point is the estimated vole density for each period, used in
regressions of vole density against the % of all-vole pellets.

              Solid line   =   'short-term' changes in vole density,
                                calculated from the solid line in Figure
                                2.1a.

              Broken line =   'long-term' changes in vole density,
                                calculated from the broken line in Figure
                                2.1a.

(b)   Percentage of all-vole pellets in samples.

     Each point is the percentage of pellets in each 2-monthly sample
that contained only vole material.

     (For key to periods see Figure 2.4).

              Estimation of vole densities for each period:

              Vole densities in each month during the study were
              estimated from Fig. 2.1a, using either the broken
              line ('long-term' vole densities) or the solid line
              ('short-term' vole densities). Vole densities for
              each 2-monthly period were found by averaging the
              relevant monthly estimates obtained from each line.

(a)
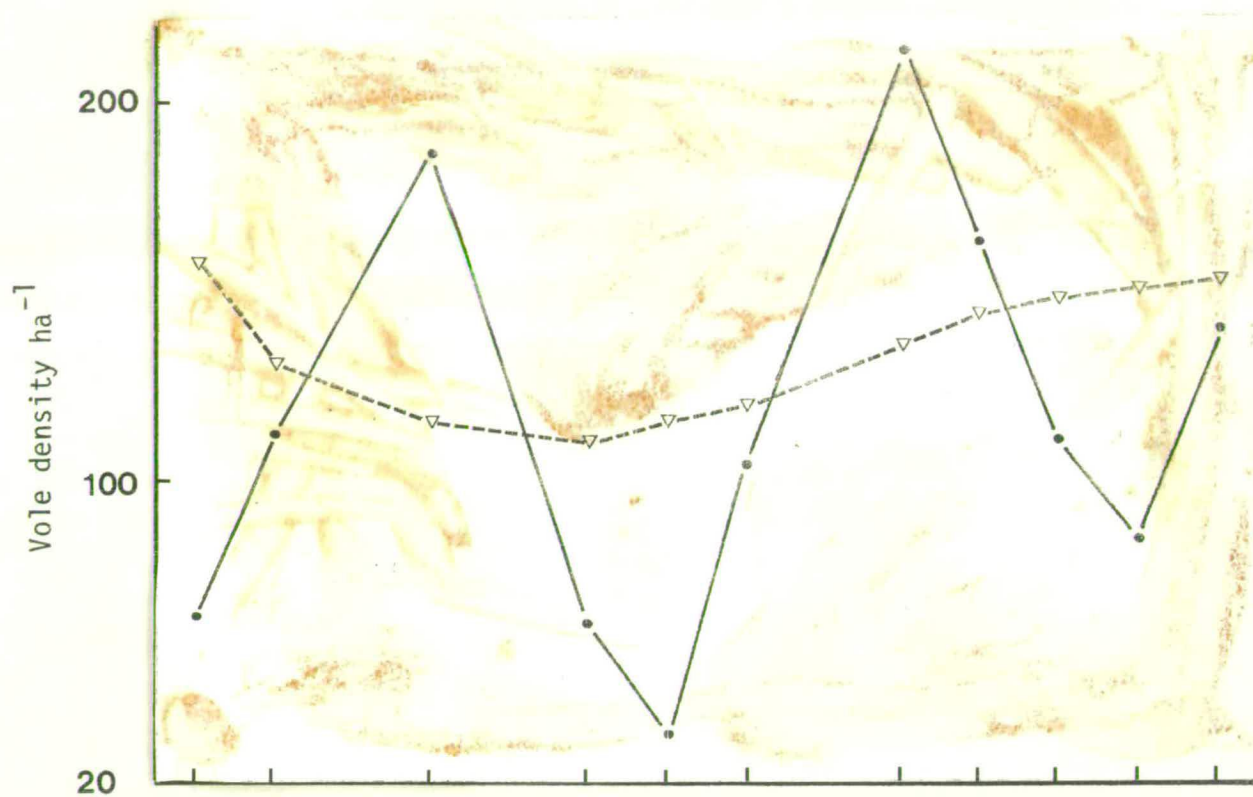
(b)
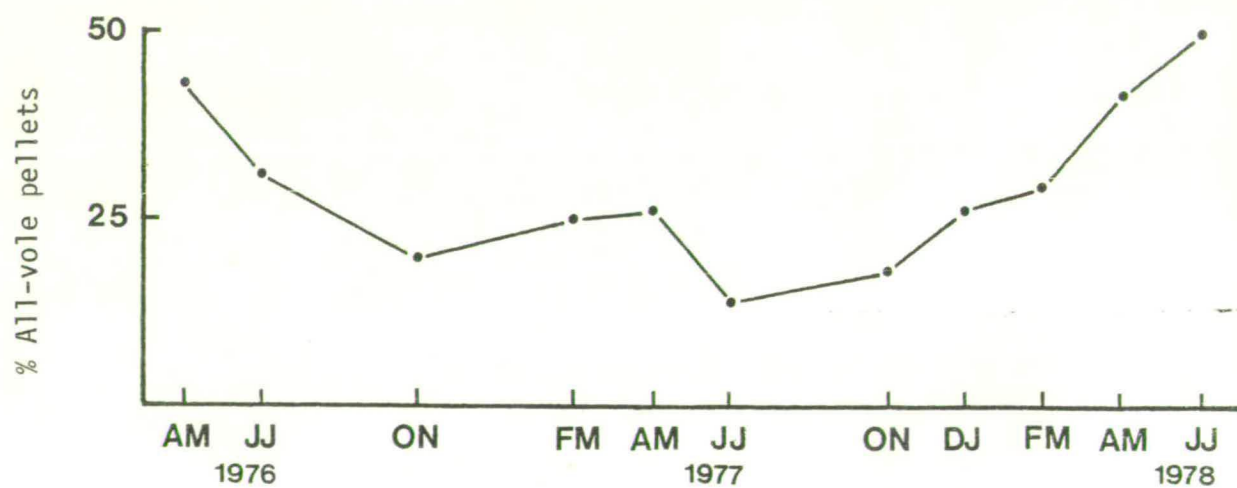
vole, shrew or bird, so analysis was limited to these items. During the three years, 561 kills were recorded; of which 382 (68%) were voles, 121 (22%) birds and 58 (10%) shrews. The low sample sizes in some months (Table 2.8) made analysis difficult, but the following trends were apparent:

(a) Data for 1978 (the only year with sufficient samples in all months) showed that the proportion of voles taken decreased as the breeding season progressed. There was a highly significant difference between months in both young plantation and grazed areas (Table 2.9a).

(b) Because of the above changes, differences between years could only be tested month for month, and sufficient data for all years was available only for June. These indicated that a lower proportion of voles was taken in 1977 than in either of the other two years. This trend was true for both habitats but was not significant at even 10% level when data from each were combined (Table 2.9b).

(c) Differences between grazed areas and young plantation were apparent only later in the breeding season. A higher proportion of voles was found in young-plantation in June and July in both 1977 and 1978, the differences being significant

at the 5% level when all data were treated together (Table 2.9c).

These data show that voles were the main prey item taken and

Table 2.8 Frequency of finding prey items at nests, 1976-1978.

		1976				1977				1978		
		V	B	S		V	B	S		V	B	S
April	YP	–	–	–		0	0	2		45	2	1
	GA	–	–	–		0	0	0		18	1	0
May	YP	3	2	1		12	4	0		61	9	3
	GA	3	0	0		0	1	1		38	1	4
June	YP	32	9	7		18	14	1		65	21	19
	GA	12	6	2		5	9	3		36	27	6
July	YP	3	0	0		10	2	2		12	3	2
	GA	1	7	0		3	1	2		5	2	2
Totals	YP	38	11	8		40	20	5		183	35	25
	GA	16	13	2		8	11	6		97	31	12
	BOTH	54	24	10		48	31	11		280	66	37

V= Voles, B= Birds, S= Shrews.

YP= young-plantation, GA= grazed areas.

Table 2.9 Tests of differences in the proportion of vole prey

items found around nests.

(a) Between months (using data for 1978 only).

(i) Young-plantation.   (ii) Grazed areas.

	V*	NV		V	NV
April	45(94)	3	April	18(95)	1
May	61(84)	12	May	38(88)	5
June	65(62)	40	June	36(52)	33
July	12(71)	5	July	5(56)	4

Chi-squared= 21.80 P<0.001   Chi-squared= 23.44 P<0.001

(b) Between years (using data for June only).

(i) Young-plantation.   (ii) Grazed areas.

	V	NV		V	NV
1976	32(67)	16	1976	12(60)	8
1977	18(55)	15	1977	5(29)	12
1978	65(62)	40	1978	36(52)	33

Chi-squared= 1.22   NS   Chi-squared= 3.18   NS

(iii) Both habitats.

	V	NV
1976	44(65)	24
1977	23(46)	27
1978	101(55)	73

Chi-squared= 4.17   NS

Table 2.9 (con.)

(c) Between young-plantation (YP) and grazed areas (GA).

(i) June 1977.

	V	NV
YP	18(55)	15
GA	5(29)	12

Chi-squared= 1.93   NS

(ii) June 1978.

	V	NV
YP	65(62)	40
GA	36(52)	33

Chi-squared= 1.24   NS

(iii) July 1977.

	V	NV
YP	10(71)	4
GA	3(50)	3

Fisher exact test, P=0.329

(iv) July 1978.

	V	NV
YP	12(71)	5
GA	5(56)	4

Fisher exact test, P=0.347

(v) June+July 1977.

	V	NV
YP	28(60)	19
GA	8(35)	15

Chi-squared= 3.80   NS

(vi) June+July 1978.

	V	NV
YP	77(63)	45
GA	41(53)	37

Chi-squared= 2.19   NS

(vii) June+July, 1977+1978.

	V	NV
YP	105(62)	64
GA	49(49)	52

Chi-squared= 4.24   P<0.05>0.01

*V=number of vole kills, NV= number of non-vole kills.

Figures in parentheses are percentages.

are in line with those from pellet analyses in equivalent periods i.e. voles were more frequent in the diet during good vole years, but, within years, the proportion decreased in summer as alternative food (mainly birds) became available. The diet of Kestrels was also more varied on grazed areas than in young-plantation, though this may have applied only late in the breeding season.

Discussion.

There was good evidence that voles were the most important item in the diet of Kestrels at Eskdalemuir. Other prey occurred in pellets at times when they were most abundant or most available, for example:

(a) Birds were rarely taken, except in summer, probably because most small birds left the area in winter and because they were most easily caught as fledglings, rather than when adult.

(b) The activity of beetles is partly dependent on temperature (Jones 1976), which may explain why fewer were taken in winter. The low frequency in summer may have been because they were under represented in items brought to the nest. In autumn, beetle populations were probably still high and they may have been the most easily caught prey, especially for juvenile Kestrels still inexperienced in hunting.

(c) Gerard (1967) found that most species of earthworm were at

least 7-10 cm below the surface when the soil was dry (from June to October) or cold (January and February), but were near the surface in the warmer, moist conditions from March to May. This is consistent with my findings as worms seem to have been most frequently taken at times of year when they were at the surface and thus vulnerable to predation. Yalden and Warburton (1979) also found signs of earthworms in Kestrel pellets collected in winter, but not in summer.

(d) Frogs were vulnerable in spring, when they congregated to breed, and were recorded mainly in pellets collected at this time.

(e) Items other than voles may have been more important on grazed areas because they were more abundant relative to voles and because the sparse vegetation cover meant that some, especially beetles and earthworms, were much more vulnerable than in young-plantation.

The results presented here confirm the findings of others that Microtine voles form the bulk of the diet where they occur. Alternative items are taken according to their availability relative to voles and may become important if they are seasonally abundant or if vole numbers decline. In habitats where voles are scarce, other prey are important, both within Eskdalemuir (i.e. between grazed areas and young-plantation) and, apparently, between studies in different areas. For example, birds may be more often taken in urban environments (Crichton 1977) and also in Ireland, where voles are absent and are replaced in the diet by birds and

woodmice (Farely 1973).

It appears that Kestrels specialize in a method of hunting (i.e. searching the ground from a fixed position, either from the air or from a perch), rather than on a prey item as such. However, in a habitat such as Eskdalemuir, this predisposes them to capturing voles, which are consequently the most important item both in terms of weight and numbers. In other habitats, such as arable farmland, the same hunting methods are used, but invertebrates and birds are more likely to be encountered than voles, and are more frequent in the diet.

PELLET·WEIGHT.

Several studies have shown that when captive raptors are fed on a single prey type, pellet weight is proportional to daily food intake (Duke et al. 1976 for a variety of raptors, Tarboton 1977 for Black-shouldered kites, Elanus caeruleus, and Crichton 1977 for Kestrels). This seems to be because diurnal raptors usually produce a single pellet a day, irrespective of the number or size of meals eaten (Duke et al. 1976), so that when they eat large or frequent meals, they produce larger pellets than when fewer, or smaller meals are eaten. Wild Kestrels have a mixed diet and pellet weight is probably affected mainly by the type of prey eaten; even so, the mean weight of single-item pellets may have been an index of daily food intake. To see if food intake varied with food supply, I related the mean weights of all-vole pellets (plus those which contained a trace of only one other item) for each 2-month period, to the prevailing vole density. The use of pellets with a trace of one other item seemed justified as there was no significant difference in their size or weight compared with all-vole pellets (Table 2.10).

Results.

There was no difference in the mean size or weight of vole pellets from grazed areas or young-plantation (Table 2.10), so results from both habitats were combined. Mean pellet weight

Table 2.10 Mean size and weights of Kestrel pellets collected

from 1976 to 1978.

Type	Habitat	Length mm	Width mm	Weight g X10	n
Vole	YP	31.5(0.7)	15.6(0.2)	11.7(0.5)	213
	GA	30.4(1.1)	15.0(0.4)	11.3(0.8)	100
	BOTH	31.1(0.6)	15.4(0.3)	11.6(0.4)	313
Trace	YP	31.6(1.0)	15.4(0.3)	11.4(0.7)	104
	GA	30.0(1.1)	15.0(0.4)	11.1(0.8)	81
	BOTH	30.9(0.7)	15.3(0.3)	11.3(0.5)	185
All	YP	31.2(0.4)	15.4(0.2)	11.3(0.3)	554
	GA	30.2(0.5)	14.9(0.2)	10.8(0.3)	460
	BOTH	30.7(0.3)	15.2(0.1)	11.0(0.2)	1014

Vole= pellets consisting entirely of vole.

Trace= pellets consisting of mainly vole, plus a trace of one other item.

All= all pellets.

YP= young-plantation, GA= grazed areas.

Figures in parentheses are 2S.E. of the mean.

differed between some periods, those from 1976 and early 1977 being generally lighter than those in 1978 (Fig. 2.7a). The changes in weight corresponded roughly with changes in vole density and the two were significantly correlated (Fig. 2.7b, r= 0.6051, P<0.05>0.01). Using the regression of pellet weight to meal weight from Crichton (1977), mean daily food intake would have varied from approximately 35 g in spring 1977 to 50 g in autumn 1977.

Discussion.

The relationship of pellet weight to vole density was surprisingly close, considering that (a) pellet weight was probably influenced by other factors besides daily food intake and (b) food intake was not solely dependent on vole density. One explanation for the above relationship is that all-vole pellets were smaller when voles were scarce because Kestrels ate fewer voles per day under these conditions. Reduction in pellet size was unlikely to have been due to changes in the size of vole-meals; if anything voles were larger, on average, when vole populations were low because a higher proportion of individuals was adult (N. Charles). Some Kestrels could probably compensate for the greater difficulty in catching voles by taking alternative prey, so that their food intake may not necessarily have been lower under poor vole conditions. However, as pellets were light in early spring, when few items other than voles were available, Kestrels unable to find alternative food may have had a reduced food intake.

Figure 2.7 Pellet weight and vole density.

(a) Mean weight of vole pellets in each 2-monthly period.

Each point is the mean weight of pellets that contained only vole, or vole plus a trace of one other item. Confidence limits are $\pm$ 2 S.E.

(b) The weight of all-vole pellets in relation to vole density.

Each point is the mean pellet weight and estimated vole density for each 2-monthly period.   Line is fitted regression.

$$Y = 0.0011X + 1.015$$

$$(r = 0.6051, P < 0.05).$$

(a)
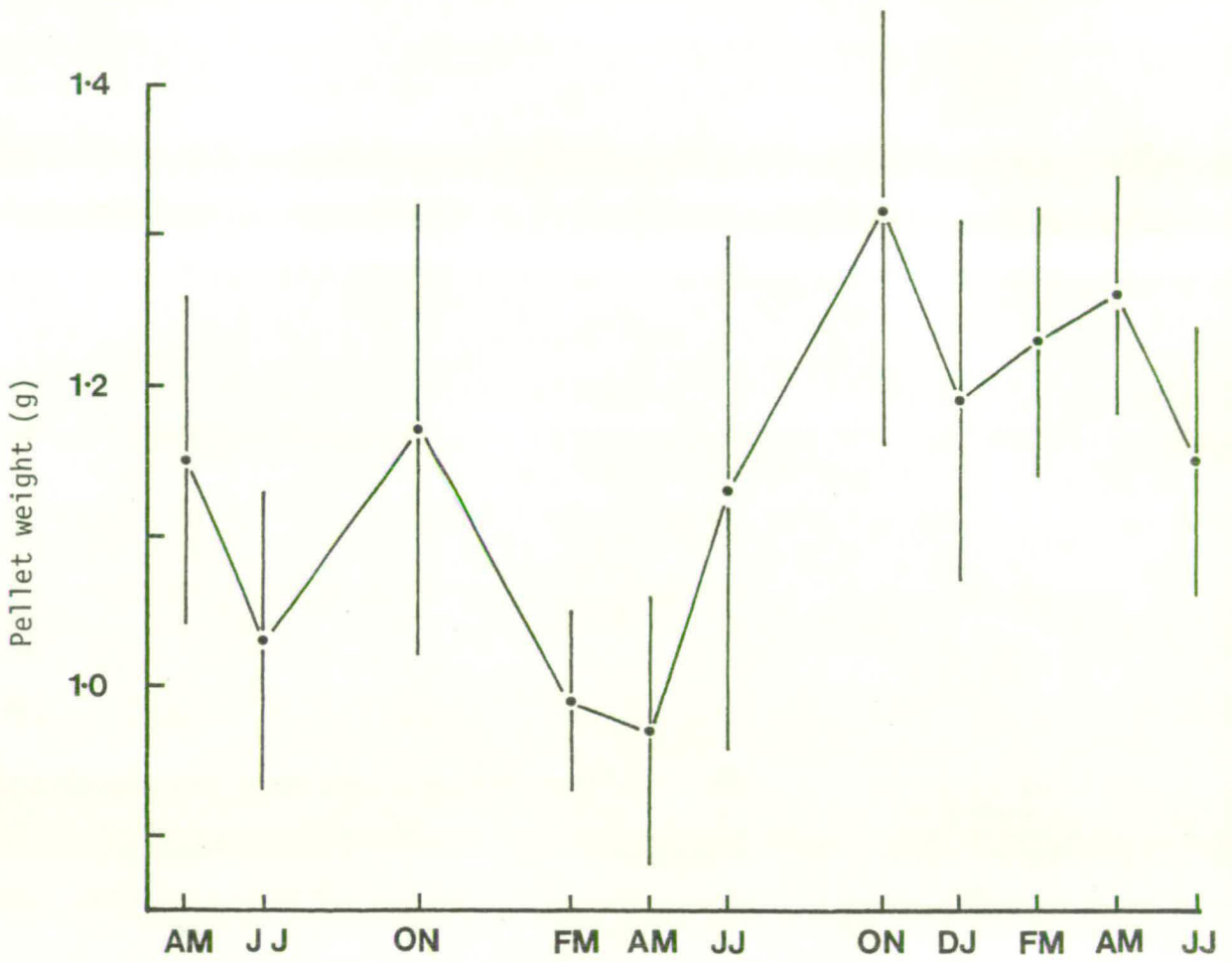
(b)
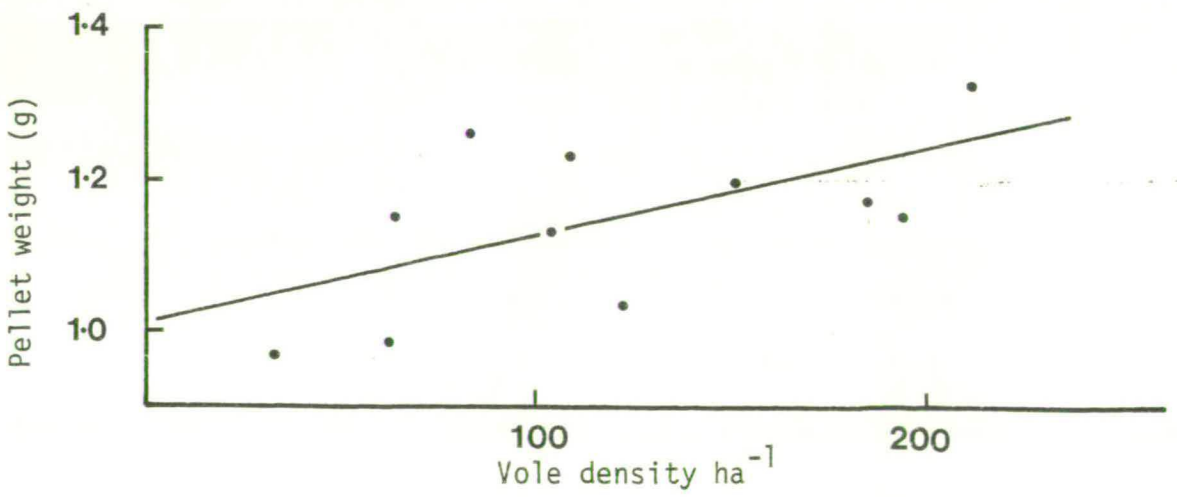
CHAPTER 3.

ENERGY BUDGETS AND HUNTING BEHAVIOUR.

This chapter examines how Kestrels allocated their time between various activities at different times of year. With this information I hoped to estimate the energy consumption of free-living birds, and in particular to compare seasonal changes in energy budgets with concurrent changes in body weight and condition. Hunting behaviour is also examined, in order to determine what influenced the choice of hunting method.

TIME BUDGETS.

Methods.

I classified the behaviour of all Kestrels when first sighted as either (a) ordinary flight, (b) flight-hunting, (c) inactive perching, (d) perched-hunting or (e) display and defence. Flight-hunting included 'hovering' (hunting in one place by continual beating of the wings), 'hanging' (maintaining a fixed position without wing beats) and 'mixed' (a combination of hovering and hanging). These were easily distinguished from displays and ordinary flight, though the latter often occurred during hunting sessions. Separating hunting from non-hunting behaviour in perched

birds was more difficult because even those engaged in activities such as preening occasionally made sudden strikes if they happened to notice prey. Individuals inactively perched sat in a hunched position, with fluffed feathers, or preened; whereas those actively hunting from perches had an upright posture, often made 'bobbing' movements of the head and frequently moved from perch to perch. Only this behaviour was considered as perch hunting, even though a few strikes were made by inactively perched birds.

The frequencies of activities recorded by these 'spot observations' were used to estimate the actual time spent on them thoughout the day. Results from radio-tracking a few Kestrels suggested that this was justified because birds often used conspicuous perches during the day (especially electricity or telegraph poles) so were generally as visible when perched as when flying. Birds were perhaps less easily seen if they were soaring very high, sheltering from rain or eating kills on the ground. Soaring was used for display rather than for hunting, so it was uncommon outside the breeding season. Kestrels sought shelter only in heavy rain and observations made under these conditions were ignored. In most cases where birds were seen eating kills on the ground, they returned to perches within 10-15 minutes and I had no evidence that satiated birds hid in thick cover. Observations were made between 0800 GMT and dusk. There was no obvious diurnal rhythm in behaviour (confirming Tinbergen 1940), so frequencies were

extrapolated to all daylight hours to estimate the total time spent on each activity per day.

The sample size in each month depended on both the population density of the birds and the intensity of my fieldwork. Few observations were made in January and none in August or September, so years were taken from October to July. In all, 4894 sightings were made, the numbers for years 1 to 3 being 1495, 1307 and 2098 respectively.

Results.

(a) Seasonal changes. The frequencies of activities were similar between years, so I combined the data for all three. Taken over the whole period, 2153 (44%) observations were of hunting birds (26% flight-hunting and 18% perched-hunting). Non-hunting activities included display and defence (8%), inactive perching (32%) and directional flying (16%). These last two showed little variation in frequency from month to month (Fig. 3.1), with no marked seasonal changes. However, daylight varied from 7 hrs in December to 17 hrs in June so that, even though the frequency remained the same, more time was spent on these activities per day in summer than in winter (see Table 3.1). Few territorial fights or displays were seen in autumn or winter, but their frequency increased in February and reached a peak in April, when laying started. Once incubation began, territorial behaviour declined

Figure 3.1 Seasonal variation in the frequencies of activities,
estimated from spot observations.

(a) Inactive perching
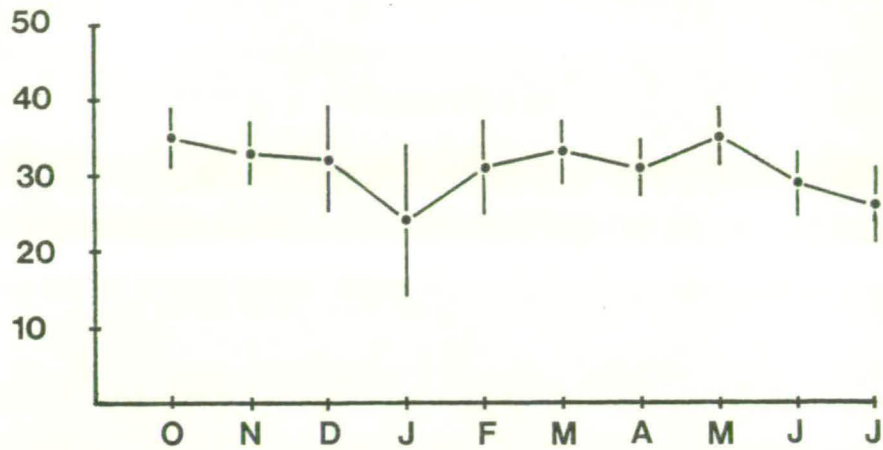
(b) Directional Flight
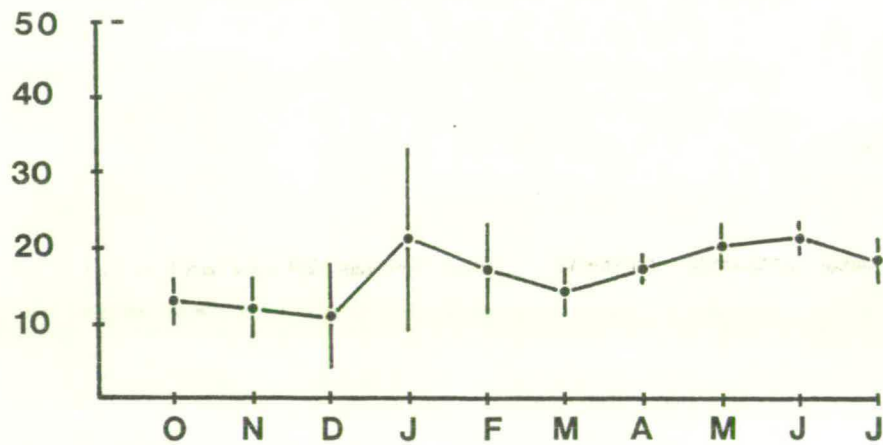
(c) Display and Defence
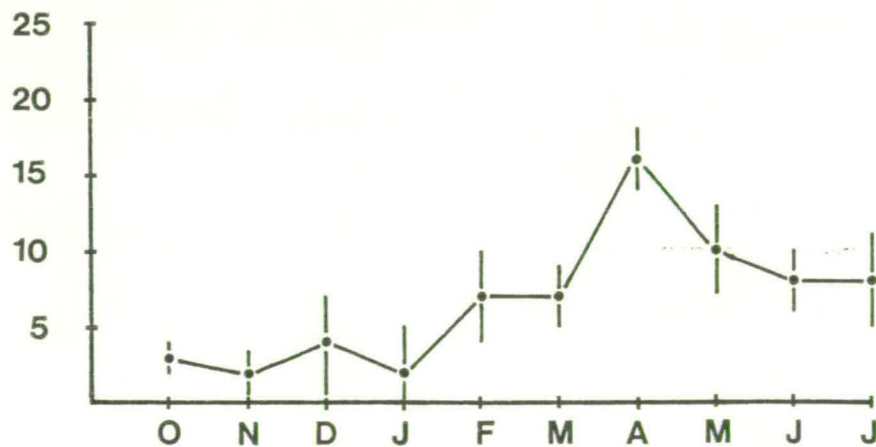
Frequencies are expressed as a percentage of the total observations
of all birds for each month, + 2 S.E.% (calculated assuming a binomial-
like distribution). Combined data, 1976-1978.

Figure 3.2   Seasonal changes in the frequency and methods of hunting.

Using combined data for 1976-78.

(a)   Frequency of hunting.

     Percentage hunting expressed as the proportion of the total
observations of all birds per month.

     Total hours of hunting per day estimated from percentage hunting
x daylength.

(b)   Seasonal changes in hunting method.

     Frequencies expressed as a percentage of the total observations
for each month, $\pm$ 2 S.E.%.   Confidence limits were calculated assuming
a binomial-like distribution, and refer to differences within each
method, but not necessarily between them.

     In both cases the values during the breeding season refer to
males and non-brooding females only.

54

(a)

Hours per day

% Hunting

% of daylight

Hours of hunting per day.

O N D J F M A M J J

(b)

%

Flight-hunting

Perched-hunting

O N D J F M A M J J

Month
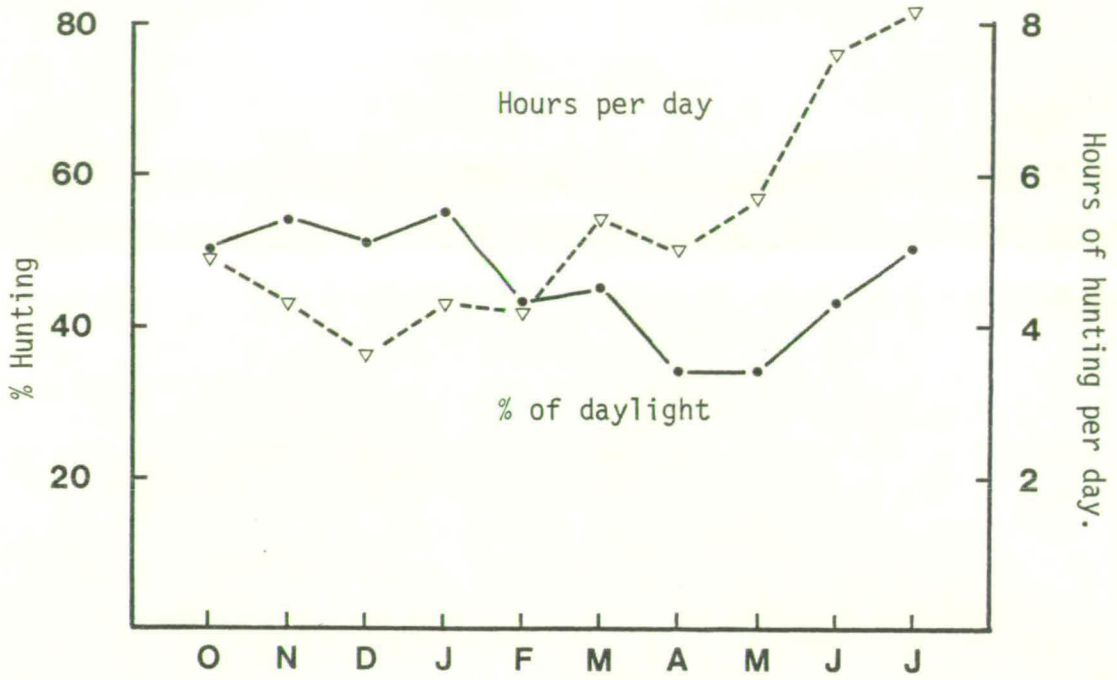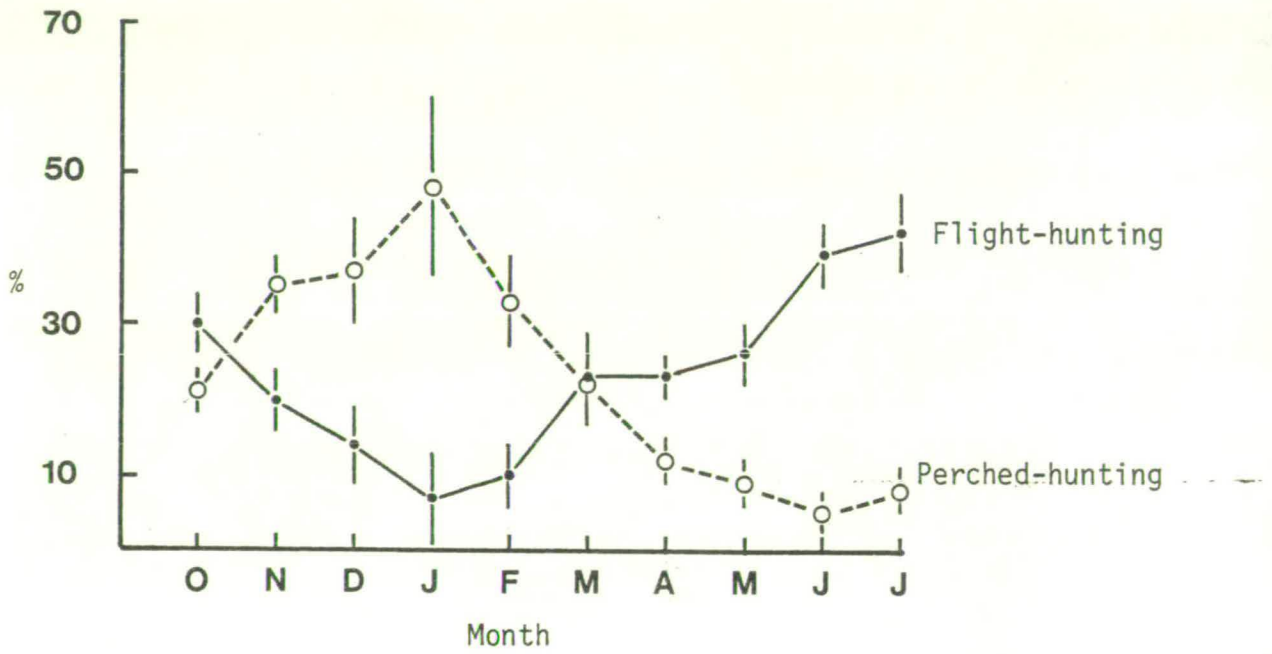
slightly and remained lower for the rest of the breeding season, both in frequency (Fig. 3.1c) and in hours per day (Table 3.1). The proportion of time spent hunting declined slightly in spring, but the actual hunting time per day increased from 3.6 hrs in December to 8.2 hrs in July (Fig. 3.2a). The predominant method of hunting varied with the time of year, changing gradually from perched-hunting in winter to flight-hunting in summer (Fig. 3.2b).

(b) The behaviour of males and females was examined separately using observations of tagged birds only, due to the difficulty in sexing untagged juveniles. Outside the breeding season there were no significant differences in behaviour between the sexes; but from April to July females did less hunting, flying and displaying, and more inactive perching, than did males (Fig. 3.3). This corresponded to the time they were brooding and were only seen when off the nest during feeds by the male. Males spent a lower proportion of the day hunting, and a higher proportion displaying, than earlier in the year, but the total time spent hunting still rose because of the increased daylength (see Table 3.3). During the late nestling period (i.e. July), males and females were more similar in their behaviour, the only significant difference being the higher frequency of inactive perching by females. Because females were less easily seen than males when breeding, they contributed only 33% (n= 1741) of the observations from April to July. Consequently, the overall results for this period reflected the activity of males, rather than of females.

Figure 3.3   Differences in the frequencies of activities between males
             and females.

Using combined data for 1976-78.

(a)   Inactive perching.

(b)   Directional flight.

(c)   Display and defence.

(d)   Hunting.

        All frequencies are expressed as a percentage of the total
observations of tagged Kestrels of each sex per month. Confidence
limits are ± 2 S.E.%, calculated assuming a binomial-like distribution,
and are only given where those of male and female do not overlap.

        Estimates for females during the breeding season are from
sightings only, and refer to non-brooding activity.
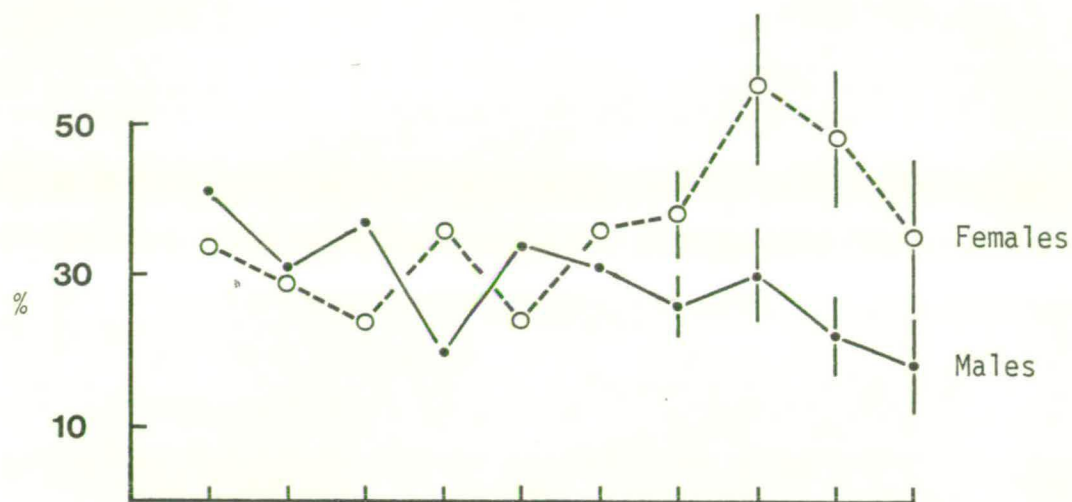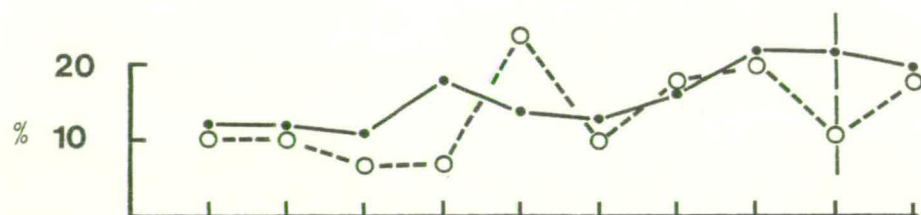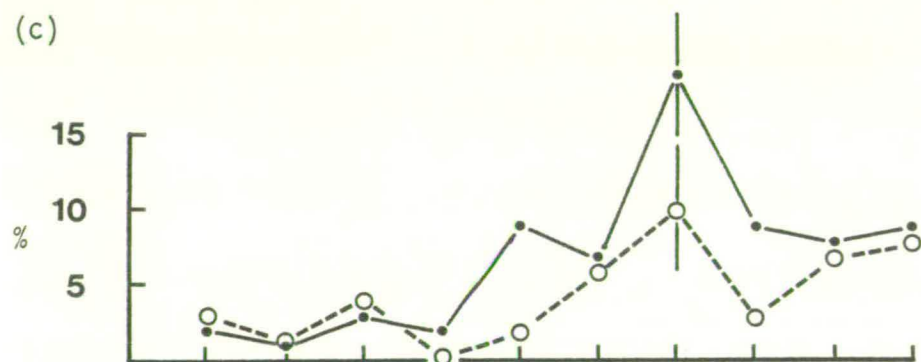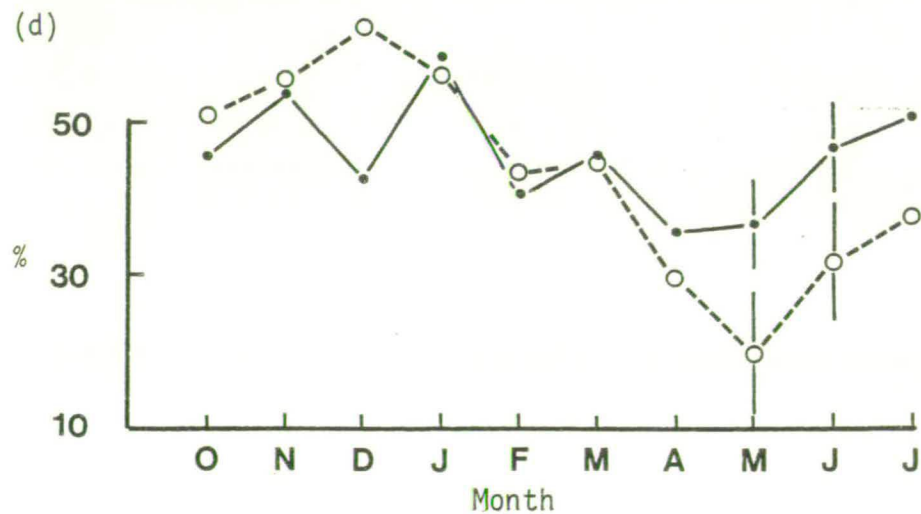
ENERGY BUDGETS.

Methods.

The energy demands of the various Kestrel activities were not measured directly, so all estimates were approximations based on published figures from other species. The Basal Metabolic Rate (BMR) was calculated from body weight using published data for non-passerine birds (Ashoff and Pohl 1970). The BMR is measured in thermoneutral conditions (i.e. at about 30 °C) and does not reflect the actual metabolic rate of birds at rest in the wild. Because of the large temperature variation through the year at Eskdalemuir, the BMR was adjusted to give the metabolic rate at the mean monthly temperature (MR_{ta}), again using published equations (Calder and King 1974). Apart from the breeding season, metabolic rates were calculated assuming a constant body weight of 218 g (Table 3.1). Although mean monthly weights varied through the year and between the sexes, the effect of this variation on the estimates of Daily Energy Expenditure (DEE) was negligible. The calorific equivalent for each activity was found by multiplying the MR_{ta} by increments given in King (1974) and Tarboton (1978). Various estimates have been used to calculate the cost of flight: Tucker (1974) suggested the value of 17.2xBMR, but other workers used values of 12-14xBMR (e.g. Custer and Pitelka 1972, Utter 1971 and Wakeley 1978). Kestrels probably expended more energy in hovering than in ordinary

flight, so I used $17 \times MR_{ta}$ for hunting flight and $12 \times MR_{ta}$ for directional flight (which included some glides). Displays varied from high-activity 'fluttering' to low-activity soaring, so energy consumption was calculated as for ordinary flight.

The estimates of DEE for each month varied considerably according to the metabolic rate chosen and the increment used to estimate the cost of flight. Therefore, in addition to calculating DEE as outlined above, I also calculated maximum and minimum likely estimates for each month and assumed the real value lay somewhere between the two. My main interest was in the changes of DEE from season to season, rather than in the values themselves. During the breeding season, energy consumption was calculated both from all sightings and for each sex separately, using tagged birds only. Most of the sightings in the breeding season were of males, so energy budgets calculated from all sightings at this time reflected the DEE of males, rather than of brooding females. The energetic costs of egg production and incubation were calculated from published figures (Ricklefs 1974), taking April, May and June to correspond approximately to the pre-lay, incubation and early nestling periods respectively. Females were assumed to average 90% of daylight hours on the nest during incubation and 50% during the nestling period, figures which seemed reasonable from observations made by Tinbergen (1940) and others.

Results.

(a) Seasonal changes in energy expenditure. Daily energy expenditure, estimated by the above methods using all sightings, varied according to the time of year, from 50.6-95.7 Kcal in December to 156.1-257.5 Kcal in June (Tables 3.1 and 3.2). These values referred to all birds from October to March, but mainly to males within the breeding season. The importance of each behaviour in affecting the size of the DEE depended on its cost and its frequency. Thus, at all times of year, flight-hunting used more energy per day than perched-hunting, even in January when Kestrels spent less than 10% of daylight hours flight-hunting (Fig. 3.4). The main cause of the seasonal changes in DEE was the increased day length in summer which meant that more hours per day were spent awake and less at roost (the least expensive activity per unit time). However, even when changes in day length were allowed for, birds still used more energy per daylight hour in summer than in winter (Table 3.1). This was because of the tendency to hunt by flying instead of perching and because more time was spent in display and defence. Thus in January, the majority of the DEE was used in roosting, perched-hunting and directional flight; whereas in July, the majority was used in flight-hunting and only a small percentage in roosting or in day-time perching (Fig. 3.4).

(b) Differences between the sexes in the breeding season. During the breeding season, the energy budgets found from all

Table 3.1 Monthly estimates of daily energy expenditure from frequencies of activities, using all sightings.

	D.L.	t_m	MR_{ta}	FLIGHT Directional		Hunting		PERCHING Inactive		Hunting		DISPLAY+ DEFENCE		ROOSTING		TOTAL DEE	EEH
	hrs	°C	Kcals	hrs	Kcals	hrs	Kcals	hrs	Kcals	hrs	Kcals	hrs	Kcals	hrs	Kcals	Kcals	Kcals
Oct	9.7	7.6	1.44	1.3	22.5	2.9	71.0	3.4	6.4	2.0	7.2	0.2	3.5	14.3	20.6	131.2	11.4
Nov	7.8	4.8	1.54	0.9	16.6	1.6	41.9	2.6	5.2	2.7	10.4	0.1	1.9	16.2	25.0	101.0	9.7
Dec	7.0	2.8	1.58	0.7	13.3	1.0	26.9	2.3	4.7	2.6	10.3	0.3	5.7	17.0	26.9	87.8	8.7
Jan	7.8	1.4	1.87	1.6	35.9	0.6	19.1	1.9	4.6	3.7	17.3	0.2	4.5	16.2	30.3	111.7	10.4
Feb	9.7	1.8	1.82	1.8	39.3	1.0	30.9	3.0	7.1	3.2	14.6	0.7	15.3	14.3	26.0	133.2	10.6
Mar	12.0	3.6	1.73	1.7	35.3	2.8	82.3	4.0	9.0	2.6	11.3	0.8	16.6	12.0	20.8	175.3	12.9
Apr	14.4	5.8	1.63	2.5	48.9	3.3	91.4	4.5	9.5	1.7	6.9	2.3	45.0	9.6	15.7	217.4	14.0
May	16.3	8.9	1.49	3.2	57.2	4.2	106.4	5.7	11.0	1.5	5.6	1.7	30.4	7.7	11.5	222.1	12.9
June	17.1	11.7	1.34	3.6	57.9	6.7	152.6	5.0	8.7	0.9	3.0	1.4	22.5	6.9	9.3	254.0	14.3
July	16.3	13.3	1.30	2.9	45.2	6.9	152.5	4.2	7.1	1.3	4.2	1.3	20.3	7.7	10.0	239.3	14.1

D.L.= Daylight hours, t_m= mean monthly temperature, DEE= Daily Energy Expenditure, EEH=Energy Expenditure/hr of daylight.

Values under 'hrs' are hours per day, energy expenditures are Kcals/day, apart from MR_{ta} and EEH which are Kcals/hr.

MR_{ta} = estimated metabolic rate at mean monthly temperature, calculated using:

Mean weight of Kestrel, m= 218g, Heat transfer coefficient, $h= 4.06m^{-0.54}$ (Calder and King 1974, non-passerines)

= 0.22 cal/g/hr/°C. Assumed body temperature, $T_b= 40°C$, Lower critical temp. $(T_{lc})= T_b - 4.73m^{0.274}$ (Calder

and King 1974, non-passerines) = 19 °C.

This is above all the mean monthly temperatures, so $MR_{ta}= h(T_b - T_a)$ (Calder and King 1974),

using t_m as T_a (ambient temperature).

Table 3.2 Maximum (#) and minimum (*) likely estimates of

Daily Energy Expenditure per month.

Estimates are based on observations of all birds and those from April to July reflect the energy expenditure of males and non-brooding females only.

Met. rate: Flight inc.:	BMR* 12	BMR 17	MR 12	MR# 17
October	76.6	98.6	110.3	142.0
November	57.6	70.6	88.7	108.7
December	50.6	60.6	79.9	95.7
January	56.7	68.7	106.1	128.5
February	68.2	85.7	124.1	156.0
March	87.3	113.8	151.1	196.9
April	116.9	157.4	190.6	256.5
May	128.1	173.6	190.8	258.6
June	156.1	214.6	209.1	257.5
July	149.5	205.1	194.4	266.6
MEAN	94.8	124.9	144.5	186.7

BMR= Basal Metabolic Rate, given by: $3.06M^{0.734}$

(Ashoff and Pohl 1970, non-passerines)

= 1.00 Kcals/hr for 218g Kestrel.

MR= Metabolic Rate at ambient temperature, (see Table 3.1)

Flight inc.= increment used for flight (see text page 57).

Figure 3.4 The contribution of various activities to the total
daily energy expenditure in different months.
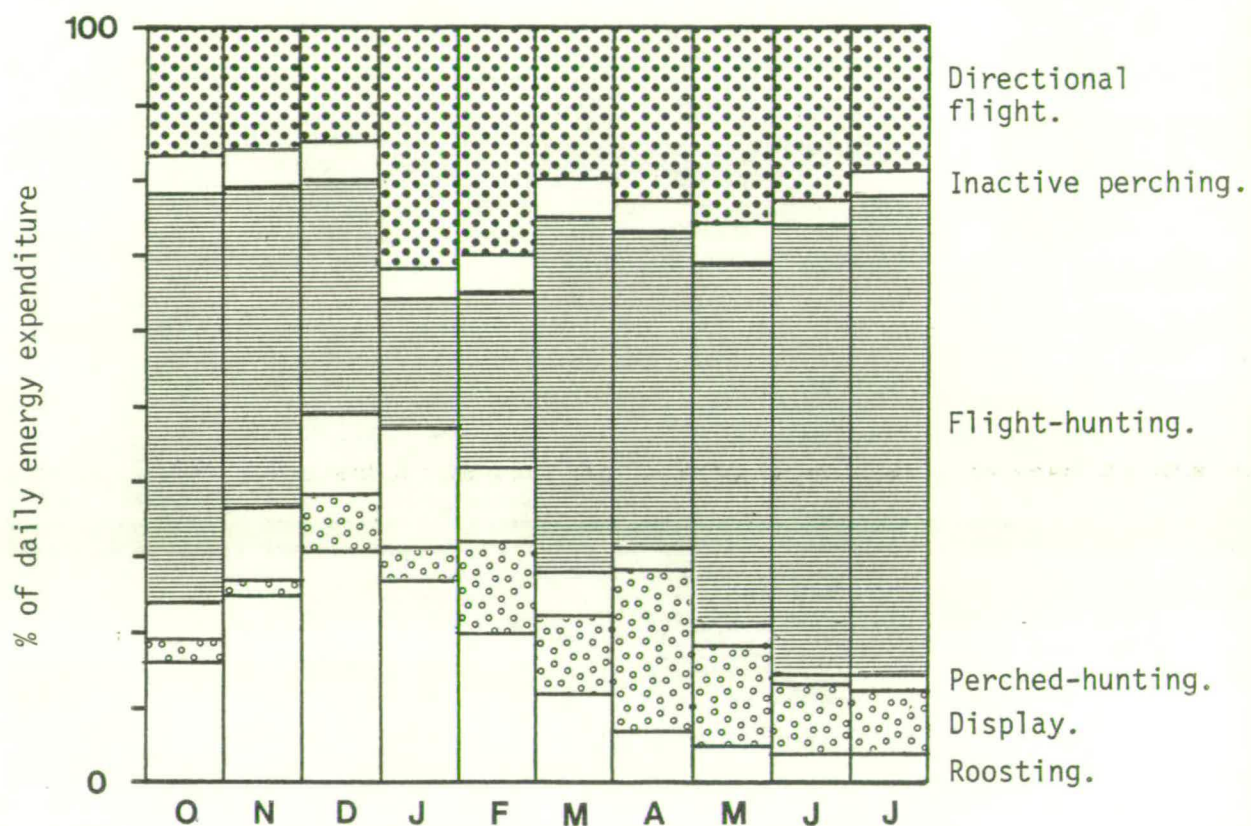
Frequency is expressed as a percentage of the daily energy
expenditure for each month, estimated from sightings of all Kestrels.

Data for the breeding season are for males and non-brooding
females only.

sightings differed by less than 5% from those found for tagged males only, for reasons explained earlier. DEE was similar between the sexes in the pre-lay period, even though females were less active than males. This was because females were assumed to have an increased energy consumption when producing eggs (Table 3.3, broken line Fig 3.5). Females used much less energy than males during the incubation and early nestling periods, but in July females increased their hunting activity and their DEE was only slightly lower than that of males.

Discussion.

The difficulties of assessing the frequencies of activities by spot observations, and the lack of direct measurements of the costs of each activity, meant that the above methods were unsuitable for calculating accurate values of daily energy expenditure. However, they were assumed to give a rough estimate of changes in energy consumption from month to month because seasonal changes in DEE showed the same trends when different methods of calculation were used (Table 3.2).

When comparable methods of estimating DEE were used, my results were in line with those found elsewhere in Kestrels and similar raptors (Table 3.4), though none of these studies estimated changes in energy expenditure through the year so it was difficult to make valid comparisons. What little work has been done on

Table 3.3 Differences in the daily energy expenditure (DEE) of males and females during the breeding season.

		WT.	BMR	MR_{ta}	FLIGHT Directional		Hunting		PERCHING Inactive		Hunting		DISPLAY+ DEFENCE		BROODING OR ROOSTING		EEP	BRE	TOTAL DEE
		g	Kcals	Kcals	hrs	Kcals	hrs	Kcals	hrs	Kcals	hrs	Kcals	hrs	Kcals	hrs	Kcals	Kcals	Kcals	Kcals
Apr	M	207	0.96	1.61	2.3	44.4	3.3	90.3	3.8	8.0	1.8	7.3	2.9	56.0	9.6	15.5	–	–	221.4
	F	222	1.01	1.66	2.3	45.8	2.4	67.7	5.5	11.9	2.0	8.3	1.5	29.9	9.6	15.9	36.4	–	215.9
May	M	210	0.97	1.48	3.6	63.9	4.6	115.7	4.9	9.4	1.5	5.6	1.6	28.4	7.7	11.4	–	–	234.4
	F	281	1.21	1.69	0.3	6.1	0.2	5.8	0.9	2.0	0.1	0.4	0.1	1.0	22.4	37.9	–	11.6	64.8
June	M	200	0.94	1.31	3.7	58.2	7.0	155.9	3.8	6.5	1.0	3.3	1.5	23.6	6.9	9.0	–	–	256.5
	F	255	1.12	1.47	0.9	15.9	2.4	60.0	4.1	7.8	0.3	1.1	0.7	12.3	15.5	22.9	–	7.2	127.1
July	M	199	0.94	1.24	3.3	49.1	6.8	143.3	3.0	4.8	1.5	4.7	1.7	25.3	7.7	9.6	–	–	236.8
	F	238	1.07	1.34	2.9	46.6	5.5	125.3	5.7	9.9	0.7	2.4	1.5	24.1	7.7	10.3	–	–	218.6

'hrs'= hours/day, Kcals are Kcals/day, apart from MR_{ta} and BMR, which are Kcals/hr.
M= males, F= females, WT.= mean weight for month (from Fig. 3.6), EEP= energy used in egg production, BRE = energy used
brooding. EEP taken as 1.5BMR/day (Ricklefs 1974). BRE found by the clutch weight method (Ricklefs 1974), assuming:
mean egg temp.=35°C (Ricklefs 1974), mean clutch size=5.0 (chapter 6), mean egg weight=21g (Newton 1977), ambient
temp. (T_a)=mean monthly temp. and calculating thermal conductance, h, as in Table 3.1. Hence: BRE =(clutch weight)x(body temp.-T_a)xh/1000 Kcals/hr =0.518 Kcals/hr in May. Values for June (i.e. early nestling period)
found by using the same method.

Figure 3.5   Seasonal changes in estimated daily energy expenditure
              (DEE) of free-living Kestrels.
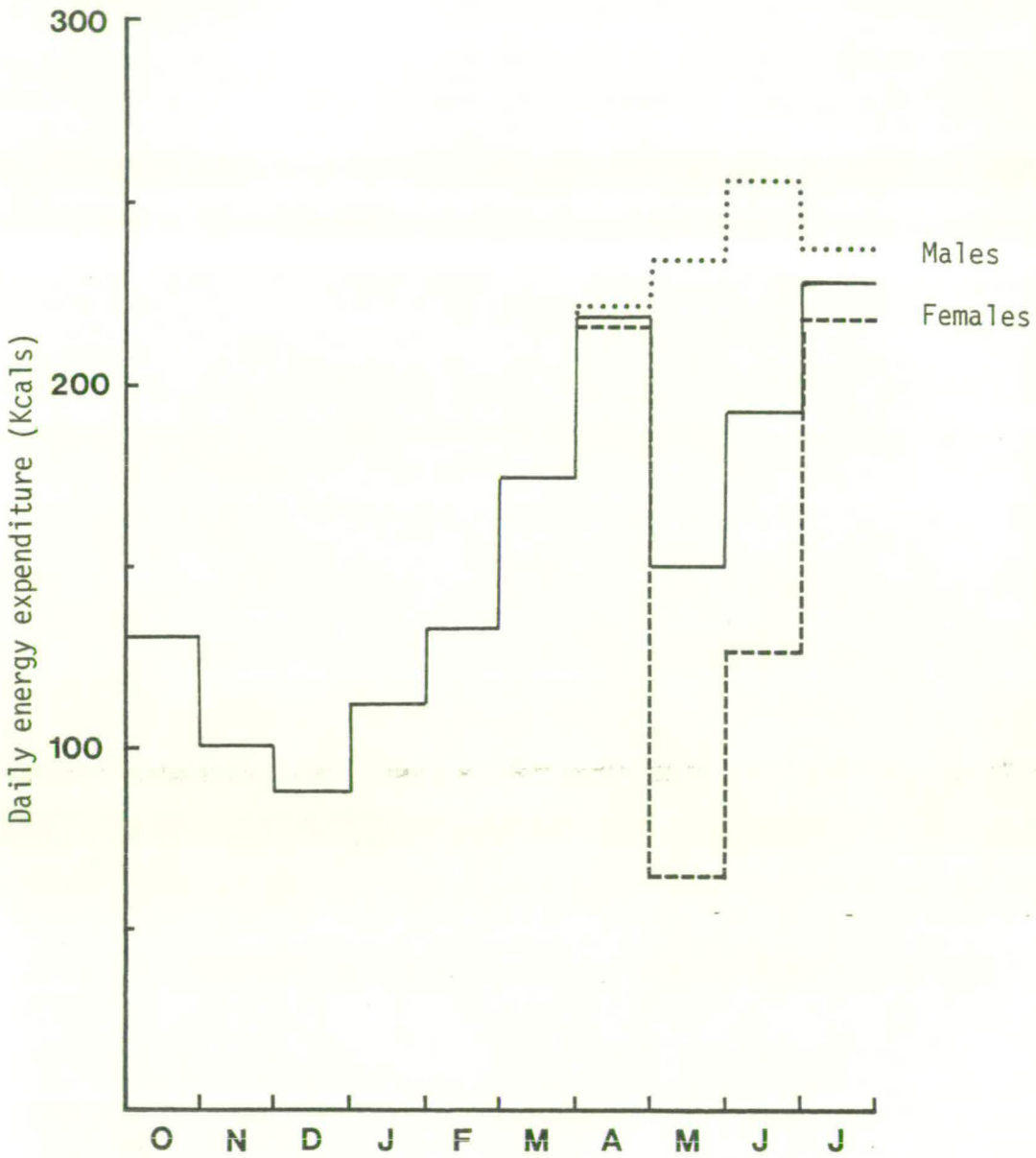
Values from October to March were taken from Table 3.1. Those
for the breeding season are of males (.....) and females (----), taken
from Table 3.3, with the mean of the two estimates (———).

seasonal changes of energy budgets in birds has suggested that DEE either does not vary by much or that it is highest in winter (King 1974). The opposite seemed to be true in Kestrels, with energy expenditure in winter being lower than in the breeding season, even allowing for the low energy consumption of incubating females. No estimate was made of the costs of moult (which in both sexes started during incubation and continued into autumn) and this would have further increased the summer DEE relative to that in winter. The low energy consumption in winter was due partly to the shorter days and partly because birds did less hunting by flying and more from perches.

The different energy consumption of males and females during the breeding season was a result of the division of labour at this time. From the pre-lay stage onwards, males did the bulk of the hunting and had to provide food for themselves, their partners and, later, their young. Females did less hunting prior to laying than earlier in the year, and the resulting decrease in energy expenditure may have made more energy available for egg production (though the main limit to egg production was probably the amount of fat and protein available for egg formation, rather than the availability of energy). Although females may have captured less prey themselves at this time, the loss was compensated by food brought by the male. The food-gathering demands on the male may have fallen once the eggs were produced, because the overall energy consumption of the pair decreased during incubation, but then

Table 3.4 Comparison of the estimated DEE of Kestrels at Eskdalemuir

with that of Kestrels or similar raptors elsewhere, from

other studies.

Species	Country	Months	Met. rate	Flight inc.	DEE Kcals	Source
Kestrel	Sweden	October	BMR	10.8	74.0	Sylven (1974)
Kestrel	Scotland	October	BMR	12.0	76.6	Village (1979)
Black-shouldered Kite	South Africa	all	BMR	17.2	82.3*	Tarboton (1979)
Kestrel	Scotland	all(mean)	BMR	17.0	124.9	Village (1979)

Met. rate= Metabolic rate used throughout.

Flight inc.= Flight increment used throughout.

DEE= Daily Energy Expenditure.

*The esimate of DEE given in this source is 98.3, but this was

based on the incorrect formula: BMR= $3.60M^{0.734}$ Kcal/hr

(Ashoff and Pohl 1970). This should be $3.06M^{0.734}$, and the

estimate given here is that recakulated from the correct formula.

increased again after the young had hatched. This suggests that the most demanding stages of the breeding cycle were: (a) prior to, and during, egg-lay, when both birds had high energy expenditures and males did most of the hunting, and (b) in the early nestling stage, when males had to meet the needs of both females and young. This may be generally true of raptors (Brown 1976, Newton 1979). Feeding rates increased later in the nestling period (Tinbergen 1940), but females did a greater share of the hunting and this may have reduced the demands on the male.

BODY WEIGHT AND CONDITION.

Methods.

To see whether the nutritional state of Kestrels reflected seasonal changes in energy consumption, I examined the mean weights and body condition of adults and juveniles throughout the year. Body condition was measured approximately, by feeling the breast of trapped birds and rating the size of the flight muscles on a scale of 1 (= small) to 5 (= large). The size of these muscles was assumed to be related to the protein content of the body (Ward 1969, Jones and Ward 1976). I did no trapping in August or September, so data for these months were taken from Kestrels caught elsewhere in Dumfrieshire from 1971 to 1977 (M. Marquiss and I. Newton). The coverage of other months was uneven; large numbers were trapped on the nest during summer, but few were caught in some other months and none in January. Body weights for each sex had to be treated separately because females were generally larger and heavier than males and had a different annual weight-cycle. Although most first-year birds caught in summer were breeding, those caught in autumn had just fledged, so were treated separately from adults.

Results.

(a) Comparison of body weight and condition between months was limited because of the low sample sizes in each category. However, the following trends were apparent (Fig. 3.6):

(i) Adult females rapidly gained weight from April to May but gradually lost it thereafter, whereas adult males showed a less pronounced decline from February onwards, with no large pre-laying peak. Adults were lightest in early autumn, but seemed to increase in weight by November. There were insufficient samples to show whether mean body weight declined during winter, but both sexes seemed to be heavier in November than in February.

(ii) Juveniles were lightest in September, about two months after fledging and, like adults, increased in weight in late autumn. During the breeding season, yearlings showed similar weight changes to adults. Although there were no significant differences in the mean weights of adults and juveniles in the few months that this could be tested, in both sexes, adults seemed heavier than juveniles in autumn.

(iii) Monthly changes in breast-muscle size were similar in both sexes and in adults and yearlings (Fig. 3.7). Body condition increased from March to April in both sexes, though this was less obvious in females, possibly because of the low samples. In males and females, body condition declined from April until July, but increased in autumn to a possible peak in October. I had insufficient data to decide whether juveniles were in poorer

Figure 3.6   Mean monthly body weights of trapped adult and juvenile
             Kestrels.

(a) Males.

(b) Females.

         Solid line = adults, broken line = juveniles.

     Points in parentheses are based on a single weight only. Values
above the graphs are the sample sizes in each age group per month,
adults on the top line, juveniles below.

     Arrows mark the approximate fledging period, the annual cycle for
juvenile birds starting at this point.

(a) Males.
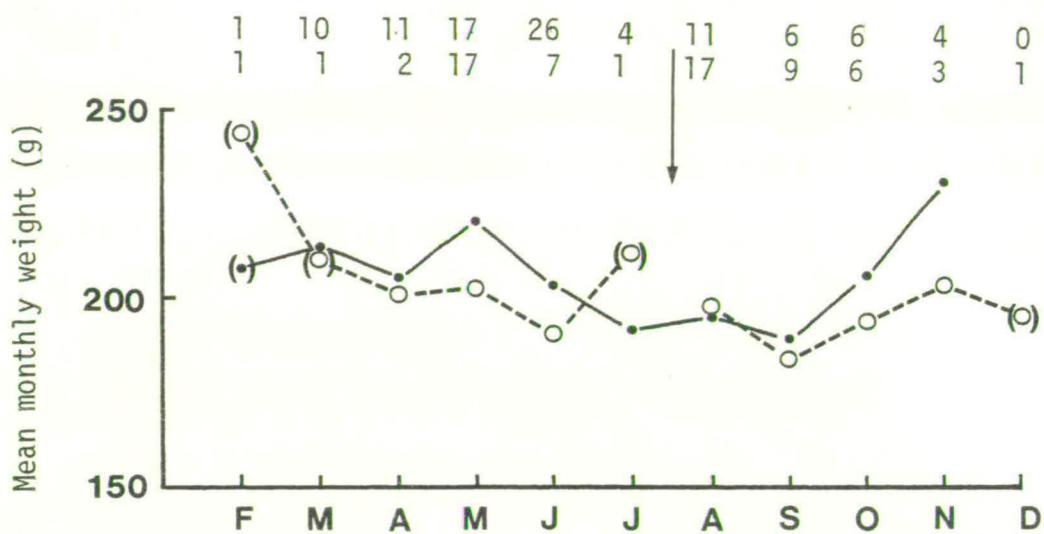
(b) Females.
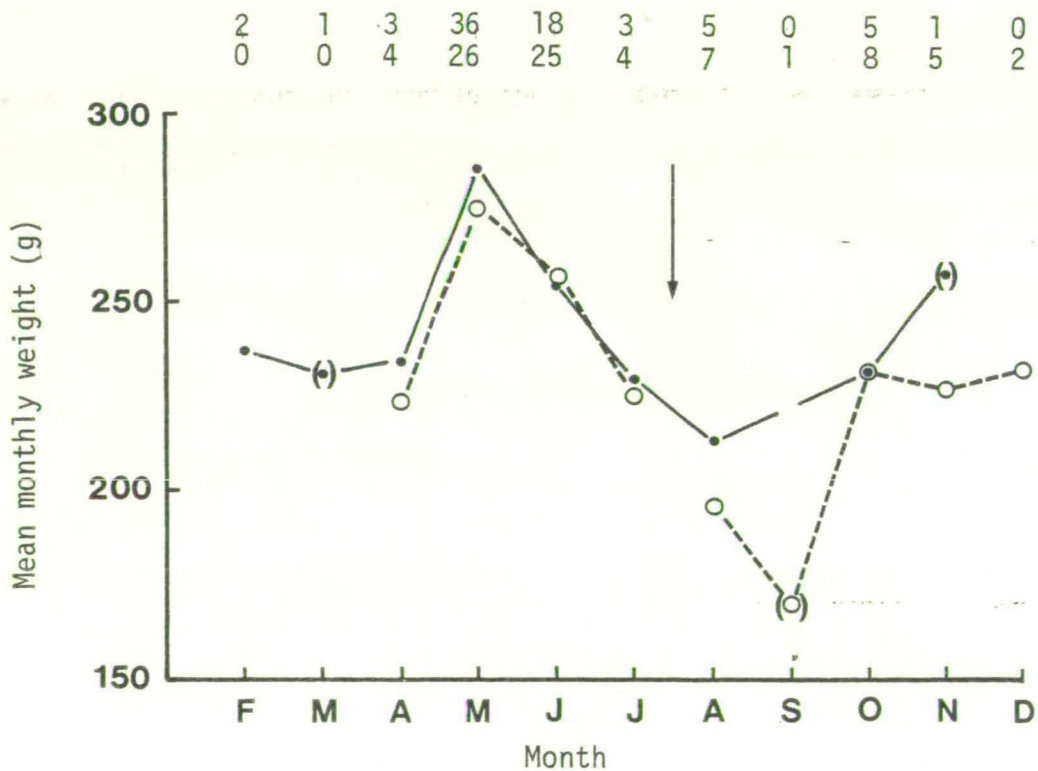
Figure 3.7 Mean monthly body condition of trapped adult and juvenile
            Kestrels

(a) Males.

(b) Females.

     Solid line = adults,   Broken line = juveniles.

     Body condition was measured as the breast-muscle size index of
trapped birds. Points in parentheses are based on a single bird. Values
above the graphs are sample sizes of each group per month.

     Arrows mark the approximate fledging period, the annual cycle for
juveniles starting at this point.
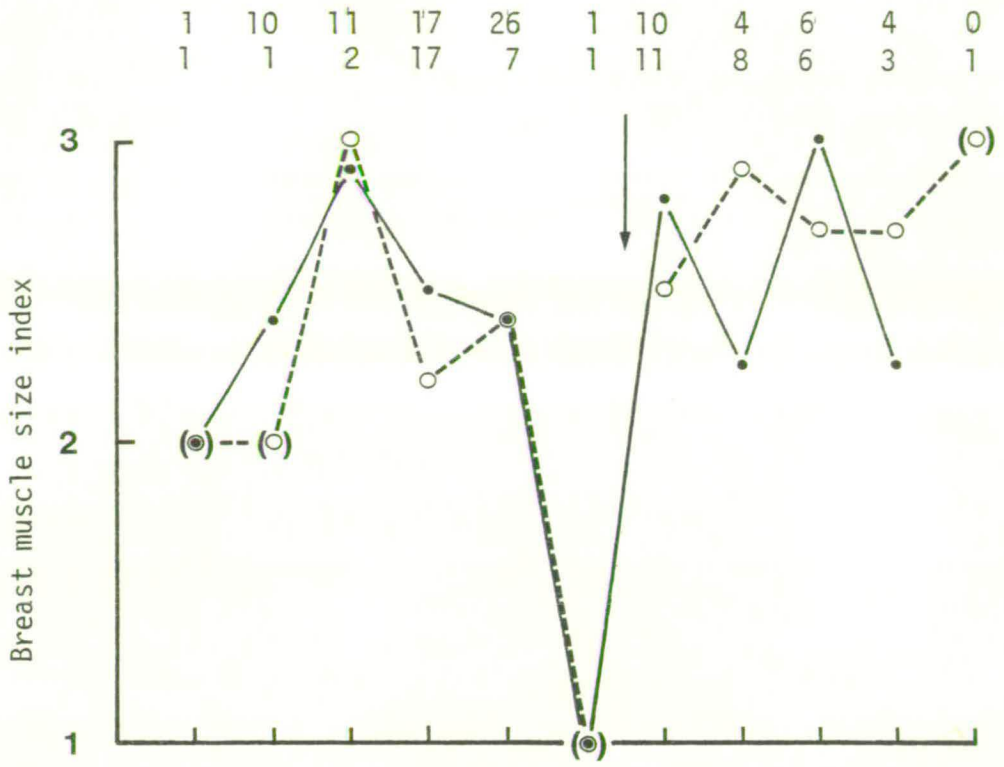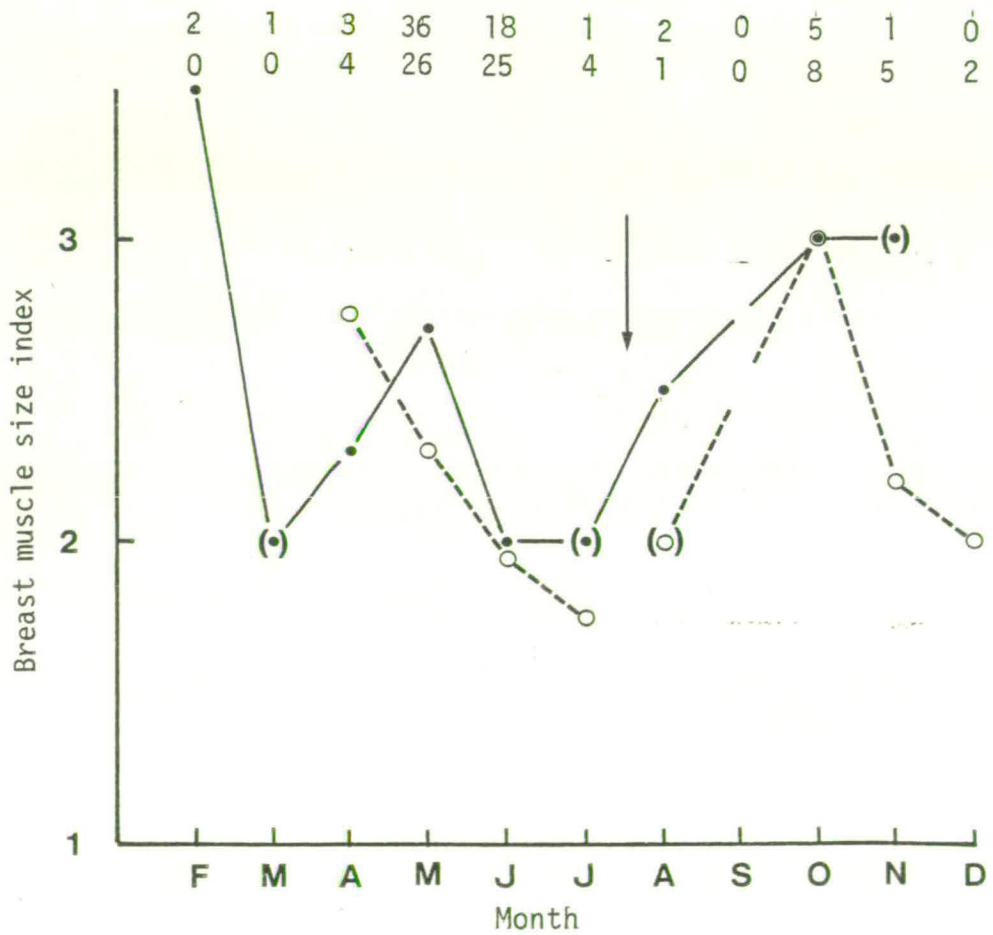
condition than adults in autumn, or whether condition decreased during winter.

(b) To examine weight changes during the breeding cycle more closely, I plotted the weights of all breeding Kestrels (expressed as weight/wing length, to reduce the variation due to body size), according to their stage of breeding when caught (Fig. 3.8). Males showed little weight change prior to clutch completion by their partners, but a significant decline thereafter. There were few weights for females prior to laying, but they indicated an increase in weight until laying and a decline thereafter.

Discussion.

The levels of protein and fat reserves in wild birds may play an important part in the proximate control of laying dates and clutch size (Ward 1969, Fogden 1972, Jones and Ward 1976, Newton 1979 for raptors). These reserves are used both for the production of eggs and for maintenance during the incubation- and nestling periods. Thus, in raptors where only the female incubates, only females gain weight in the prelay period; whereas in raptors where incubation is shared, both sexes increase in weight prior to lay (Newton 1979). Extra nutritional stores seem to be required by the female during incubation to reduce the effects of temporary food shortages, which have been shown to lead to clutch-desertion or even death in some species (Cave´ 1968, Newton 1976, Jones and Ward 1979).

Figure 3.8   Changes in the body weight of males and females during the
             breeding cycle.

(a)   Males.

      Lines are fitted regressions:
           Prior to laying -
                Y =   0.0012X + 0.85
                          (S.E. b=0.0031, not significant).

           After laying -
                Y =   -0.0056X + 0.93
                          (S.E. b=0.0026, P < 0.05).

(b)   Females.

      Lines are fitted regressions:
           Prior to laying -
                Y =   0.0347X + 0.79
                          (r =   0.6815, P < 0.01).

           After laying -
                Y =   -0.0217X + 1.33
                          (S.E. b=0.0031, P < 0.001).

      Body weight expressed as weight/wing length.   Breeding cycle taken
from 10 weeks prior to clutch completion.   Arrows mark the week in which
the clutch was completed.

(a) Males.

(b) Females.
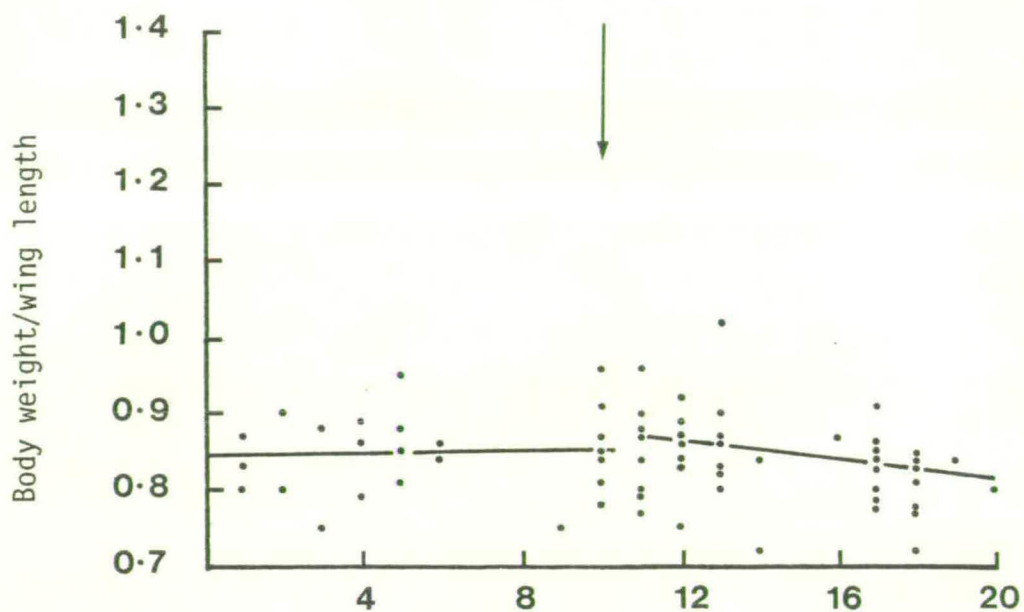
Stage of breeding cycle (weeks)
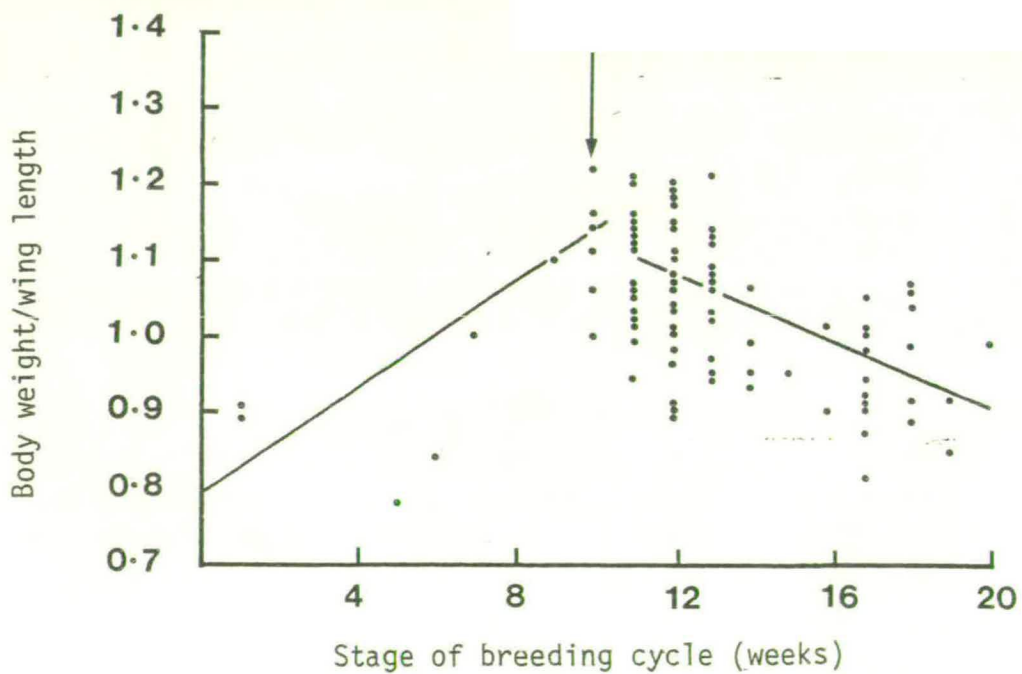
The observed changes in the weight and condition of Kestrels during the breeding cycle are in line with those noted in other raptors in which only the female incubates (e.g. Sparrowhawks, Newton 1979; Tawny Owls, Hirons 1976). Thus females, but not males, gained weight prior to lay and remained heavy even after all eggs had been laid. Some of this weight gain may have been caused by enlargement of the egg-producing organs, but most of it was probably due to a build up of body reserves. The mean breast-muscle size of females showed only a slight increase corresponding to their gain in weight from April to May, and was not significantly different from that of males (who showed no gain in weight). This could be because the increase in female weight was due largely to a build up of fat rather than of protein, but more measurements are needed to confirm this as few females were caught before laying. Both sexes lost weight slowly after clutch completion, suggesting that body reserves were gradually depleted during the incubation and nestling periods. The loss in females was more noticeable because of the increase in weight prior to laying. Although this loss may have been due in part to atrophy of the oviduct, the decline in condition at this time indicated that a general loss of nutritional reserves was the main cause.

Although energy reserves were only part of the nutritional balance during the breeding season, the changes in body weight were roughly in line with the activity and DEE of each sex. Thus females

gained weight around the time they began hunting less and so had a reduced energy consumption. Courtship feeding prior to laying may have helped females to gain weight faster, and so lay earlier, than if they had fed themselves. Males became lighter through the breeding season, when they were feeding their mates or young and had a high DEE. The loss of weight during incubation by both sexes indicated that this was a period of considerable nutritional stress and that food shortage could have been a major factor in causing clutch desertion (as suggested by Cave´ 1968).

Adults and juveniles may have had low body weights in early autumn for different reasons. In juveniles, this may have been because they were still growing or because they had recently fledged and found it more difficult to obtain food than did adults. The low weight of adults in September was probably because their body reserves were depleted during breeding. The increase in mean weights from August to October may also have occurred for different reasons, with breeding adults recovering their condition and juveniles improving their hunting ability. Alternatively, mean weights may have increased because low-weight individuals of both groups died.

HUNTING BEHAVIOUR.

Whether Kestrels hunted from perches or from the wing may have been affected by the relative capture rates of the two techniques and by the weather. Unfortunately, lack of time prevented any measurments of prey capture rates during the study, but I collected some data in autumn 1979, which are included below.

Methods.

(a) Hunting success was measured by following birds for as long as possible during hunting sessions and recording the number of kills they made. Kestrels killed by diving at prey, either from a perch or while flying. The term 'full strike' was used for dives that ended on the ground, and 'half strike' for dives abandoned before landing (following Tarboton 1978). Strikes made at vertebrate prey ended in sudden dives that were easily distinguished from the more gradual dives at invertebrates. This allowed most sessions to be classed according to the main prey-type hunted, even if no kills were made. Sessions with no strikes, or those including fast and slow dives, were not used to test between the hunting of different prey types. The classification of kills was easier, invertebrates being eaten immediately (either on the ground or on the wing), whereas larger prey were first carried to a suitable perch. This meant that some invertebrate kills were probably missed, as I could not always see if birds captured small

prey, so capture rates for invertebrates were minimum values.

(b) Weather and hunting. To examine the relationship of wind and temperature to hunting, I used data from October 1976 to July 1978, for the periods October/November, March/April and June/July. Each time a bird was seen hunting its location and method were recorded. Whenever possible I further classified flying-hunting birds as either 'hovering', 'hanging' or 'mixed'. Wind speed and direction were assigned later using hourly values recorded at Eskdalemuir meterological observatory, which was approximately in the centre of the study area. Within each period, observations were grouped if they were made at the same windspeed (using windspeed classes spanning 2 knots) and the percentage of activities was then found for each class. Similarly, daily temperatures were found by averaging the day-maximum and day-minimum values and observations were grouped if they occurred at the same daily temperature. To make results from each period compatible, I used only those sightings made between 1000 and 1500 GMT. Precipitation may have affected hunting, so I discounted records made on days when more than 1 mm of rain fell between 0900 and 2100 GMT.

Results.

Hunting performance.

The overall capture rate during the 21.1 hours of hunting observed was 2.42 kills/hr, 51(40%) of the 129 strikes being successful. However, the capture rate during any session depended on the prey sought and the hunting method used (Table 3.5):

(a) The capture rate was significantly higher when Kestrels hunted invertebrates than when they hunted vertebrates, both for flight-hunting ($X2= 11.34$, $P<0.001$) and perched-hunting ($X2= 12.29$, $P<0.001$). This was mainly because of the higher strike rate when hunting smaller prey, rather than a higher proportion of successful strikes. The actual differences may have been larger than those observed because vertebrate captures were more easily seen than invertebrate ones.

(b) Kestrels had a higher strike rate when flight-hunting than when hunting perched, both for vertebrates ($X2= 24.81$, $P<0.001$) and for invertebrates ($X2= 8.31$, $P<0.01>0.001$). The difference in the methods was even larger when the overall data were used, because hunting sessions without strikes (which could not therefore be classified by prey type) were more frequent in perched than flying Kestrels. The proportion of successful strikes was similar in each method, so flight-hunting gave a higher capture rate than perched-hunting ($X2= 12.08$ $P<0.001$). There was no evidence that a

Table 3.5 Hunting performance of Kestrels in Eskdalemuir, autumn 1979.

	Flight-hunting				Perched-hunting				Both
	V	I	?	TOT	V	I	?	TOT	GTOT
Total time hrs	4.6	2.8	1.2	8.6	4.7	2.9	4.9	12.5	21.1
Full strikes	29	39	2	70	8	21	3	32	102
Half strikes	16	6	1	23	1	1	2	4	27
Total strikes	45	45	3	93	9	22	5	36	129
Strike rate/hr	9.8	16.1		10.8	1.9	7.6		2.9	6.1
No. kills	11	22	0	33	3	13	2	18	51
Success as % of:									
Full strikes	38	56		47	38	62		56	50
All strikes	24	49		36	33	59		50	40
Kill rate/hr	2.4	7.9		3.9	0.7	4.6	-	1.4	2.4

V= sessions where vertebrates were the main prey sought.

I= sessions where invertebrates were the main prey sought.

?= sessions where main prey type unknown.

TOT= total for method, GTOT= total for both methods.

higher proportion of vertebrate kills was taken when perched-hunting ($X2$= 1.12, P= 0.6), so the different capture rates of the two methods were not due to the type of prey hunted.

(c) To estimate the net energy gain from using each hunting method after each prey type, I used the capture rates in Table 3.5 to calculate the energy gain per hour of hunting (i.e. that gained from food minus that used in hunting) assuming that flight-hunting used 17xBMR Kcal/hr and perched-hunting 2.5xBMR Kcal/hr. Energy intake per item was estimated from published figures, assuming vertebrate prey to be equivalent to the averaged sized vole, and 'invertebrates' to be equivalent to an intake of equal numbers of earthworms and beetles (Fig. 3.9). The results suggested that flight-hunting gave a much greater energy return than perched-hunting if large prey were taken. As prey size fell, capture rates increased in both methods, but net energy gain still decreased because of the lower energy value of each item. The advantage of flight-hunting was lost as prey size fell, and both methods yielded similar energy gains when invertebrates were taken. Below this size of prey, flight-hunting may have created energy deficits sooner than hunting perched, because of its extra energy costs.

Figure 3.9   Estimated net energy gain per hour of hunting in relation
              to hunting method and prey size. (see text page 81).

CALCULATIONS:

Energy value of vertebrates:
     Mean weight of vole = 20g (N. Charles)
     Energy value   = 1.6 Kcals/g fresh wt.
                                (after Tarboton 1978).
     Energy value/vole   = approx. 30 Kcal.

Energy value of a diet of equal numbers of beetles and earthworms:
     Mean weight of Carabids
     and Geotrupids   = 0.8g (Yalden and Warburton 1979)
     Mean wt. Lumbricus   = 5.0g ("   "   "   ")
     Mean wt. per item   = 2.9g

Using 75% water content, mean dry wt. = 0.7g
     Energy value invertebrates   = 5.4 Kcal/g dry wt
                                          (after Pernetta 1976)
                                       = 3.9 Kcal/item

Capture rates for each method and item taken from Table 3.5.

Flight-hunting assumed to use 17xBMR = 17 Kcal/hr
Perched-hunting assumed to use 2.5xBMR = 2.5 Kcals/hr.
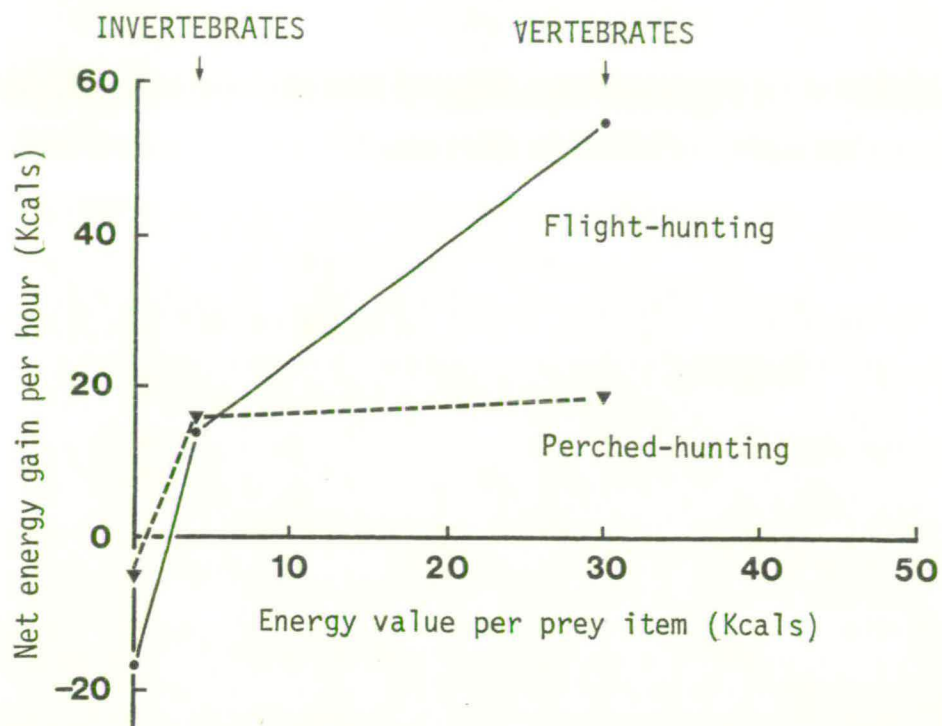
Hunting and weather.

1. Wind.

No relationship was apparent in any period between the overall frequency of hunting (i.e. the proportion of all observations that were of individuals hunting) and wind speed. Mean wind speeds were similar between months, but the proportion of hunting done by flying versus perching had to be tested separately for each period because the level of the two behaviours varied with time of year. Flight-hunting (as a percentage of hunting observations) was positively correlated with wind speed, the relationship being significant at the 0.1% level in October/November, 2% level in March/April but not significant in June/July (Fig. 3.10). Thus in summer, when young were being fed, birds flight-hunted regardless of wind conditions, whereas in autumn they hunted increasingly by flying as the wind became stronger. In March and April the method of hunting was still affected by the windspeed, but birds did more flight-hunting at lower windspeeds.

The way Kestrels hunted when flying depended on the uplift of the airstream, which in turn was related to the speed of the wind and the slope of the ground. This relationship was unlikely to have changed through the year, so data for all periods were combined for this analysis. The frequency of 'hovering' (expressed as a percentage of flying-hunting observations) was inversely correlated with wind speed (Fig. 3.11a, $r = -0.9658$, $P < 0.001$). The

Figure 3.10 The proportion of hunting observations that were flight-
hunting in relation to wind speed.

(a) October/November.

$$Y = 10.7X - 5.9$$
(S.E. b=1.49, $P < 0.001$)

(b) March/April.

$$Y = 5.2X + 24.8$$
(S.E. b=1.48, $P < 0.02$)

(c) June/July.

$$Y = 0.8X + 89.3$$
(S.E. b=1.39, lot significant)

Frequencies are expressed as a percentage of all hunting
observations that were flight-hunting per 2-monthly period. The total
of hunting observations at each windspeed is shown above each point.

(a)

(b)

(c)

Wind speed (Knots)
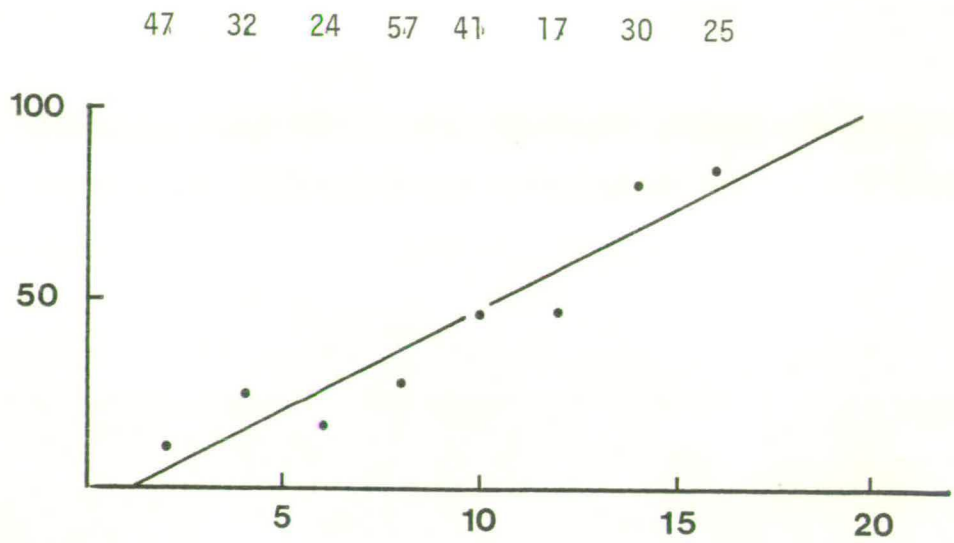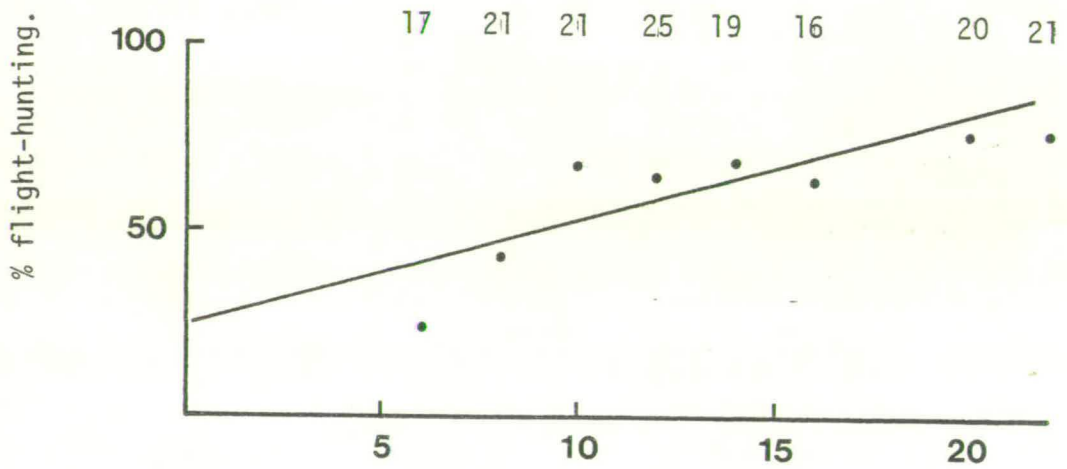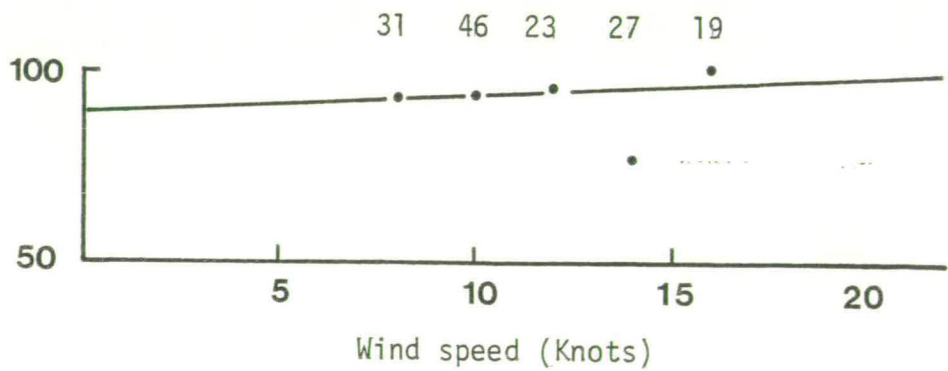
Figure 3.11   Relationship of the method of flight-hunting to wind speed
              (see text page 83).

(a)   Hovering.

      $Y = -10.7X + 109.3$
         (S.E. b=0.95, P < 0.001)

(b)   Mixed.

      $Y = 6.6X - 16.7$
         (S.E. b=1.37, P < 0.001)

(c)   Hanging.

      $Y = 4.0X + 7.4$
         (S.E. b=1.50, P < 0.05)

      The frequency of each method is expressed as a percentage of the
total flight-hunting observations at each wind speed. (This total is
given at the head of the opposite page.)

(a)

(b)

(c)
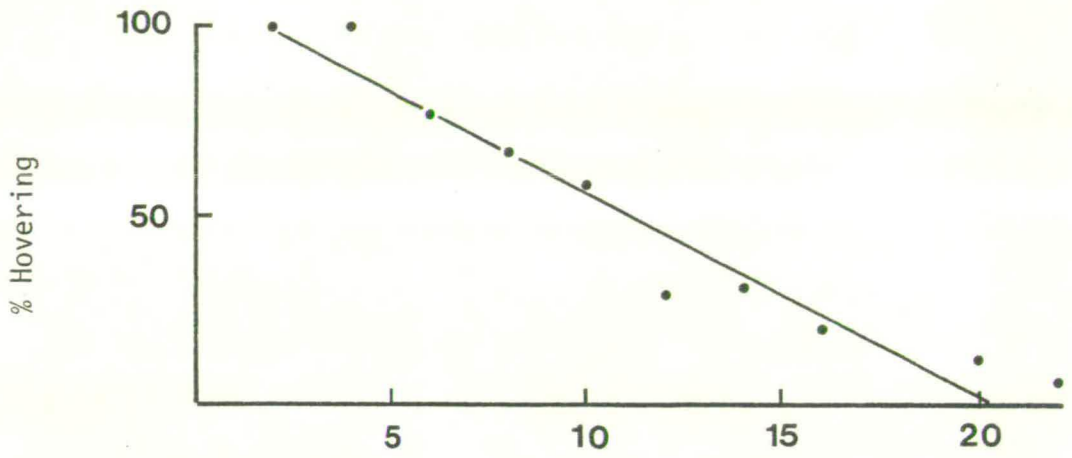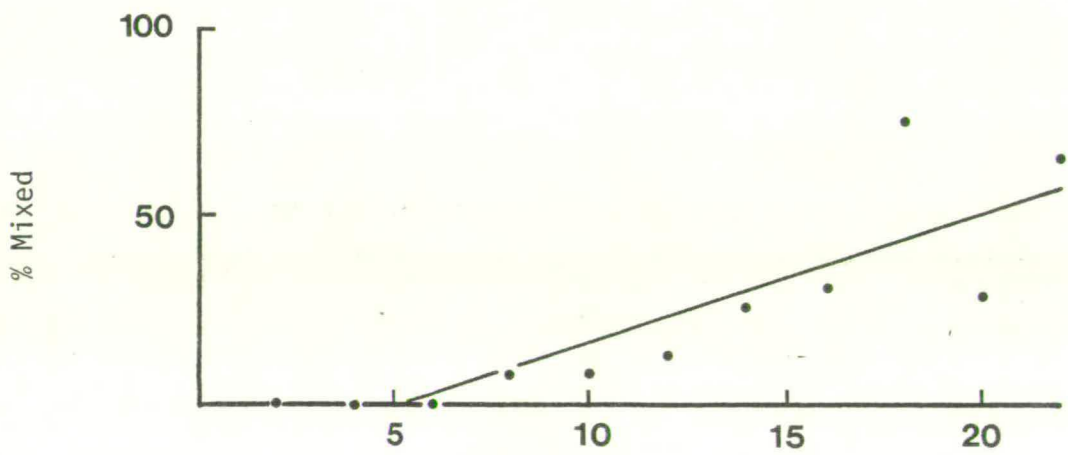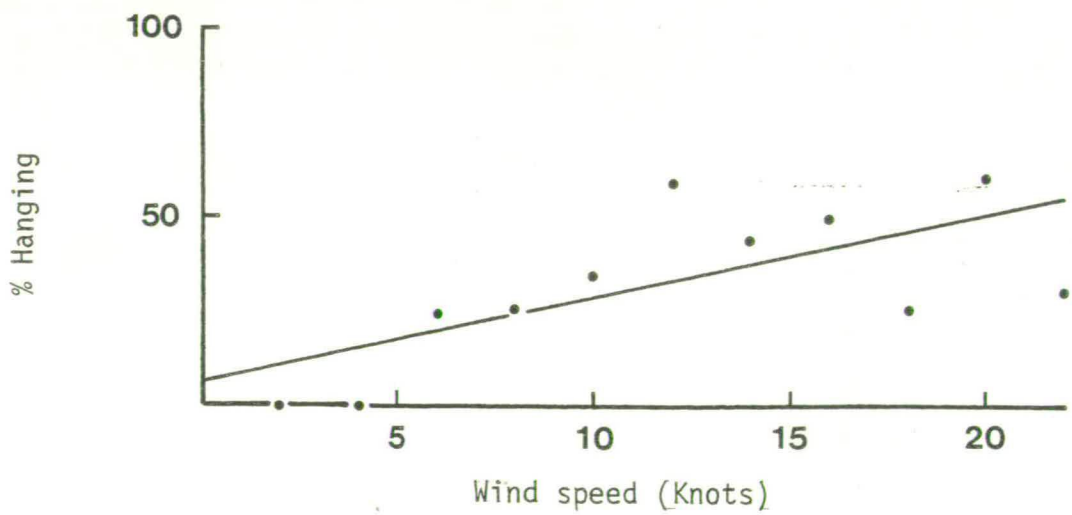
relationships for 'mixed' and 'hanging' hunting were less precise, probably because the two were more difficult to separate from one another (Fig. 3.11b-c). In strong winds, Kestrels sometimes had to beat their wings to prevent themselves being blown off position, and this was recorded as mixed rather than hanging hunting. Furthermore, the ability to hang in the air also depended on the the slope of the ground and this meant that, under the same wind conditions, birds could hang-hunt in some places but not in others.

Birds also tended to hunt on slopes which faced into the wind; to test this, I used data from October/November as this period had the most observations. The position of each flight-hunting bird was marked on a 1:20000 scale map and the slope direction was estimated from the contour lines. The few sightings which were not obviously on a slope, or were made on calm days, were ignored. Differences between wind and slope direction were then expressed as a frequency histogram (Fig. 3.12). There was a highly significant tendency for birds to hunt on the windward, rather than the leeward, slopes and in particular to use slopes that faced within 10 degees of the wind direction.

Figure 3.12   Histogram of observed and expected frequencies of the differences between wind direction
              and the direction of slopes used by flight-hunting Kestrels.   (See text page 86).

$$\frac{(Obs.-Ex.)^2}{Ex.} : 40.0 \quad 12.1 \quad 6.4 \quad 0.9 \quad 0.9 \quad 3.6 \quad 6.4 \quad 8.1 \quad 8.1$$

Wind direction minus slope direction (°)
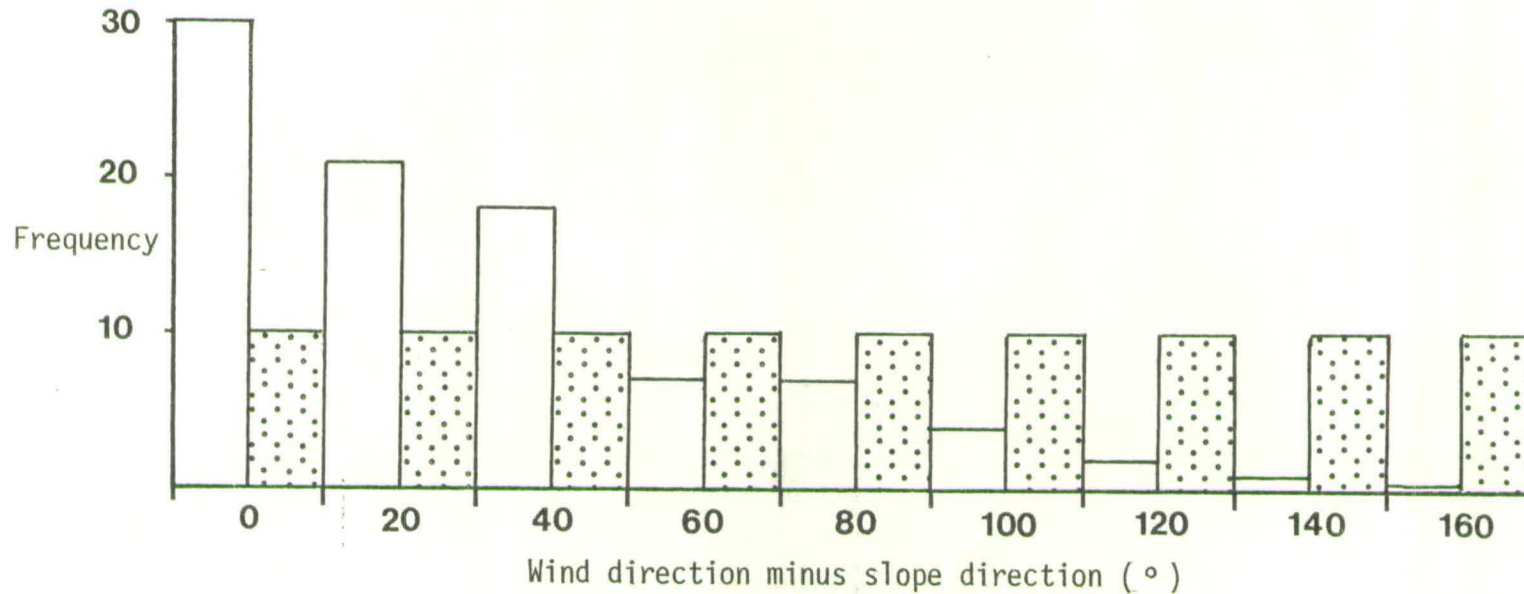
Chi-squared = 86.5   df = 8, P < 0.001.

     Classes span 20 and are labelled by their lowest value.   Expected frequencies calculated assuming slopes in
all directions were equally likely to be used by flight-hunting Kestrels.
Shaded area = expected frequencies,   unshaded = observed frequencies.

2. Temperature.

Wind speed explained much of the variation in hunting methods within some months, but it did not vary significantly between months so was unlikely to have caused the seasonal changes in the amount of perched versus flight-hunting. The seasonal change in hunting method did follow that of mean monthly temperature, and the two were significantly correlated (Fig. 3.13a, r= 0.8957, P<0.001). If temperature was important in affecting the mode of hunting used, birds would be expected to hunt more by flying on warm days and by perching on cold ones, within the same month. I tested this by comparing the frequency of the two activities at different daily temperatures using the same periods as in the wind speed analysis. In each case no relationship was evident between daily temperature and the proportion of hunting by flying (Fig. 3.13b). Unfortunately, no very hot days occurred in autumn and no very cold days in summer, so I could not examine each period over the full temperature range. Even so, there was no evidence of any relationship over ranges of -2 to +16 °C in autumn and 10 to 22 °C in summer, which suggests that, at least on a daily basis, birds did not alter their hunting method according to temperature.

The strong correlation of mean monthly temperature and hunting method might suggest that the two were related in the longer term, but this relationship may not imply cause and effect. The gradual increase in energy demands from winter to summer also coincided

Figure 3.13 The frequency of flight-hunting in relation to temperature.

(a) Flight-hunting and mean monthly temperature.
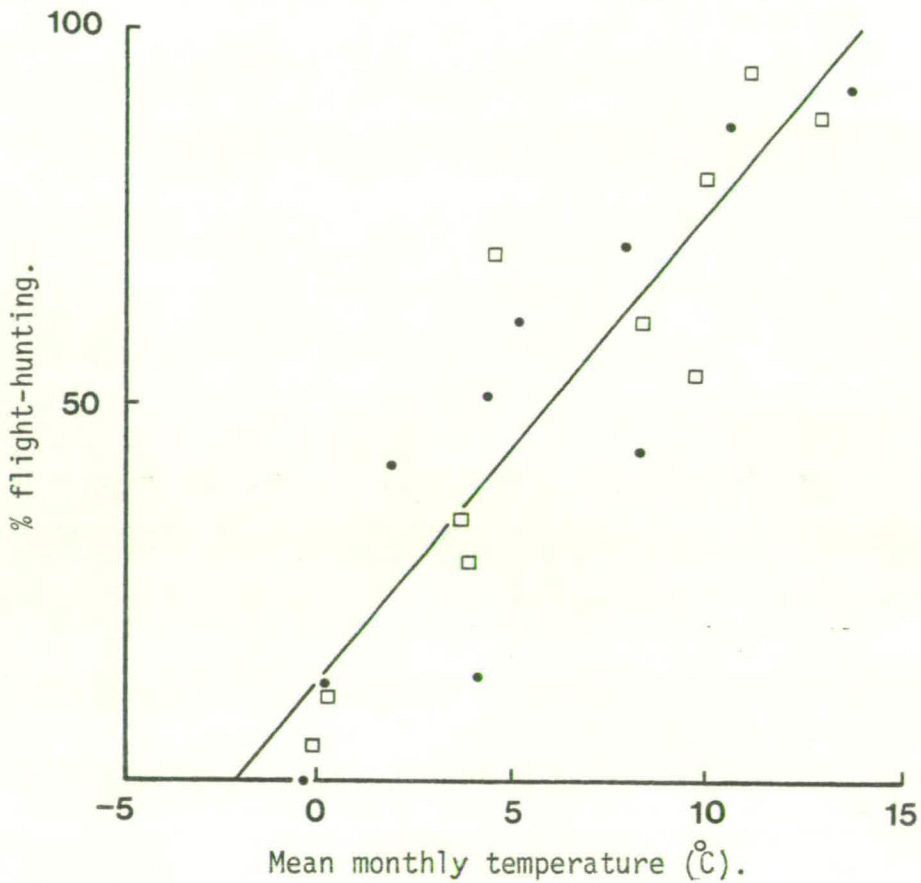
Frequencies are expressed as a percentage of hunting observations that were flight-hunting in each month. Data are from October 1976 to July 1977 (•) and from October 1977 to July 1978 (□). Line is fitted regression for both periods:

$$Y = 6.3X + 12.8$$

(S.E. b=0.74, P < 0.001).

Figure 3.13   (contd.)

(b)   Flight-hunting and mean daily temperature.

   (i)   October/November.
        Y   =   1.0X + 31.8
        (S.E. b=1.55, Not significant)

   (ii)   March/April.
        Y   =   -0.8X + 60.2
        (S.E. b=1.56, Not significant)

   (iii)   June/July.
        Y   =   0.2X + 89.7
        (S.E. b=1.09, Not significant)

   Frequencies expressed as a percentage of hunting observations at
each daily temperature that were flight-hunting. Total number of
hunting observations at each daily temperature is given above each
point.
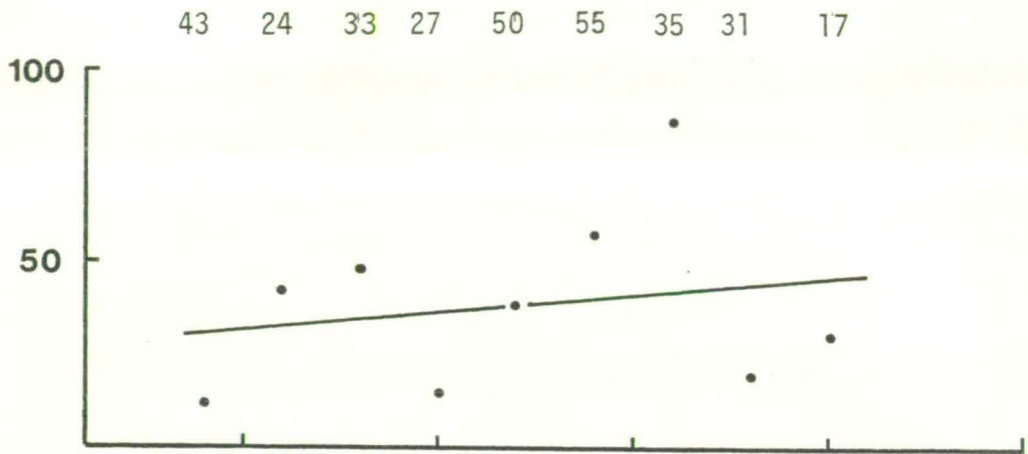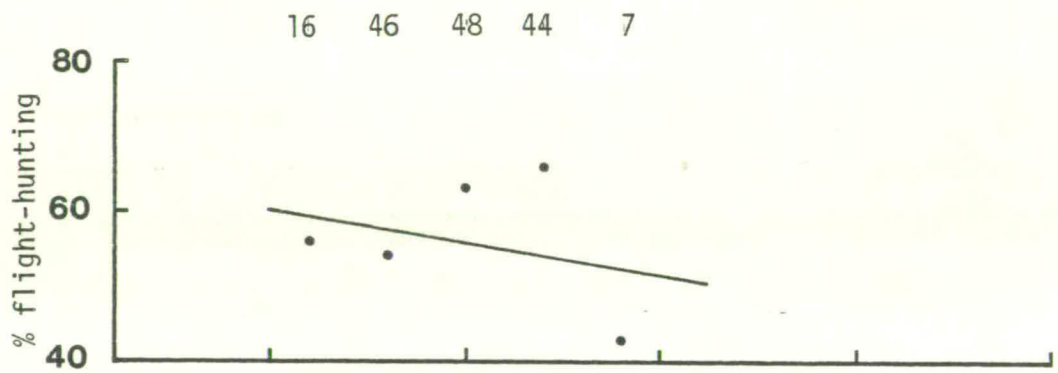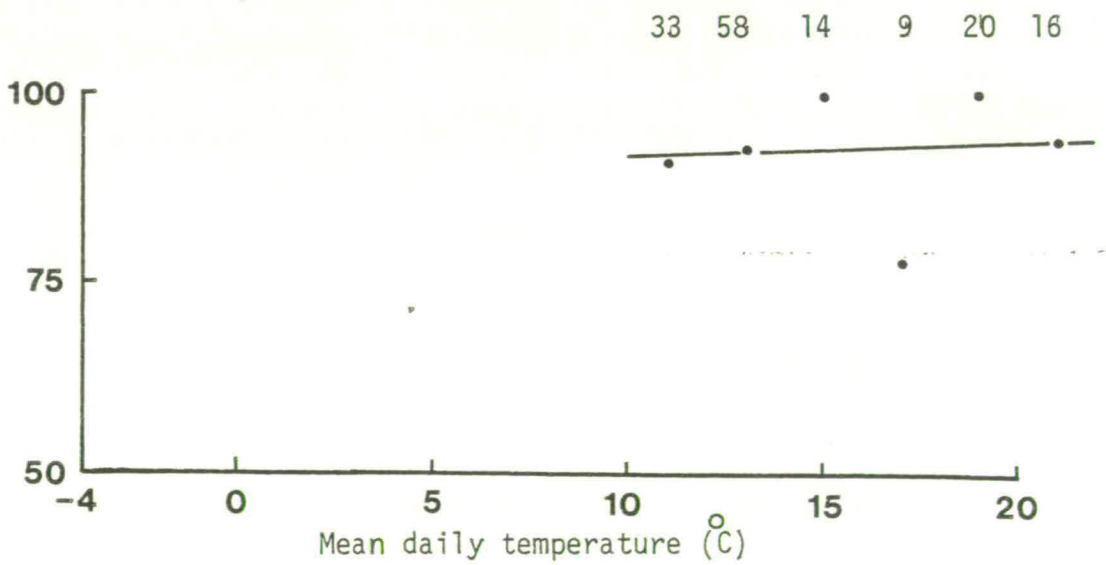
with the rise in temperature, but the two were only indirectly related.

3. Rain.

During heavy rain I noticed that Kestrels were reluctant to fly and often sought shelter in thick trees or under overhanging banks. Similar observations were made by Cave´ (1968), who also found that fewer prey items were brought to the nest on a wet day than on dry ones. Rain probably reduced the amount of hunting, but I could not test this using sightings of birds because those sheltering from rain were usually hidden.

Discussion.

1. The efficiency of perched- and flight-hunting.

While flight-hunting consumed more energy than perched-hunting, it was also a more effective method of capturing prey (3.9 kills/hr flight-hunting versus 1.4 kills/hr hunting perched). This seems to be true in similar raptors as well; for example Black-shouldered Kites in South Africa made an average of 1.2 kills/hr hovering but only 0.2 kills/hr hunting from perches (Tarboton 1978, from table 2).

The estimates of energy gain per hour of hunting were only

approximate because I had insufficient data to tell exactly how capture rates varied with prey size. Nonetheless, Fig. 3.9 illustrates the main differences, in energy terms, between the two modes of hunting. Flight-hunting requires considerable energy, but yields greater energy per unit time, provided captures are made at a high enough rate and that large prey items are taken. Perched-hunting uses up less energy but has slower capture rates and is therefore more suitable if the overall energy demands are low and the bird has plenty of time in which to meet them (as in winter). Furthermore, perched Kestrels may exploit small prey without incurring an energy deficit, whereas the high energy-cost of flight makes this more difficult for flight-hunting birds.

2. Wind speed and hunting.

The use of wind uplift to maintain height in the air must have been a considerable saving of energy, compared with that needed to hover in windless conditions. It is likely, therefore, that the use of perched- rather than flight-hunting at low windspeeds, at certain times of year, was to conserve energy because flying was too costly. On windy days, flying required less energy because birds could use uplift to avoid the need to hover-hunt, and the higher capture rate of flight-hunting made it a more efficient method. Areas of open hill with no perches could also be exploited using less energy on windy days, provided the wind was in the right direction. This may also have allowed Kestrels to search areas away

from their usual hunting perches and so reduced the effects of local depletion of prey. Finding a windward slope may have been an important factor in affecting where birds hunted, and on several occasions I noticed marked inidividuals, outside their normal range, using windward slopes which were not available where they usually hunted. The fact that there was no relationship of windspeed to hunting method in the breeding season suggests that birds may have sacrificed energetic efficiency in order to gain the maximum amount of food per unit time.

3. Seasonal changes in hunting methods.

The change from mainly perched-hunting in winter to mainly flight-hunting in summer may have been due to changes in energy demands on Kestrels. In winter birds could probably afford the low rate of energy gain associated with perched-hunting, because they only had to meet the needs of their own body maintenance. Flying may have provided the daily food intake more quickly, but carried a greater risk of creating an energy deficit if no captures were made. Furthermore, once enough food was caught, birds would probably return to perches anyway, to advertise their ownership of the territory and to spot any intruders, and this activity could easily be combined with perched-hunting. Thus in winter, Kestrels may have resorted to flight-hunting only if they failed to catch sufficient food from perches or if the wind made hovering cheaper.

Energy demands increased in early spring as birds prepared for breeding. Males had to find sufficient food not only for themselves, but also for their partners and, later, the nestlings. Although daylength increased in spring, not all this extra time could be spent hunting because of the demands of courtship and nest defence. Hunting from perches would probably have taken the birds away from the nest for long periods, whereas maximising capture rates by hovering would have reduced the time spent hunting (i.e. away from the nest) and still have allowed birds to meet the increased energy demands of breeding.

Changes in hunting method may also have been affected by the availability of prey. It was suggested earlier that flight-hunting was worthwhile only if the prey taken were large and could be caught at a fast enough rate. During winter voles may have been less easily caught than in summer so that perch hunting may have been the most appropriate method at that time. Furthermore, nestlings were fed mainly on large items (chapter 2), and these may have been most efficiently caught by flight-hunting, which may explain the greater use of flight-hunting in summer.

CHAPTER 4.

POPULATION SIZE, TURNOVER, AGE/SEX RATIOS AND MOVEMENTS.

This chapter examines the size and structure of the Kestrel population at Eskdalemuir. My aims were to measure population density, turnover and age/sex ratios throughout the study to see how these parameters varied within and between years.

KESTREL NUMBERS.

Methods.

Kestrel numbers were assessed (a) by the density of breeding pairs and (b) by counting individuals seen while driving. The former measure has been obtained elsewhere on Kestrels, so was best suited for comparing densities with those in other areas. The second measure enabled me to monitor changes in numbers outside the breeding season and to include non-breeding birds during the summer.

(a) Breeding density. This is dealt with here only for comparison with other studies, and the regulation of breeding numbers is covered in more detail in chapter 6. Breeding density, as used in this chapter, was measured over an area of 100 km^2 (the 10 km national grid square number NT20) and was the number of pairs recorded each year, including those that failed to lay.

(b) Counts made while driving. Raptors have been counted in several studies by driving a fixed route and correcting the number seen to allow for variations in the terrain, weather or speed of driving (e.g. Craighead and Craighead 1956, Enderson 1960, Smeenk 1974). Such counts necessitated special trips for the purpose of censusing, making them time consuming. The collection of other data for my study involved driving long distances over minor roads or forest tracks, and I made use of this time by counting all the Kestrels I saw.

Counting was done from 31 roads of known length. I recorded how many times each was used per month, and the number of Kestrels seen on each occasion. Roads were not covered systematically, but I tried as far as possible to use a variety in each month. No allowance was made for differences in visibility between roads; instead I assumed that the average visibility of the roads used was similar in each month. There were only a few deciduous trees in the area, so visibility was relatively unaffected by seasonal changes in vegetation. Heavy rain and hill fog reduced the numbers seen, so trips made during such weather were ignored. Kestrels seemed to be equally visible in all months, apart from during the breeding season, when brooding females were seldom seen. I partially corrected for this from a knowledge of the proportion of breeding females that were brooding in any month, though counts for May and June were probably still underestimates. To calculate the density index, I found the mean number of Kestrels seen per km driven on

each road, and from this the mean value for all roads used in any period.

As a check on the method, the index was compared with density as found by careful searches (on foot and by car) of restricted parts of the study area. Searches were made during three periods each year:

(a) 'autumn' (1 October to 31 November);

(b) 'winter' (1 December to 28/29 February) and

(c) 'summer' (1 April to 31 July).

(March was excluded because of the rapid changes in Kestrel numbers during that month. Changes in other months were usually more gradual (see Fig 4.3) and the density in each period was assumed to be roughly stable.) The maximum number of Kestrels present in each period was estimated using a combination of the number of different individuals seen, the number of occupied roosts and, in summer, the number of occupied nests. Kestrel density was calculated by dividing the number of birds present by the total size of the areas searched. This method was less satisfactory than using the census index because it measured numbers over only a restricted area. Furthermore, it was sometimes difficult to separate untagged birds and to define the exact limits of the areas searched. The density estimates for each period were compared with the corresponding density index found from driving-counts made over the whole area. Estimates of Kestrels per km^2 during the breeding season included those that moved away after failure. They were thus

maximum densities, rather than averages, so were compared with the highest monthly density index recorded in the breeding season. The results from the two methods were highly significantly correlated (Fig 4.1 r= 0.9442, P<0.001), suggesting that a reasonable index of Kestrel numbers could be obtained by making simple counts.

Results.

1. Kestrel breeding density.

This varied between years from 0.24 to 0.43 pairs per km^2. The maximum figure included pairs using artificial sites and may not have been reached under natural conditions. Discounting artificial sites, the densities each year were (in pairs/km^2): 0.24 in 1976, 0.27 in 1977 and 0.34 in 1978. There were a number of problems in comparing these estimates with those in the literature.

(a) Most published work was based on data collected by a number of people covering a wide area. In some cases only frequently used sites were counted, or areas were visited late in the season so that early failures would probably have been missed.

(b) Some densities were based on a small number of pairs and may have been unrepresentative of the habitat sampled. This was especially true if nest sites were clumped, because the density in a 'clump' may have been be much higher than in the surrounding area, though the latter may not have been included in the estimate.

Figure 4.1 Comparison of Kestrel numbers estimated from counts made while driving with density found from detailed searches of restricted parts of the study area.
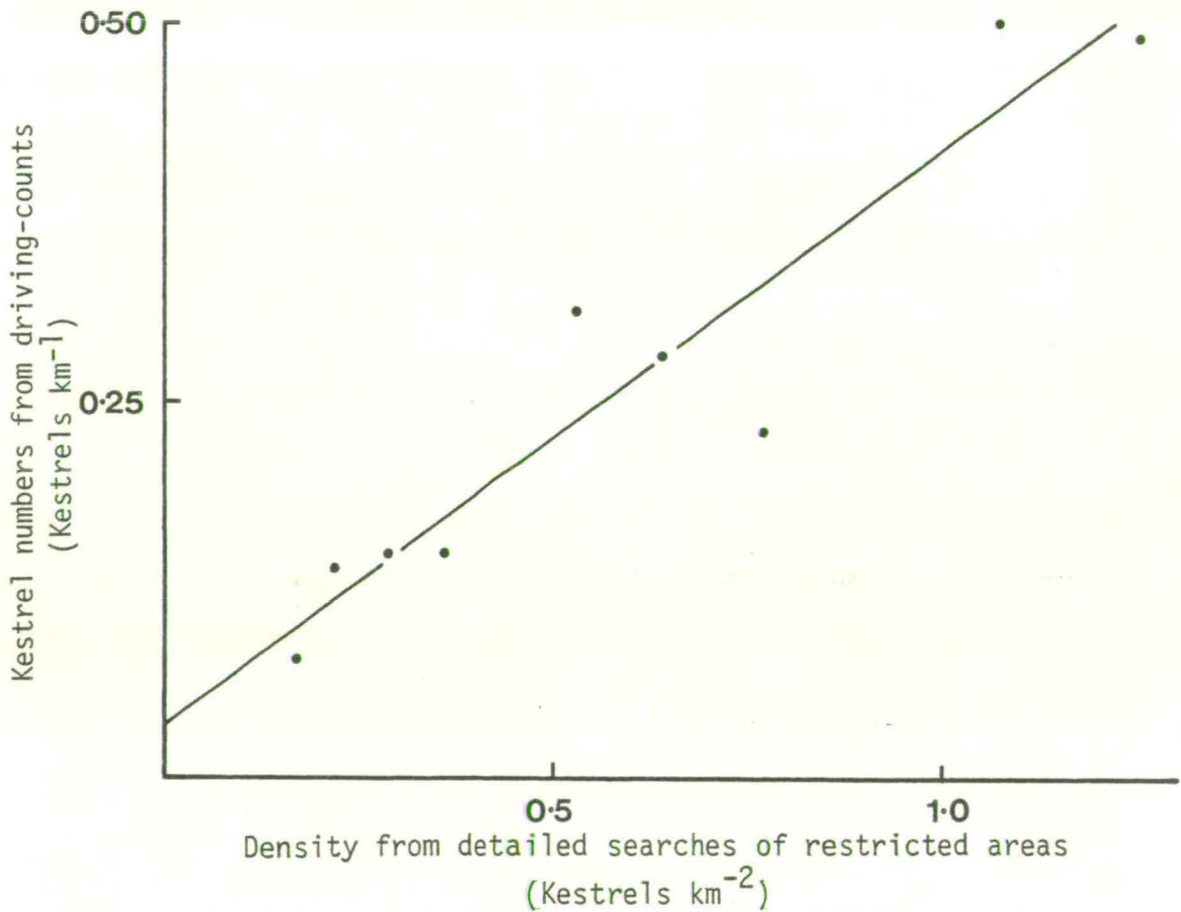
Each point is the estimated density per period. For a definition of these periods see text page 97 .

Line is fitted regression:

$$Y = 0.3772X + 0.0367$$
(S.E. b=0.05, $p < 0.001$).

A summary of data from various European sources is shown in Table 4.1, which includes, where possible, the separate values for each individual study area within the county or region. Data from Cave´ (1968) were excluded because birds were breeding in nest boxes erected at regular intervals in blocks which were separate from the main feeding areas. When the densities within and between studies were plotted against the size of the area searched, there was an approximate trend for estimates to be higher when the area searched was smaller (Fig. 4.2). This was generally true within studies and held to some extent between them, though there were exceptions (the densities quoted in Griffiths 1967, for example, were consistently lower than others measured over the same area). This implied that nests were missed if large areas were searched, and/or that densities from small areas were those found only in clumps of nesting sites and not over a wider area.

Nonetheless, taken with my data, the results in Table 4.1 suggest that numbers in arable and urban habitats are lower than those in upland sheepwalk or young-plantation. This is consistent with likely differences in vole densities between these habitats, but could have arisen for other reasons. Few of the quoted studies indicated whether nest sites were limiting to breeding in their area and this may account for some of the observed variation in densities. Furthermore, a few estimates were made during the nineteen-sixties in southern Britain, when the reduction of breeding pairs by pesticides was at its height (Cramp 1963, Prestt

Table 4.1 Estimates of Kestrel breeding density from other studies.

County or Region	Habitat	Density (prs/km^2)	Area searched (km^2)	Source	Symb.
Leicestershire	Arable farmland	0.08	36	Griffiths (1967)	X
		0.07	59		
		0.03	91		
	Urban	0.06	47		
	(Total	0.06	233)		
Somerset and Gloucestershire	Arable farmland	0.04	1168	Taylor (1967)	T
Surrey	Urban grass park	2.22	9	Parr (1969)	+
	Grass scrubland	0.44	16		
London	Urban	0.04	3255	Montier (1968)	M
South Germany		0.40	400	Rockenbauch (1968)	R
		1.07	15		
Speyside	Conifer plantation and heather moor	0.07	518	Macmillan (1969)	S
Sussex	Arable farmland	0.22	74	Shrubb (1970)	O
		0.18	28		
		0.17	85		
		0.18	110		
		0.17	90		
	Sandy heath/farmland	0.11	202		
		0.15	21		
		0.16	51		
		0.14	51		
	Marsh	0.39	13		
	(Total	0.16	3800)		
Ayrshire	Upland sheepwalk and young-plant.	0.25	40	Riddle (1979)	*
		0.22	36		
		0.26	35		
		0.22	63		
		1.00	9		
	Arable farmland	0.40	70		
	(Total	0.31	253)		
Dumfries	Upland sheepwalk and young plant.	0.27	100	Village (1979)	V
		0.42	17	Picozzi and Hewson (1970)	P

Symb.= symbol used in Fig. 4.2.

Figure 4.2 Estimates of Kestrel breeding density from various European sources, in relation to the size of the study area.
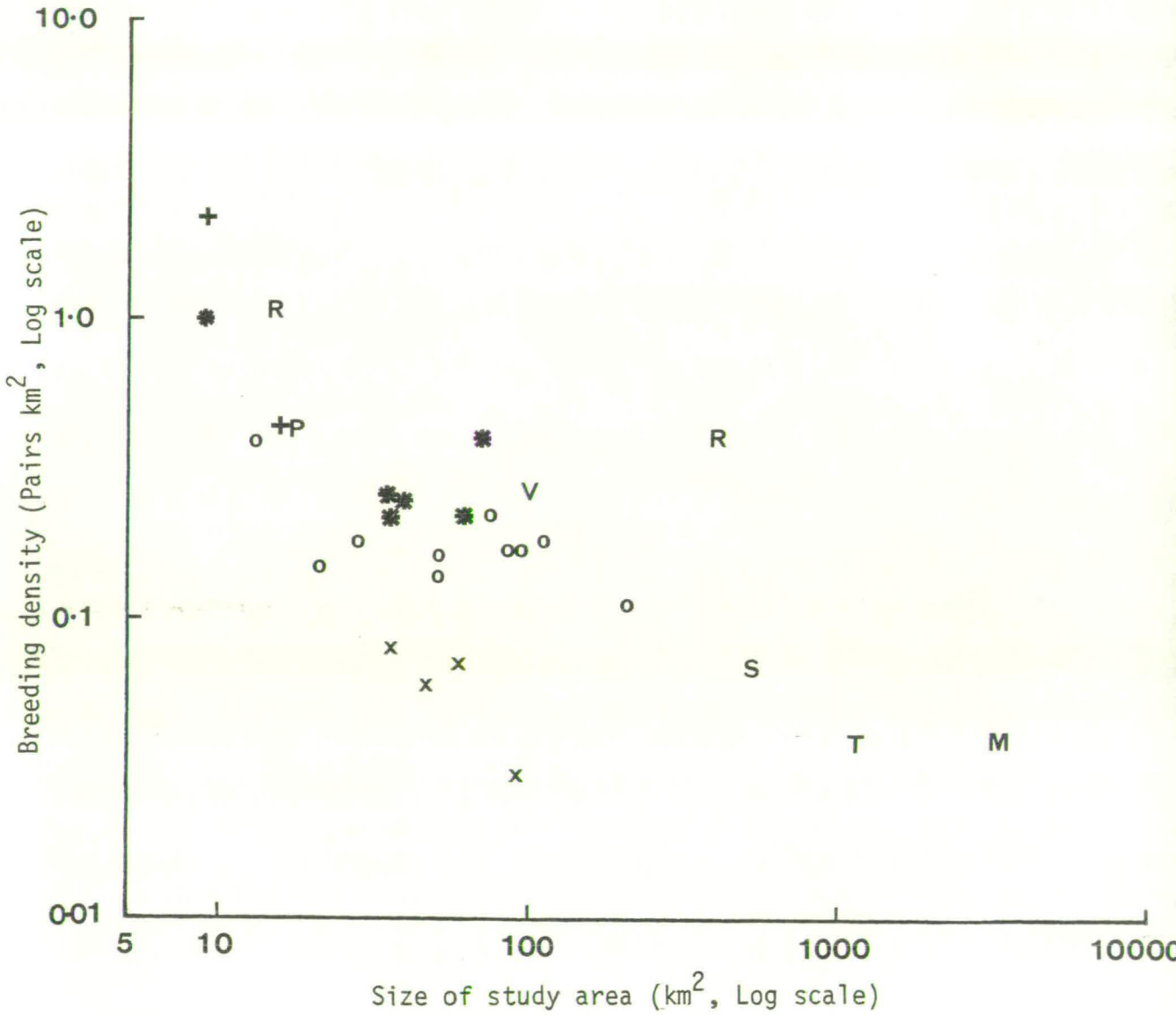
Each point represents an individual study area quoted in the sources given in Table 4.1, which also gives a key to the symbols used.

1965). This may explain the unusually low densities given in Griffiths (1967).

2. Kestrel numbers from road-counts.

I did not attempt any detailed statistical analysis of the density index because of problems caused by the way the data were collected. Instead, general trends were estimated from the mean monthly index (Fig 4.3) and by obtaining means for the periods defined earlier (Fig. 4.4). The confidence limits for these means were only approximate because the data may not have been normally distributed. However, the results suggested the following.

(a) Seasonal changes in population size were similar in each year. Numbers were lowest around January and February, rose sharply during March, and levelled off during the breeding season. Kestrels were most abundant between July and October, but the exact timing of the peak was uncertain as no data were collected in August or September.

(b) Kestrel numbers varied between years, being lower in the year ending July 1977 than in eqivalent periods in either of the other two years (Fig 4.4). The autumn peak in 1977 seemed to be later than in 1976 but, again, it was hard to be sure.

The density index was unsuitable for measuring variation in Kestrel numbers between habitats because few roads ran through unplanted areas. My impression was that there were fewer Kestrels on sheepwalk in winter, though the only evidence I had to support

Figure 4.3   Mean number of Kestrels seen per km driven per month, October 1975 to July 1978.

O = October
A = April

Solid line   = corrected estimate

Broken line = estimates in breeding season uncorrected for the number of brooding females.
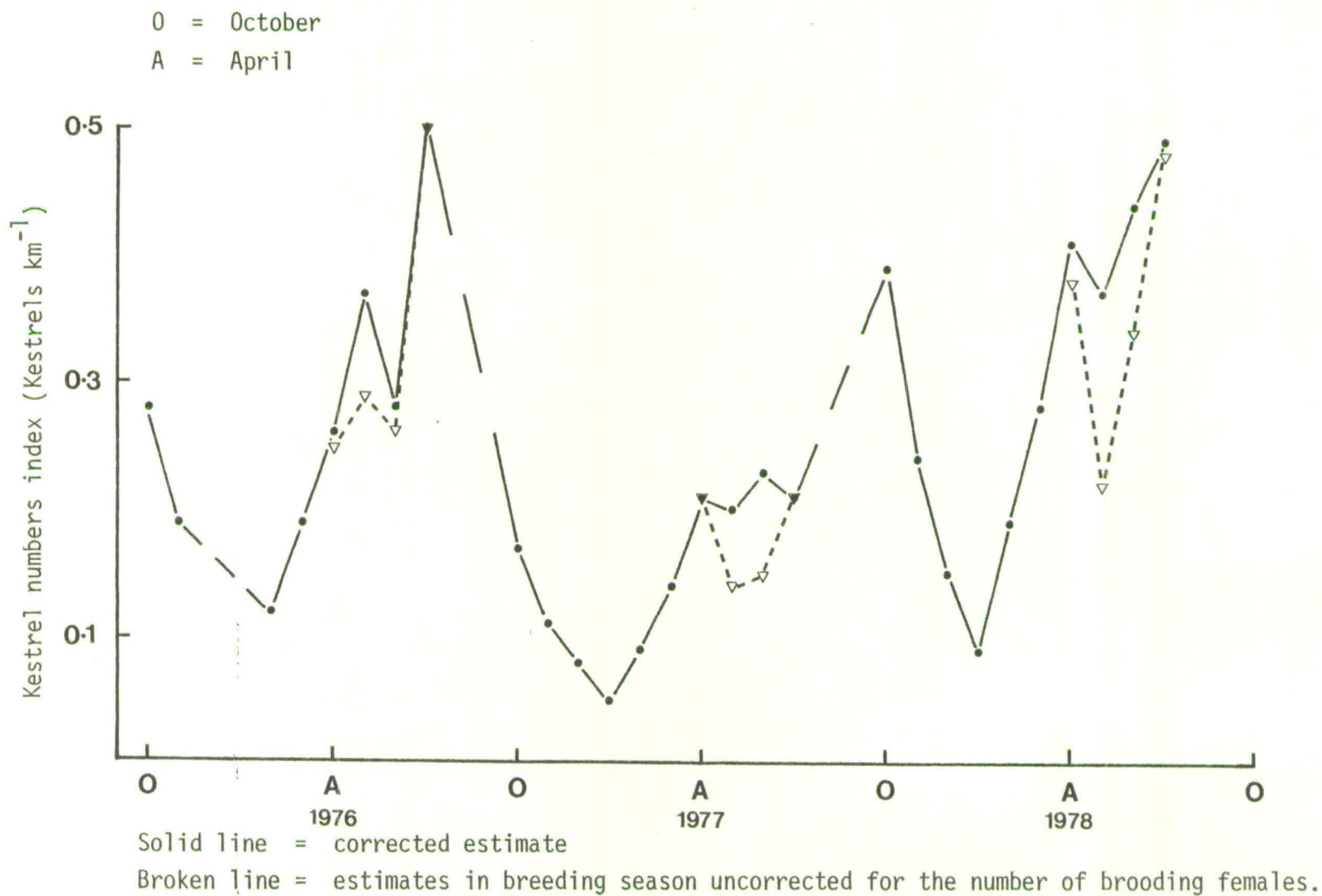
Figure 4.4 Estimates of Kestrel numbers per period.
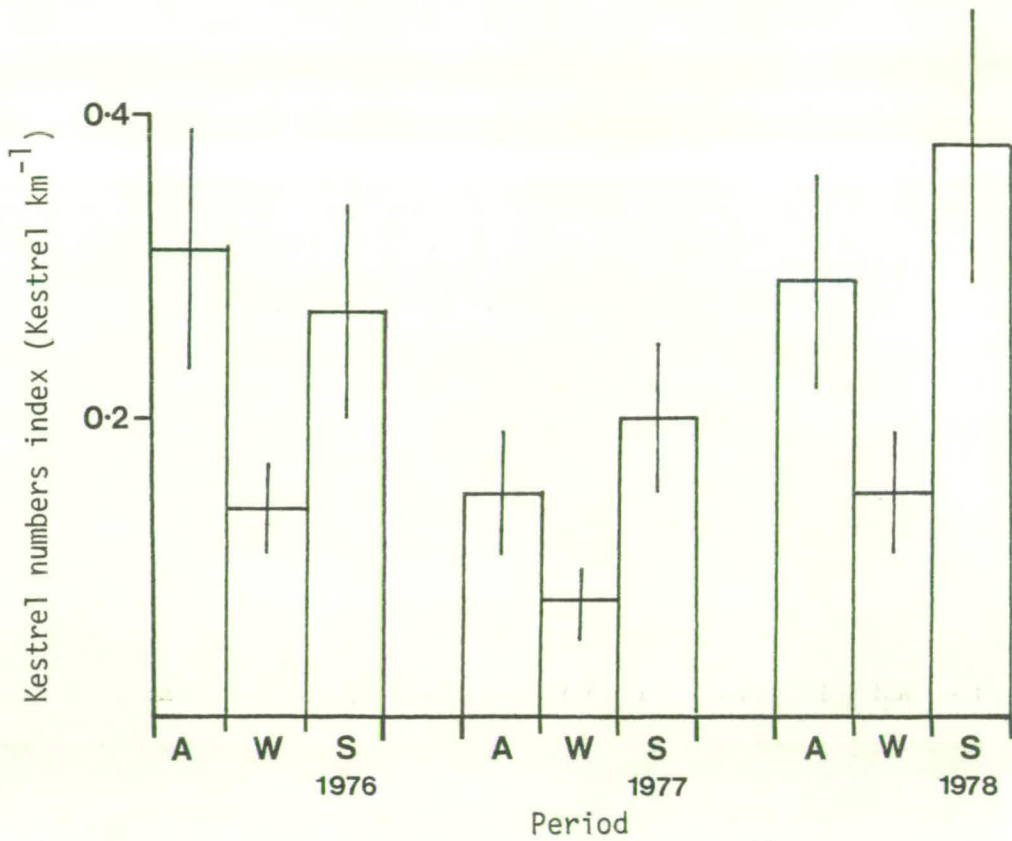
Each bar is the mean number of Kestrels seen per km driven in each period. Confidence limits are only approximate and are ± 2S.E.

KEY TO PERIODS:

    A = autumn (October/November)
    W = winter (December to February)
    S = summer (April to July)

this was circumstantial. On several occasions marked Kestrels, which subsequently nested in sheepwalk areas, were seen hunting mainly in adjacent young-plantation during February and March. One of these was an adult male, followed by radio-tracking, which was always located in the young-plantation by day, but which roosted near its future nest some 2 km away on sheepwalk. Later in the summer such birds usually hunted in sheepwalk surrounding the nest and there was no evidence that young-plantation was a preferred habitat except in winter.

3. Kestrel numbers and vole density.

Fig. 4.5 shows that changes in vole density between the twice-yearly trapping periods were reflected in corresponding fluctuations in Kestrel numbers. However, regressing estimates of monthly vole densities against monthly Kestrel numbers gave no significant relationship. (r= -0.0389, P= NS.). This was probably because vole density was estimated only twice a year, and the exact timing of the annual maxima and minima were unknown. Because of the relatively rapid changes in both vole and Kestrel numbers in spring and autumn, even slight errors in either estimate meant that the two appeared to be asynchronous. This problem was partially solved by comparing longer periods than months, which reduced some of the lack of synchrony. A more detailed discussion of Kestrel numbers and home range in relation to vole density is given in chapter 5.

Figure 4.5   Comparison of monthly estimates of Kestrel numbers with twice-yearly estimates of vole density.
O = October
A = April
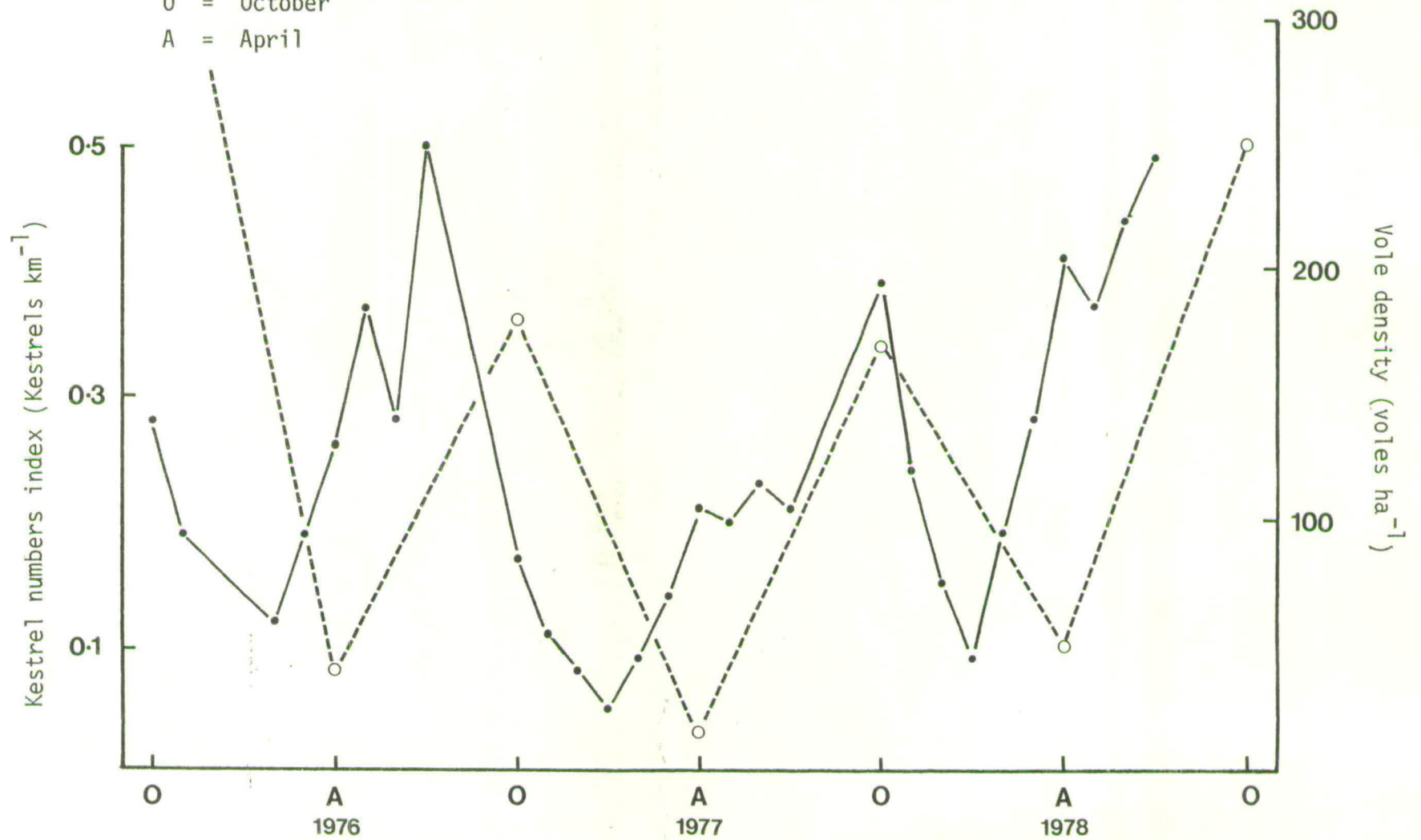
Solid line = Kestrel numbers index,   broken line = estimated vole density.

POPULATION TURNOVER.

Methods.

Turnover, in this context, refers to the gain or loss of individuals either through death or movements. Estimates of the arrival and departure (or death) of wing tagged birds were made by recording the dates on which they were first and last seen. Most birds showed fidelity to a particular range so that the arrival of untagged birds that were subsequently caught was taken as the date on which a bird of similar age and sex was first seen in the territory, provided that there was no evidence of an intervening change in the occupant. Birds were unlikely to be recorded on the precise day they arrived (or left), but the first and last sightings gave a rough estimate of the timing of movements, accurate to within a few weeks. As this method was based on birds which remained in the area long enough to be caught, the turnover calculated referred to long- and short-term residents and not to transients that were in the area for only a few days or less. Some birds left the area over winter, but returned in spring; a bird was considered to have done so if it was not seen between 1 December and 1 March.

For each month, two figures were calculated:

(a) The Percentage Gain. This was the proportion of marked birds (or those subsequently marked) present at the end of the

month, that arrived during it. As I did no fieldwork in August or September, birds first seen in October which were not present the previous July were assumed to have arrived during the intervening months and the 'autumn' gains were averaged over the three months from 1 August to 31 October.

(b) The Percentage Loss. This was the proportion of marked birds lost during the month. Coverage in June and July was more difficult because of other work done at that time, so successful breeding birds present at the end of May, but not in October, were assumed to have disappeared in August or September, even though they may not have been seen in June or July. It is likely that most breeding birds which successfully fledged young did not leave until autumn, although I could not be sure of this in all cases.

For both of the above, autumn estimates were minimum values because some Kestrels may have arrived early in the period and left toward the end without being recorded. Some of these probably stayed long enough to be caught, but were missed because I did no fieldwork during this period.

Results.

1. Seasonal changes in population turnover.

The pattern of turnover was similar in each year, and Fig. 4.6 shows the mean monthly values of the combined data from all three years. The two main periods of high turnover were early autumn and

Figure 4.6 Monthly estimates of turnover in the Kestrel population
            at Eskdalemuir.

(a) Mean percentage gain.
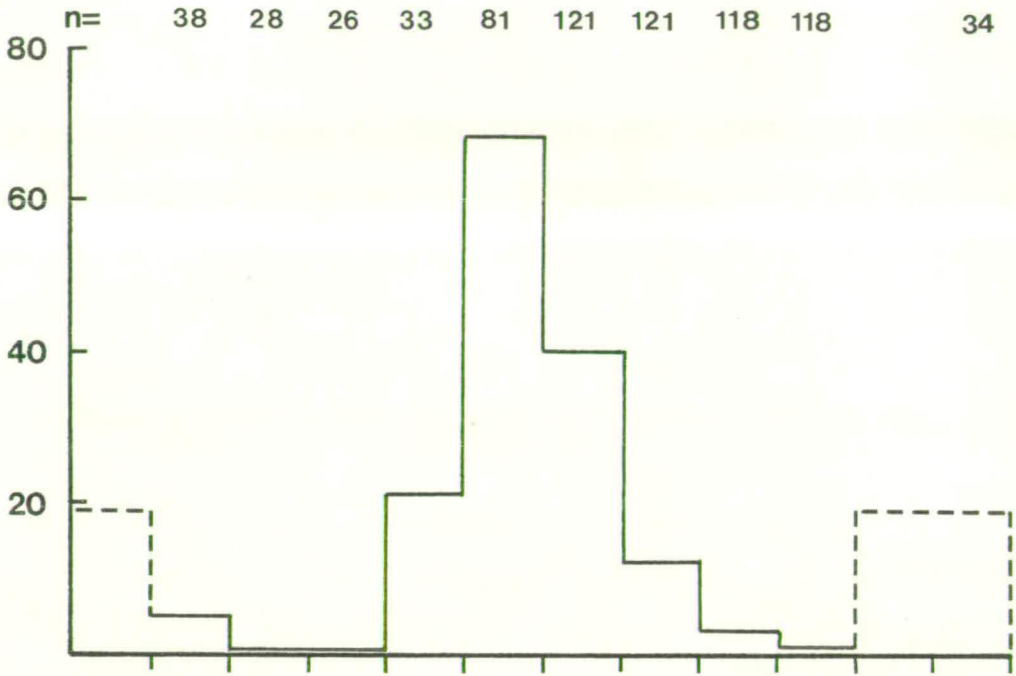
(b) Mean percentage loss.
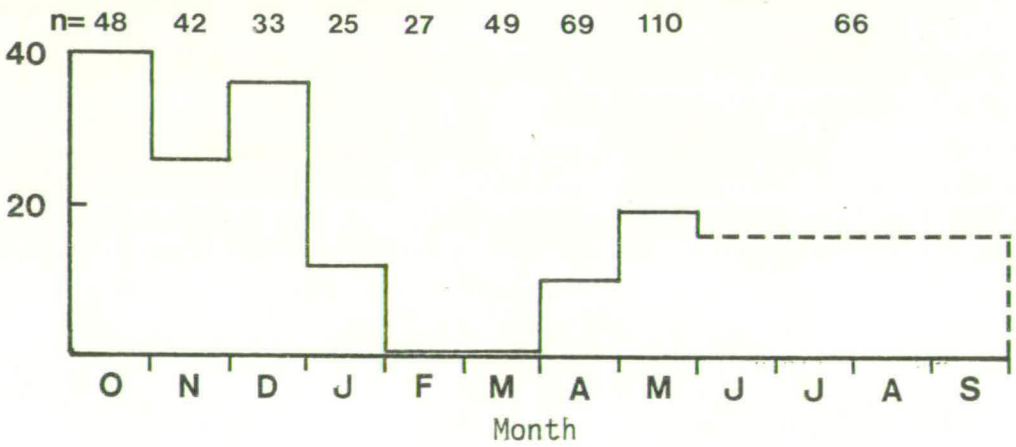
Month

Results for each month show the average for the three years,
October 1975 to July 1978. In addition, the autumn estimates of %
gain are averaged over the period August to October and those of % loss
are averaged over the period June to September.

spring. Between July and October Kestrels were both gained and lost (though the exact extent of this was hard to judge) so that those present in late autumn were not necessarily the same individuals as in the previous summer, even if the population density was similar. From October to February there were gradually declining losses but few gains, so the population size steadily decreased. In February and March the numbers of birds increased rapidly as there were high gains with no losses. Thereafter there was a reduced turnover, with low gains and losses so that population size remained reasonably steady until the end of July.

2. Sex and age differences in turnover.

There was some variation in turnover between birds of different age or sex. For example, in 18 cases where one member of a breeding pair remained on the home range over winter, it was the male on 14 occasions, significantly more than expected if both sexes were equally likely to stay ($X2= 5.56$, $P<0.02>0.01$). Males were also more likely to occupy the same, rather than a different nesting area in successive years (15 out of 18 times in males versus 5 out of 12 for females, $P= 0.024$, Fisher exact test).

Birds of different ages and sex also seemed to arrive, on average, on slightly different dates in spring. To test this, I examined the arrival of birds from February onwards, ignoring those that had overwintered. Samples were low, so months were grouped and

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Table 4.2 The date of arrival of Kestrels in spring

in relation to their age and sex.

For explanation, see text page 111.

(a) 1977.

    (i) Adults versus yearlings.

	Females	
*	adults	yearlings
FM	6	4
AM	11	5

P= 0.44 (Fisher Exact Test).

    (ii) Males versus females.

	Adults	
	males	females
FM	14	9
AM	6	11

Chi-squared= 1.64 df=1 P NS.20

(b) 1978.

    (i) Adults versus yearlings.

	Males				Females	
	adults	yearlings			adults	yearlings
FM	14	1		FM	13	2
AM	6	11		AM	5	13

Chi-squared= 9.11   Chi-squared= 9.26
df=1 P<0.01>0.001   df=1 P<0.01>0.001

    (ii) Males versus females.

	Adults				Yearlings	
	males	females			males	females
FM	14	13		FM	1	2
AM	6	5		AM	11	13

Chi-squared= 0.26   P= 0.55 (Fisher Exact Test)
df=1 NS.5

*FM= February/March, AM= April/May.

comparison was limited to 'early spring' (February and March) versus 'late spring' (April and May). Data for 1976 was excluded as too few birds were marked that year, while in 1977 comparisons were limited because no yearling males bred. The tests that could be made (Table 4.2), suggested no difference in the arrival of males and females, but adults of both sexes arrived before yearlings in 1978.

Discussion.

The above results suggest that there were fairly stable summer and winter populations, with periods of transition in early autumn and spring. This is as expected of a partial migrant at this latitude and similar results have been found in other raptor studies (e.g. Craighead and Craighead 1956, Newton 1979). The results also fitted the observed changes in density, periods of high gain and low loss corresponding to times of population increase and vice versa. The importance of movements in affecting Kestrel density (as opposed to breeding production or mortality) was not known for certain as I could not tell if birds that disappeared had left the area or died. However, the rapid increase in density in March was entirely due to immigration and a number of birds that disappeared in winter returned the following spring, suggesting that movements played a major role in affecting density. I had insufficient data to tell whether numbers in autumn were

directly related to breeding production the previous summer; though they were low in autumn 1976, following poor breeding performance in the area, and higher in autumn 1977 after more successful breeding. Although some of the yearlings caught in autumn 1977 were reared in Eskdalemuir, most were not and it is likely that the high numbers at that time reflected a greater settling in the study area because of better food conditions and better breeding over a wide area.

AGE AND SEX RATIOS.

Methods.

The age and sex ratios in the population were measured in two ways:

(a) The proportion of each age group trapped (or already marked) at breeding sites. This gave the most reliable estimate of adult/yearling ratios but was limited to the breeding population.

(b) From the proportion of adult males seen. At most times of year, adult females and juveniles were difficult to distinguish in the field and the only sector of the population which could be reliably identified were adult males (i.e. those in their second year or later). I assumed that the frequency with which I saw adult males was proportional to their frequency in the population. This was better than using either estimates of the number present at any one time, which were biased because residents were more likely to be included than transients, or the age and sex ratios of trapped birds, because yearlings were more easily caught than adults and I avoided trapping birds that were already marked.

Results.

(a) Birds at breeding sites. Results for 1976 were too few to analyse, but the other years showed that:

(i) More females bred as yearlings than did males (Table 4.3a X2= 6.31, P<0.02>0.01), a trend that was present in both years.

(ii) A significantly higher proportion of the breeding population were yearlings in 1978, than in 1977 (Table 4.3b X2= 16.78, P<0.001). This was true for both males and females.

(iii) Assortative mating. Data from 1978 (the only year in which sufficient numbers of yearlings bred) were used to test for assortative mating. The results showed there were significantly more adult and yearling pairs, and fewer mixed pairs, than expected if mating had been at random in the population (Table 4.4 X2= 11.5, P<0.001).

(b) Ratio of adult males sighted. The first two years were similar (Fig. 4.7), in that the ratio reached a peak in winter, especially that of 1976-77 when 90% of the birds seen were adult males (the peak in 1975-76 may have been less obvious because there were no data from January). Both these years showed an apparent increase in adult males in summer. This was probably not a real increase, but corresponded to the time when females were incubating and therefore less easily seen. (The summer increase was later in 1977 than in 1976, which was consistent with the later mean laying date in that year, see chapter 6.) In autumn 1977 there was a sharp fall in the proportion of adult males in the population. Observation suggested this corresponded to an increase in Kestrel numbers brought about by an influx of juveniles, an idea supported by trapping results (of the 16 birds other than adult males caught

Table 4.3 Numbers of adults and yearlings occupying

nesting areas in 1976-1978.

Table gives the numbers of birds of known age
and sex recorded as paired at nesting areas.

	Adults		Yearlings	
	males	females	males	females
1976	11	8	0	0
1977	25	19	1	4
1978	24	18	13	24

(a) Differences in the proportion of each sex breeding
as yearlings.

Tests of males versus females:

	Chi-squared	df	P
1977	1.21	1	*
1978	3.00	1	0.1
Both years	6.31	1	0.02

(b) Differences in the proportion of yearlings
in the breeding population.

Tests of 1977 versus 1978:

	Chi-squared	df	P
Males	6.96	1	0.01
Females	8.05	1	0.01
Both sexes	16.78	1	0.001

* Expected values too low to use this test.

Table 4.4 Assortative mating of adults and yearlings in 1978.

Table gives the number of pairs of each type recorded,
based on marked pairs only.

		Age Group of Female	
		adult	yearling
Age Group of Male	adult	17	7
	yearling	1	10

Chi-squared= 11.5 df=1 P<0.001

Figure 4.7 Proportion of the total observation of Kestrels per month that were of adult males ($\pm$ 2S.E.).

O = October

A = April
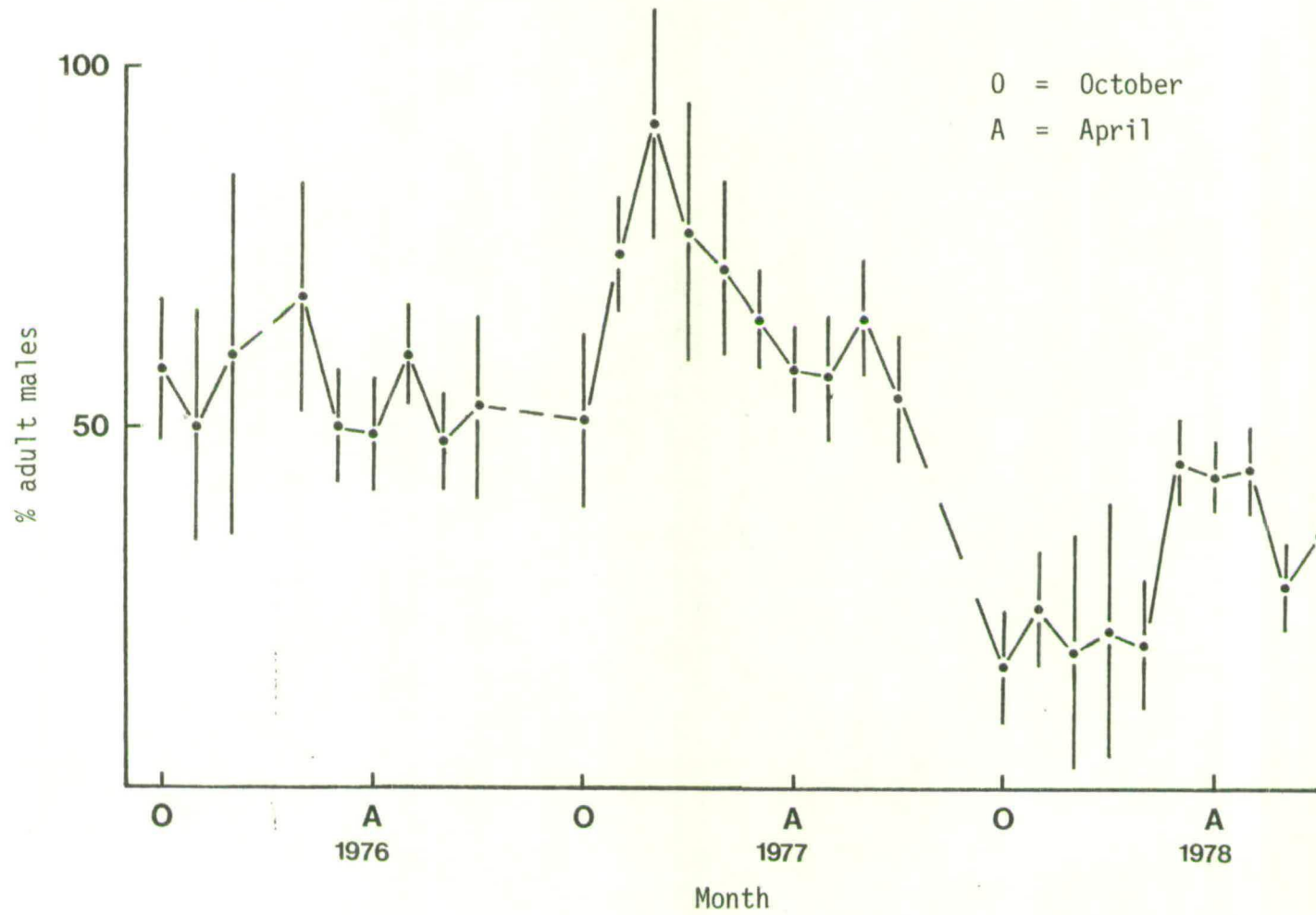
at this time, all were juveniles, 7 males and 9 females). The percentage of adult male sightings rose slightly the following March, but remained below that in previous years, which was consistent with the increase in yearling males in the breeding population found by trapping.

Thus, outside the breeding season, the proportion of adult males in the population was approximately related to the population size, being highest when Kestrel numbers were lowest (Fig. 4.8 r= -0.6511, P<0.05>0.01). During the breeding season, however, no such relationship was evident.

Discussion.

(a) The greater proportion of yearlings breeding in 1978 (a good vole year) than in 1977 (a poor vole year), implies that this age group could either (i) obtain enough food to reach breeding condition only when food was plentiful, (ii) that they were more able to compete for breeding places with adults in a good year than in a poor one, or (iii) that more juveniles survived in a good vole year. This is in line with differences in breeding performance between yearlings and adults (see chapter 6), and has been noted in a few other raptors (Newton 1979) and in some other birds (Lack 1966). The influx of juveniles in the winter population of 1977/78 occurred when food supply was high, and supports the ideas of Snow (1968) and Newton (1979), who suggested that Kestrels in their

Figure 4.8   The proportion of observations that were adult males per
             month in relation to Kestrel numbers.

             Using data from outside the breeding season only.
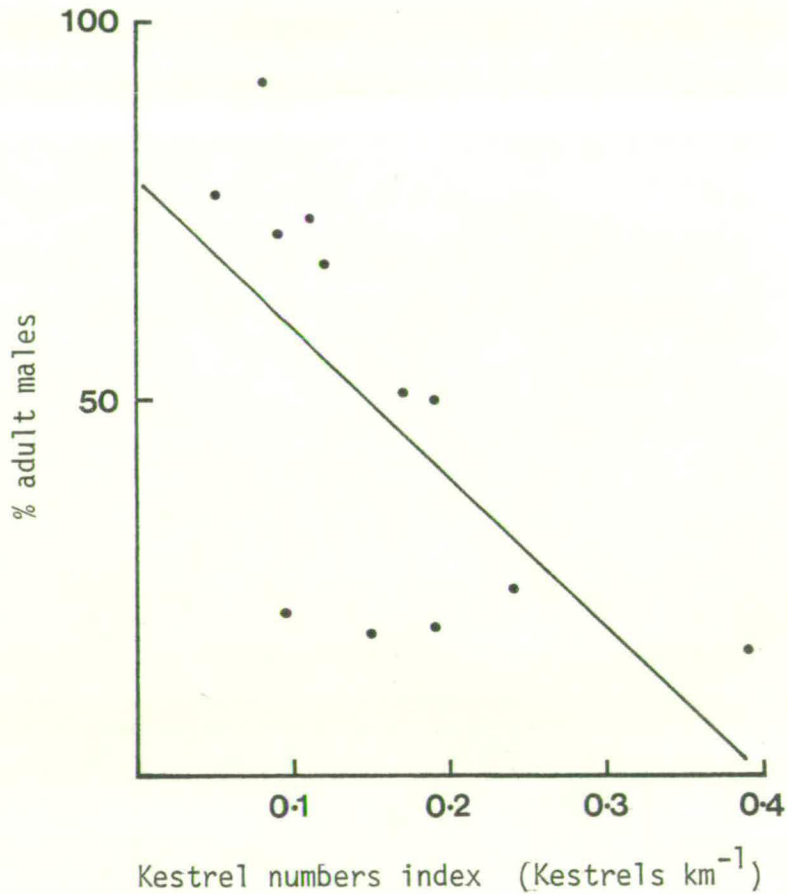
Each point represents data for one month between October and
February from 1975/76 to 1977/78. No data were available for October
or December 1975, or from January 1976.

Line is fitted regression:

$$Y = -193.1X + 79.0$$
(S.E. b=71.2, $P < 0.05$).

first year may be less tied to particular areas and thus better able to take advantage of local increases in food supply. The lack of juveniles settling in the area when food supply was poor, and the apparent difficulty they had in breeding, suggests that juveniles were less successful at capturing prey than were adults, though this was not tested directly.

(b) The reason why more females than males were able to breed as yearlings was not known for certain. Males may have had greater difficulty in maintaining a breeding territory than females, for several reasons:

(i) The mortality of females may have been greater than that of males, so producing more vacant breeding places for females than for males.

(ii) Mainly adult males wintered in the area, and these may have occupied the better quality nesting areas (i.e. those offering the greatest chance of successful breeding, see chapter 6), leaving fewer for males arriving in spring. Yearlings may have been unable to breed in poor quality areas unless food supply was generally good, so in most years yearling males would be unable to find a suitable place to breed. However, yearling females arriving in spring may more often have found good quality nesting areas available because fewer adult females wintered in the study area.

(iii) Pair formation and maintenance may have depended primarily on the ability of the male to defend the nest and to feed himself and his partner. Thus yearling females could breed by

pairing with adult males, but yearling males could not so easily breed with adult or yearling females.

I could not tell which, if any, of the above hypotheses were correct. Unfortunately, I had no independent measure of the mortality of each sex with which to test (i). The apparently later arrival of yearlings in spring would argue against (ii), because adult females would be expected to fill the vacant good quality nesting areas before the yearling females arrived. The greater role of the male in pair maintenance is supported by the higher frequency of nest defence in males (Tinbergen 1940 and chapter 3), and by the fact that only one yearling male-adult female pair was recorded during the study (though this may have been due to assortative mating- see below).

(c) Assortative mating of adults and yearlings may have been due to the different times of arrival and settling of the two age groups, or because at least some birds preferred to mate with individuals of the same age group as themselves. As adult pairs had a higher breeding performance than yearling pairs, there may have been some advantage in adults preferring to mate with each other. There may have been no advantage to yearlings of pairing together and the paucity of mixed-aged pairs could have been due solely to adults rejecting yearlings as partners.

Yearling females seemed more likely to mate with an adult than did yearling males (Table 4.4). Apart from reasons outlined in (b), this may have arisen because yearling females bore a greater

resemblance to adult females than yearling males did to adult males. This may have prevented adult males (but not adult females) from recognising whether a potential partner was a yearling or an adult, and so increased the likelihood of yearling females (but not yearling males) being accepted by an adult partner. This may have been an advantage to yearling females because those paired to adults had a better breeding success than those paired to yearlings (chapter 6).

Assortative mating among adults and yearlings also occurs in Sparrowhawks (Newton et al. 1979). In this case males were more likely than females to breed as yearlings and yearling males were more likely to form mixed pairs than yearling females.

(d) A greater tendency for males, rather than females, to remain on their breeding grounds in winter has been reported elsewhere in other falcons (Hodson 1975), and may be typical of the genus (Newton 1979). In Eskdalemuir, wintering on the breeding ground was related to breeding success, though the relationship was difficult to interpret (see chapter 6 for a fuller treatment of this). Males may have gained more advantage than females from wintering at their nesting areas if they thereby reduced the difficulty of acquiring a nest in spring. Alternatively, they may have been more able survive the decline in food supply in winter than were females.

MOVEMENTS.

Of the 400 or so Kestrels ringed in Eskdalemuir, 20 have so far been recovered. Their locations are shown in Fig. 4.9, with 9 recoveries of Kestrels ringed elsewhere in Dumfries. Of 22 individuals ringed as pulli, 21 were found before March of their first year. Most first-year birds were found in north-east or south-east England and northern France, and 16 were east and south of the study area. These results are consistent with the findings of Thompson (1958) and Snow (1968), who showed that movements of over 150 km in Kestrels from northern Britain tended to be in a south to south-easterly direction, and that this may have changed to west of south after crossing the Channel.

Five of the Kestrels recovered were first ringed as adults in Eskdalemuir, and two are of particular interest as their previous history was known. An adult female, first caught on 8 March 1977, subsequently bred with an adult male caught at the same time. The female was in the area until the end of October when she left. The following March she returned and remated with the same male, which had overwintered in the study area. After another successful breeding attempt, the female was again seen until October, but not afterwards and was subsequently 'found sick' in South Shields (County Durham), 115 km east-south-east, on 8 November 1978. The second was an adult male, caught at the nest on 15 June 1977, which

Figure 4.9   Recoveries of Kestrels ringed in Eskdalemuir and elsewhere
             in Dumfries.
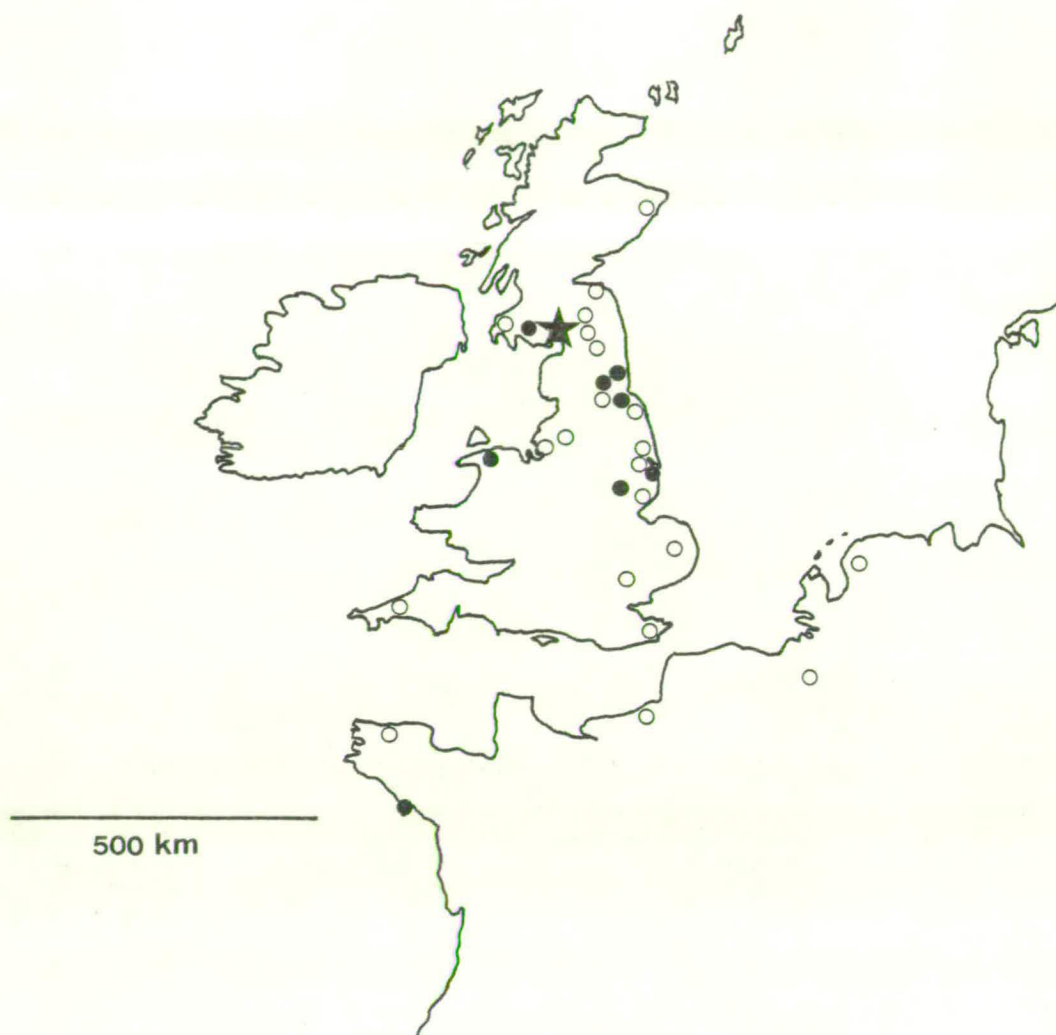
KEY:

★ = ringing location.

○ = finding location of individuals originally
    ringed as pulli or recently fledged juveniles.

● = finding location of individuals originally
    ringed as adults or breeding yearlings.

did not subsequently overwinter in the area, but was caught the following March breeding at the same nesting area. Having reared young in 1978, it left its range and was recovered on 2 November in western France.

These records were the only recoveries of birds previously known to have left the study area over winter and returned the following spring. (A tagged adult male, caught in March 1976, returned to breed in three successive years and was possibly, but not reliably, reported in two winters some 10-15 km south of its breeding site.) Return to the area after not being seen in winter was fairly common in 1978 (9 males and 10 females) but how far such birds normally travelled was unknown.

CHAPTER 5.

HOME RANGE AND TERRITORY.

INTRODUCTION.

The concepts of home range and territory have been comprehensively reviewed in the literature (Lack and Lack 1933, Nice 1941, Burt 1943, Hinde 1956, Carpenter 1958, Brown and Orians 1970) so will only be discussed here in order to clarify some problems and to define the terms with respect to this study.

1. Home range.

This was originally defined by Burt (1943) as 'that area traversed by an individual in its normal activities of food gathering, mating and caring for young'. Although a simple concept, home range is not easily quantified and most measurements rely on some sort of index of size. These usually assume that data collection is unbiased so that the locations obtained represent a random sample of points reflecting the utilization of the range by the animal. This assumption is not easily tested and, even if true, the distribution of the points may not reflect the relative importance of different places to the animal. Furthermore, because most descriptions are indices, their areas or boundaries may have

little direct significance to the individual concerned. In most of this study, I have used indices which may not have been the actual home range of the bird. This was because I was mainly concerned with relative, rather than absolute, range size and the exact position of boundaries was less important.

When animals are followed over long periods of time, the areas they use often change from day to day, month to month and from year to year. An animal suddenly recorded in a new location may either have shifted (or expanded) its range, or be visiting part of its existing range that is seldom used. It is often difficult to separate these two alternatives, especially if range data can only be collected slowly, and in many cases a true reflection of range size at any point in time is never obtained. This may have been the case in my study and, to lessen the problem, I measured ranges over similar lengths of time within and between years. As these periods had to be long enough to to allow sufficient data to be collected, but not so long that ranges altered while they were being measured, they were necessarily times when ranges were fairly stable. This may have implied greater range stability than there actually was, but this was unavoidable as rapidly changing ranges could not be accurately measured. Kestrels often changed their ranges suddenly if they gained or lost a neighbour. These changes were allowed for by slightly adjusting the exact period used for any individual so that disruption of its range due to changes in surrounding birds was minimised. Thus, unless otherwise stated, ranges refer to

seasonal home ranges, with the data for individuals within a season collected over roughly (but sometimes not exactly) the same period.

2. Territory

This has been defined in two main ways:

(a) The standard, most widely used definition is 'any defended area' (Noble 1939), 'defence' covering a wide variety of behaviours, from displays which advertise the individual, to direct fighting. Although this broadness makes it widely applicable, this definition is hard to apply if active defence is infrequent or not easily seen.

(b) To overcome this problem, Pitelka (1959) suggested territory be defined as 'an exclusive area'. This avoids the need to deal with the mechanism of territory maintenance (i.e. behaviour) by looking at its result instead (i.e. the exclusion of other individuals). However, non-overlap can also arise for other reasons (e.g. mutual avoidance, lack of neighbours, physical barriers or habitat selection) and, although an exclusive area may be of significance to an individual, it is not strictly correct to equate this with a territory unless it is maintained by defence.

In Kestrels, defence of the nest was common in summer but territorial fights were seldom seen outside the breeding season, even though most ranges were exclusive at that time. Detailed examination of ranges (see below) suggested that they were

exclusive as a result of territorial defence, so the exclusive area was used as an index of territory size.

3. Aims.

By measuring the ranges of birds over several years, I hoped to examine:

(a) seasonal and annual changes in range size and overlap;

(b) individual differences in ranges during any one season;

(c) the relationship of home range and territory size to Kestrel numbers and food supply.

METHODS.

Collection of Data.

Home range was assessed mainly by spot observations, noting the location of all birds when first seen. I occasionally followed individuals continuously and took records at variable intervals, whenever they changed location. Such records formed only a small part of the overall data so they were grouped with the spot observations and treated as such, with each shift representing a new observation. At most times of year ranges were exclusive and boundaries well defined so that individuals could often be separated from one another even if unmarked. Unmarked Kestrels were either birds that were eventually caught and marked, or those that were never caught. The latter were comparatively few in most periods and were not used to calculate range size. Sightings of unmarked birds were used where I could reliably assign them to an individual that was eventually marked. This introduced a slight bias in the data because such observations were mainly of birds that were near the centre of their range (i.e. where I could be most sure of their identity). However, comparison with results obtained using only marked birds showed this was not a serious bias and was out-weighed by the advantages of including some observations of birds before they were marked.

Details of observations were numerically coded and punched

onto cards for computer analysis. Each record contained the following information.

(a) The date and time of day.

(b) The ring number of marked birds.

(c) An eight figure grid reference which allowed locations to be described to within about 50 m.

(d) The behaviour of the bird when first sighted (see chapter 3 for a description of the categories used).

For marked birds, home range was computed over the same periods used in the estimation of density i.e. 'autumn' (1 October to 30 November); 'winter' (1 December to 28/29 February) and 'summer' (1 April to 31 July). Home ranges were unstable in March with many new arrivals settling, so I used data from this month only for birds that showed no shift of range from March to April.

Treatment of Data.

1. Home range size.

Different methods of analysing home range size have been reviewed by Jennrich and Turner (1969) and Van Winkle (1975). Three indices of range size were tried in this study.

(a) Maximum (or Convex) Polygon Area (MPA). This is the smallest convex polygon which contains all the observations of an individual. It has the advantage of being easy to compute and of

making no assumptions about the distribution of the data, but with few locations tends to increase in size with the number of observations.

(b) Capture Radius (CR). This, and the following index, are probabilistic models which assume an underlying bivariate normal distribution to the home range utilization, centred at the geometric mean of all the points (i.e. that the animal centres its activity on a point given by the means of the X and Y co-ordinates of the locations). The capture radius method (originally used on small mammals) assumes a circular home range and gives the area of the circle, whose centre is the geometric mean, and which includes 95% of all the observations. The assumption of range circularity is often unjustified in Kestrels, so this index tended to overestimate range size.

(c) Ellipse Area (EA). Jennrich and Turner (1969) suggested this as a more general index than the capture radius as it does not assume that the range is circular. They also showed that, at small sample sizes, the ellipse area is less dependent on the number of observations than the MPA and so should give a more realistic estimate. However, the assumption that observations are a random sample from a bivariate normal distribution is not easily testable (Van Winkle 1975).

To assess these indices, and to evaluate their response to sample size in my own study, I plotted MPA and ellipse index size

against the number of observations for all marked birds in each period. The results for different periods were similar, those for summer being typical (Fig. 5.1a-b). The number of observations per bird ranged from 4-80 and both indices gave positive regressions with sample size that were significantly different from zero. With the ellipse index, the points were widely scattered and the bias of sample size was probably confined to birds with less than 10 observations. Apart from a few widely scattered points, the MPA increased with the number of observations up to about 20 and levelled off thereafter.

I examined a few ranges in more detail by plotting cumulative range size against the number of observations for five males that had at least 50 observations in one period. The results for one male (Fig. 5.2) were fairly typical of all five, and illustrated a number of points.

(a) The difference in the three indices was fairly consistent, the radius estimate being much larger than the ellipse area if the range was strongly elliptical but fairly similar if, as in this case, the range was almost circular. The MPA was smaller than the ellipse, but the two approached each other as the number of observations increased.

(b) Although the ellipse index showed little consistent relationship to sample size, it changed suddenly between observations in some individuals, especially at samples of less than 10. There was usually a rapid rise in the ellipse index if the

Figure 5.1 The effect of sample size on home range indicies.

(a) Maximum polygon area.
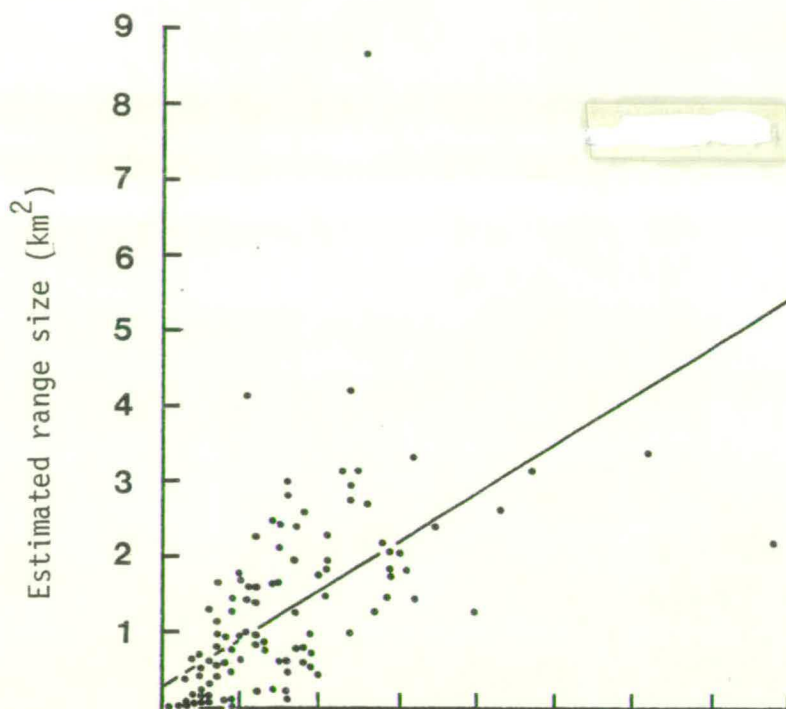
(b) Ellipse area index.
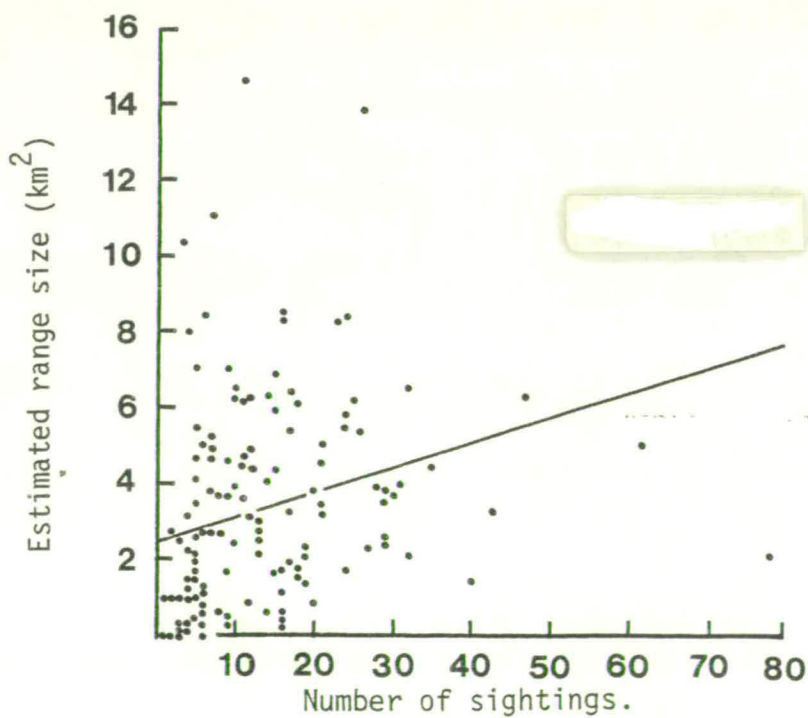
Data from summers 1976-78. Solid lines are fitted regressions, both significantly different from zero at the 0.1% level.

Figure 5.2 Estimates of range size with increasing numbers of
observations.
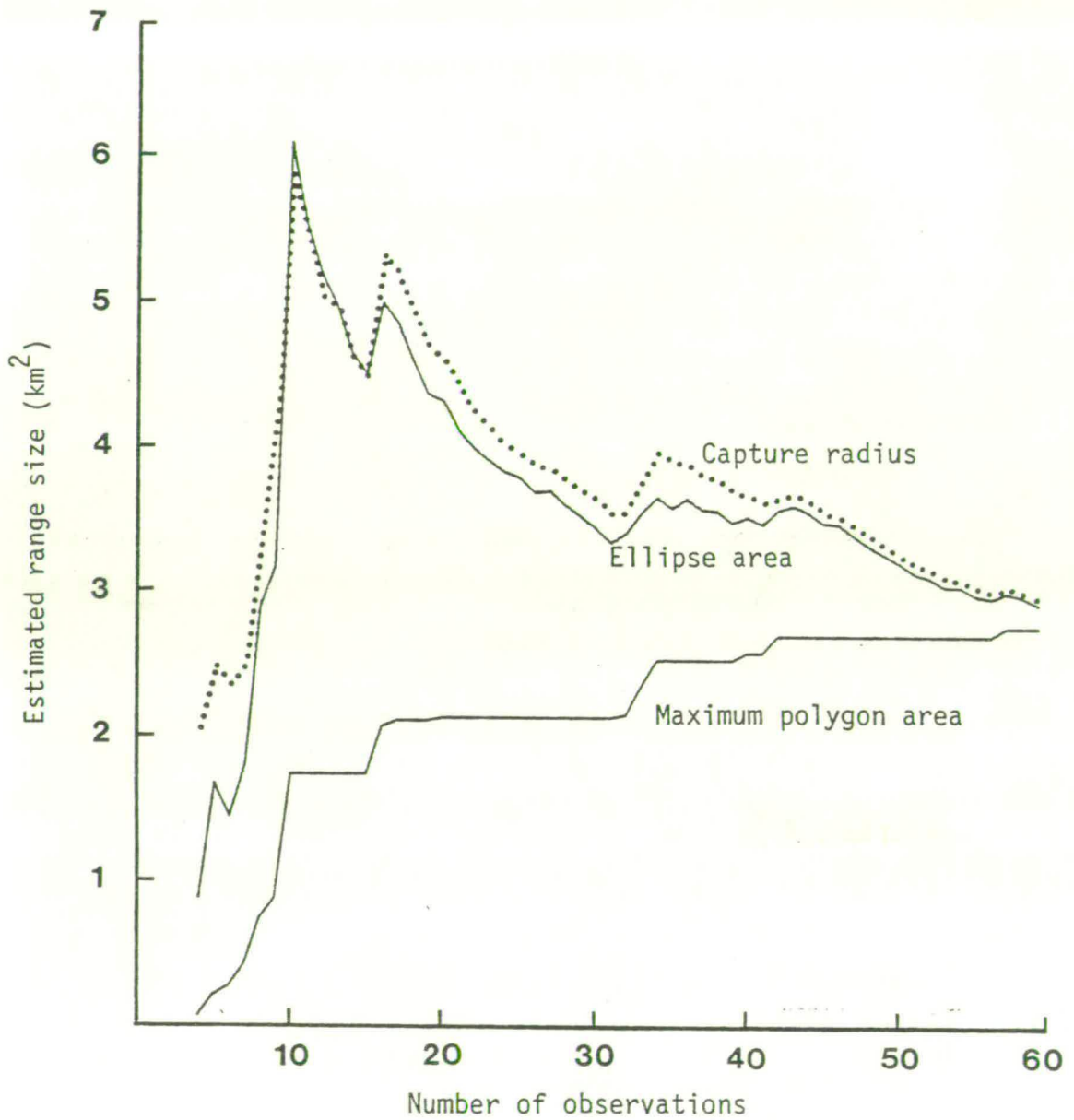
Data are sightings of a yearling male, collected between 25.1.78
and 1.4.78. For explanation of indices see text page 132.

MPA increased, but a gradual decline if the MPA was constant for several observations. This decline in size seemed to be due to the probabilistic nature of the index; outlying locations, included if samples were small, exerted less influence on the index as the number of locations near the range centre incieased. This showed the ellipse index was not necessarily free from sample bias, at least for small numbers of observations. Because it was difficult to compute, and made assumptions about the data which could not be tested, the ellipse area index was of no particular advantage in this case, though the results are listed in Table 5.7 for comparison with the other two indices.

(c) The MPA showed the most consistent response to sample size. In most cases the rate of increase in range size per observation was fairly constant over a range of approximately 5-20 observations. Above this the rate declined (Table 5.1) and the asymptote was usually reached between 20-40 observations. This suggested that, for any individual, the home range size index at the asymptote (called here the 'final MPA') was roughly proportional to the rate of increase in MPA between 10-20 observations. To test this, the rates of increase at 5,10,15 and 20 observations were plotted against the final MPA for 16 birds that had at at least 25 observations. At each sample size there was a highly significant correlation between the rate of range size increase per observation and the final range size, the plot for n=15 being typical (Fig.5.3). The correlation was lowest at n=5,

Table 5.1 Mean rate of increase of range size at different

numbers of observations.

Number of observations	Mean rate of increase in range size	2 S.E.	Number of birds
5	0.06	0.03	16
10	0.09	0.04	16
15	0.09	0.03	16
20	0.09	0.04	16
25	0.05	0.02	13
30	0.06	0.02	10
35	0.04	0.02	7
40	0.04	0.02	6

Based on data for the same 16 birds.

Rate expressed as km^2 per observation.

Table 5.2 Regressions of rate of increase in maximum polygon

area versus final range size.

For explanation, see text page137.

Number of observations.	5	10	15	20
Correlation coefficient.	0.7503	0.9037	0.9410	0.9526
Regression coefficient.	3.90	5.25	4.37	4.13
Number of birds.	16	16	16	16
't' statistic.	4.25	7.90	10.40	11.72
Significance level.	0.1%	0.1%	0.01%	0.01%
95% limits of regression coefficient.	1.93- -5.86	1.83- -7.81	3.47- -5.28	3.37- -4.88

Figure 5.3 Rate of range size increase per observation in relation
to the final size of the range.
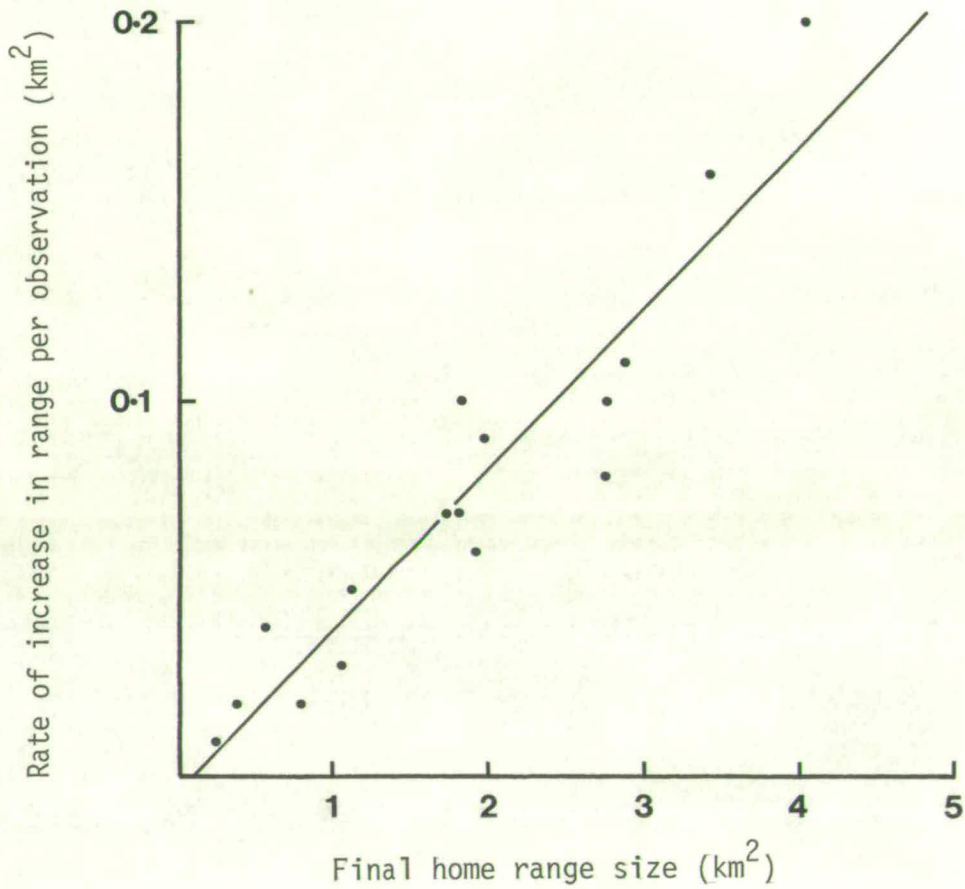
Rate of increase taken at 15 observations. Data are Maximum
Polygon Areas calculated from the sightings of the same 16 individuals
that had at least 25 observations at the final home range size.
Line is fitted regression:

Y = 0.04X -0.004
(r = 0.9410, P < 0.001)

but improved thereafter so that the fit for n=20 was closest (Table 5.2).

I used the above relationship to correct the MPA of birds that had fewer than 20 observations in any period. Detailed coverage of all birds was impossible, so some inevitably had less than 20 locations and their results could not be used unless allowance was made for this. To do this, the MPA was divided by the number of observations to give a rate of range increase per observation, which was assumed to be equal to that at n=15. The corrected MPA was then calculated using the rate at n=15 (R15) regression shown in Fig. 5.3. Birds with less than 10 observations were not used because the rates below this number were less reliable; those with over 20 observations were assumed to have reached their final range size so the index used was the MPA at their maximum number of observations. Although this method may have given a few inaccurate results, it allowed the use of data from more birds and so probably gave a better overall mean for any period than the alternatives of either not correcting or of ignoring birds with fewer than 20 observations.

2. Home range overlap and exclusive area size.

The extent of overlap indicates how much of the range is exclusive, which in turn may be an index of territory size. The range overlap of an individual was taken as the percentage of its

uncorrected MPA which was shared with the MPA of other birds. Outside the breeding season this was computed for all birds, but in summer overlap was assessed between males only. This was because data for females were limited and because their ranges were usually small and completely within those of their males. The measurement of overlap in this way was only possible if most birds had accurately assessed ranges, because those with underestimated areas had reduced overlap themselves and also reduced the estimates of their neighbours. This meant that data from October 1975 to July 1976 could not be used as there was a high proportion of unmarked birds in that period. Only birds which had a MPA based on at least 10 observations were included; individuals with fewer locations may have affected the results even when ignored, but the bias was probably no different between the periods.

3. The use of exclusive area as an index of territory size.

To evaluate the assumption that the exclusive parts of ranges were in fact territories, I examined the way in which birds utilized and defended their range. If the exclusive area was equivalent to a territory, birds may have used and defended it with greater intensity than the rest of the range. To see if all parts of the range were equally used, or whether activity was concentrated at certain points, I assumed that when the sightings of several birds were combined the distribution of points reflected

the average use of the home range relative to the centre. This seemed justified as most ranges were fairly similar in size within periods

Distribution was measured by finding the frequency of locations in bands at varying distances from either the nest (in summer) or the range geometric mean centre (GMC). The bands were at 0.25 km intervals for the first km and thereafter at 1.5 km and 2 km. To find whether all parts of the range were equally defended (or equally avoided by intruders), I also examined the amount of range overlap and the frequency of sighting intruders in the range, at different distances from the range centre. Thus for each range the following were recorded:

(a) the number of observations of the range owner in each band;

(b) the amount of MPA overlapped with other ranges in each band;

(c) the number of intruders observed within each band.

Results for each period were then expressed as totals for each band, to give the overall disribution of points in the range, relative to the centre. This showed that:

(a) Range Utilization. The distribution of 'owner' observations was similar between the seasons, being higher at the centre and falling off towards the edges (Fig. 5.4a). The summer results were slightly different in that the fall was sharp between 0-0.5 km, but there was little difference over the rest of the

Figure 5.4   Changes in range parameters in relation to distance from
              the range centre.

(a)   Density of observations of range owners.

(b)   Proportion of the range that was exclusive.

(c)   Density of observations of intruders to range.

        Range centre taken as the Geometric Mean Centre of the range
in autumn and winter, and as the nest in summer.   Data collected
autumn 1976 to summer 1978.

              • =   autumn (October/November)
              ▽ =   winter (December-February)
              ■ =   summer (April-July)

(a)
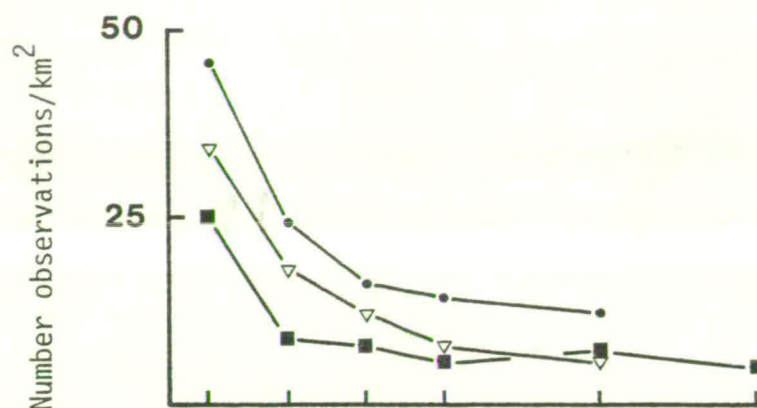
(b)
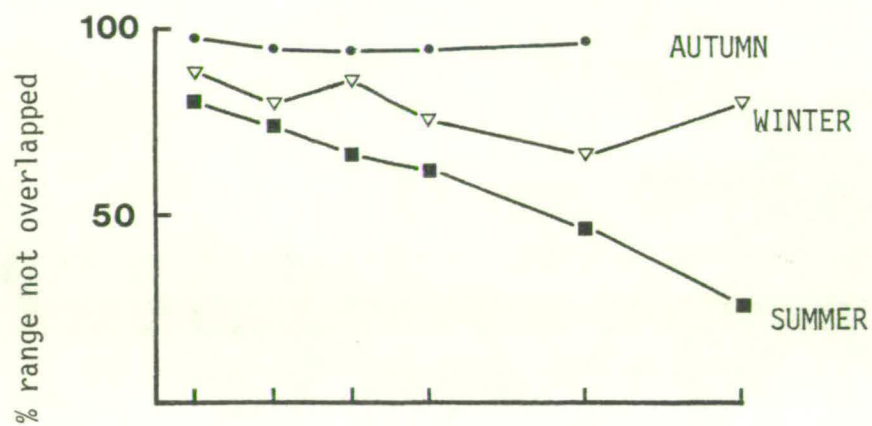
(c)
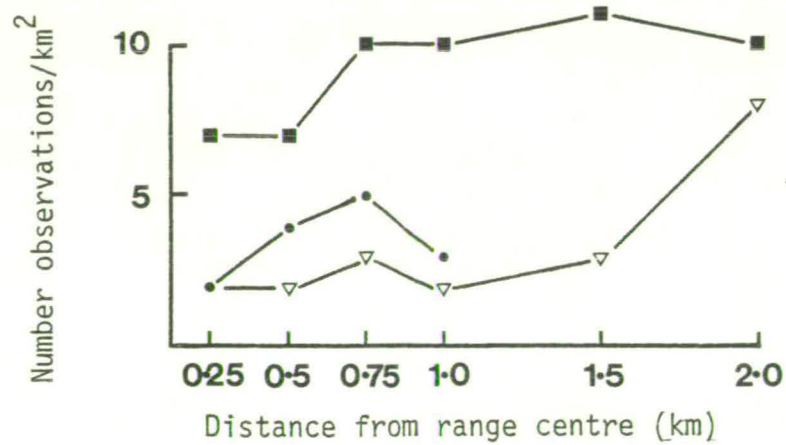
range, showing that birds were concentrating activity in a small area around the nest. The frequency of observations in each band was compared with that expected if all bands had an equal chance of being used (Table 5.3). In all seasons there were significantly more observations near the centre, and fewer further away, than expected if ranges were used equally throughout, although this effect was most evident in summer.

(b) Exclusive Area. In autumn and winter the home range was almost entirely exclusive at all distances from the geometric centre; whereas in summer overlap increased rapidly away from the nest (Fig. 5.4b). The GMC of most of the male ranges in summer was within 0.5 km of the nest and measuring from the two points gave similar results. Thus, outside the breeding season, ranges were equally exclusive at all distances from the centre, whereas in summer they were exclusive only in a 'core area' around the nest.

(c) Intruders. In autumn, the distribution of observations of intruders to the home range was the opposite to that of owners, being higher at the edges than at the centre (Fig. 5.4c and Table 5.4). However, the distribution of points in winter was no different than expected if intruders were equally likely in all parts of the range and the numbers were low in all bands. Such a result would occur if the range was defended equally throughout. In summer, the density of intruders was generally higher in all bands but showed a sudden increase between 0.5 and 0.75 km, again suggesting that birds may have excluded others only from areas

Table 5.3 Distribution of observations of owners at
          varying distances from the range centre.

(a) Autmun.

Distance from centre (km).	0.25	0.50	0.75	1.00
Total range area in band (km^2).	4.8	9.3	6.0	2.8
Number of observations.	217	224	96	38
Expected number.	122	233	150	71
$(Obs-Ex)^2/Ex.$	74.0	0.4	19.4	15.3

Chi-squared= 109.1 df=3 P<0.0001

(b) Winter.

Distance from centre (km).	0.25	0.50	0.75	1.00
Total range area in band (km^2).	2.9	6.6	8.1	5.9
Number of observations.	99	121	96	44
Expected number.	44	102	124	91
$(Obs-Ex)^2/Ex.$	68.8	3.5	6.3	24.3

Chi-squared= 102.9 df=3 P<0.0001

(c) Summer.

Distance from centre (km).	0.25	0.50	0.75	1.00	1.50
Total range area in band (km^2).	6.7	16.6	19.9	17.6	20.6
Number of observations.	169	142	161	124	142
Expected number.	61	150	181	159	187
$(Obs-Ex)^2/Ex.$	191.2	0.4	2.2	7.7	10.8

Chi-squared= 212.4 df=4 P<0.0001

Expected values calculated assuming owners were equally
likely to be seen at all distances from the range centre.

Table 5.4 Distribution of observations of intruders at

varying distances from the range centre.

(a) Autmun.

Distance from centre (km).	0.25	0.50	0.75	1.00
Total range area in band (km^2).	4.8	9.3	6.0	2.8
Number of observations.	8	37	28	7
Expected number.	17	32	21	10
$(Obs-Ex)^2/Ex.$	4.8	0.8	2.3	0.9

Chi-squared= 8.8   df=3   P<0.05 >0.01

(b) Winter.

Distance from centre (km).	0.25	0.50	0.75	1.00
Total range area in band (km^2).	2.9	6.6	8.1	5.9
Number of observations.	5	11	19	13
Expected number.	6	14	17	12
$(Obs-Ex)^2/Ex.$	0.2	0.6	0.2	0.1

Chi-squared= 1.1   df=3   P=0.5

(c) Summer.

Distance from centre (km).	0.25	0.50	0.75	1.00	1.50
Total range area in band (km^2).	6.7	16.6	19.9	17.6	20.6
Number of observations.	44	121	205	182	224
Expected number.	64	158	190	166	197
$(Obs-Ex)^2/Ex.$	6.3	8.7	1.2	1.5	3.7

Chi-squared= 21.3   df=4   P<0.001

Expected values calculated assuming intruders were equally

likely to be seen at all distances from the range centre.

around their nest. The distributions of owner and intruder sightings were combined by finding the proportion of observations within the range that were not of the owner and relating this to the distance from the range centre (Fig. 5.5). The results again emphasised the difference between the breeding season and the rest of the year.

Thus, birds concentrated their activity near the range centre (or nest), where there was a higher proportion of exclusive area, and fewer intrusions, than near the range edges. From the observed distributions I concluded that the individual ranges in autumn and winter were almost entirely exclusive. Though only a few prolonged combats were seen at this time of year, they were extremely hard fought and usually took the form of talon grappling on the ground at the range boundaries. This implied that the exclusion of others was the result of defence and that most of the ranges were territories. The low frequency of fighting at this time of year may have been because individuals soon learnt their neighbour's territory boundaries and seldom crossed them. In summer active defence was more frequent but males excluded each other only from an area around their nest. The mean distance from these fights to the owner's nest was 0.51 km in 1977 (n=12) and 0.25 km in 1978 (n=37), which roughly corresponded to the distance at which intruders increased and exclusive area decreased. Although not all the range may have been defended at this time, the above evidence

Figure 5.5 Proportion of observations that were intruders in relation to distance from the range centre.
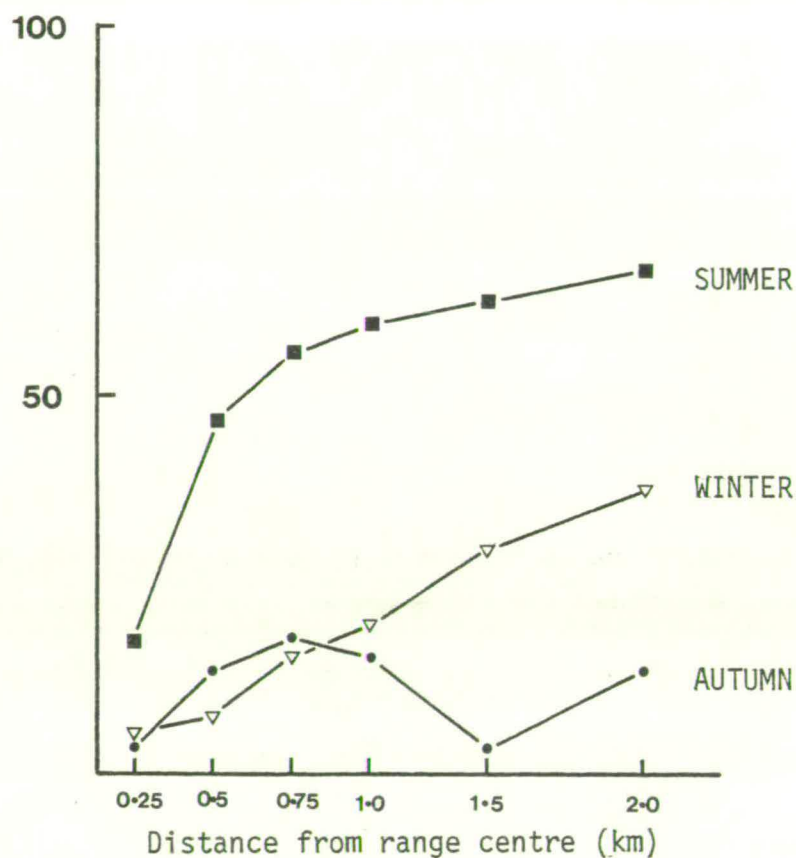
Frequencies expressed as a percentage of the total number of observations at each distance from the range centre that were intruders to the range. Range centre taken as the Geometric Mean Centre of the range in autumn and winter, and as the nest in summer. Data collected from autumn 1976 to summer 1978.

seemed to justify the use of exclusive area as an index of territory size.

Assessment of the Accuracy of Sightings.

Although Kestrels spent most of their time in the open and were fairly conspicuous, the accuracy of ranges collected by sight was unknown so I decided to check them by radio-tracking a few individuals. This was done at various times between February 1977 and July 1978, using 'AVM SM1' transmitters. Because few transmitters were available, I used only males known to have been in the area for some time, as these were thought less likely to move away than other birds. Transmitters were attached to the central tail feathers and, with the largest batteries used, weighed about 8 g and lasted up to 5 months. Ranges were generally found by spot observations, either by moving from one bird to the next after location was fixed, or 'at random', whenever I happened to be in the area. In order to compare radio-tracked observations (called here 'telemetry observations') with those obtained purely by sight ('sightings'), a bird was first searched for by sight and only if this failed was telemetry used. Thus, each radio-tracked bird had a number of sightings as well as a larger number of telemetry observations, the latter including locations made by sight alone. Collecting the two types of observation simultaneously may have

increased the likelihood of locating a bird by sight if the telemetry results increased the amount of searching in areas where the bird was most often located. However, I felt that this method was better than comparing range size before and after the transmitter was attached because it ruled out the effects of any changes between the observation periods. I tried to ensure that the effort put into visual searching for birds with transmitters was similar to that for birds without.

In comparing sight and telemetry observations, I examined three main aspects:

(a) The period required to estimate the final home range size. With telemetry it was nearly always possible to locate a bird once a search was begun, but this was not so when only sight was used. Thus the rate of increase of range size with time was faster with telemetry because more observations were obtained over the same period. However, the rate of increase per observation was similar between the two methods, at least for the first 20 observations (Fig. 5.6). This suggested the sampling methods were basically similar, the main advantage of telemetry being a rapid estimation which reduced the possibility of ranges changing during the measurement period.

(b) Range size. The results from radio-tracking a bird did not enable me to find it more easily by sight, and the mean sightings MPA of radio-tracked birds was similar to the mean sightings MPA of birds without transmitters (Table 5.5). This also showed that

Figure 5.6 Comparison of the rate of increase of range size per
            observation when data were collected by radio-telemetry
            or by sight alone.
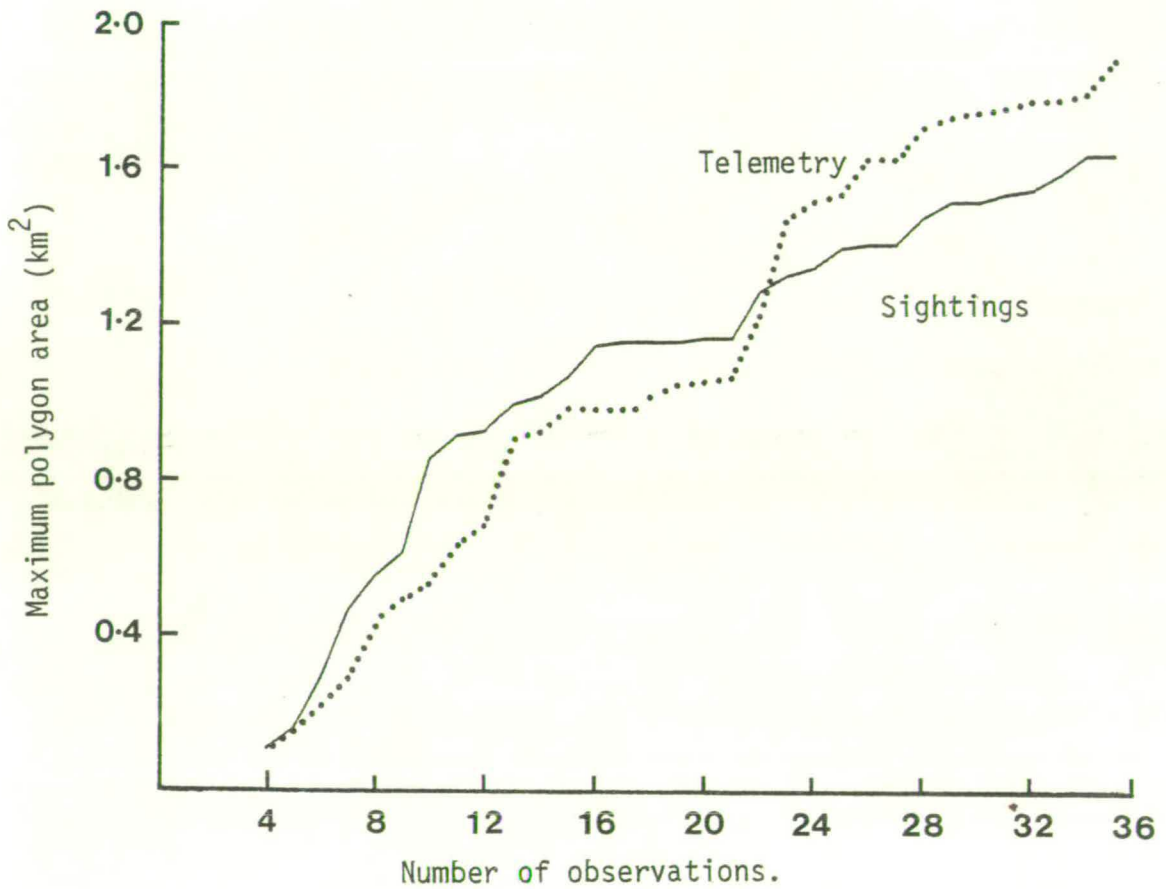
Data refer to the means of the same 5 males, estimates for the
two methods being made over the same period for each male.

Table 5.5 Range size estimates based on sightings of

Kestrels carrying radio-transmitters and those

carrying only wing tags, summer 1978.

	Mean range size (2 S.E.)	Number of birds
Birds carrying radio-transmitters and wing tags.	2.49 (0.29)	15
Birds carrying wing tags only.	2.50 (0.44)	7

The two groups were different males with ranges

collected by sight alone over the same period in summer 1978.

Ranges are maximum polygon areas in km^2, estimated from

sightings only.

attaching a radio-transmitter to a bird did not significantly alter its range size. It was therefore reasonable to assume that the difference between sightings and telemetry observations for radio-tracked birds reflected the accuracy of finding ranges by sight alone.

The size estimates from the two methods were significantly correlated (Fig. 5.7, r= 0.9667, P<0.001), though telemetry estimates were always larger than those from sightings. This was increasingly so for larger ranges so that, whereas the sightings estimate of range size was over 90% of the telemetry estimate when the range was 1 km^2, it was only 50% for ranges of over 7 km^2. It was therefore necessary to correct the sightings results because they gave more accurate estimates of size when ranges were small than when they were large. Thus, unless otherwise stated, home range size refers to the mean R15 MPA index of sightings, corrected using the regression in Fig. 5.7. This 'telemetry corrected MPA' (TMPA), calculated for birds with over 10 sightings, showed no significant correlation with the number of observations (e.g. for summer ranges: r= -0.0363, NS).

(c) The distribution of the points within the home range. In many cases there was considerable variation in the visibility at different points in the same home range. A bird was more easily seen if it was near a road or on a prominent perch than when it was some distance from a road or hidden in a wood. Because of 'blind spots', the distribution of sighting records may not necessarily

Figure 5.7   Home range size as estimated from sightings alone,
             compared with that estimated using radio-telemetry.
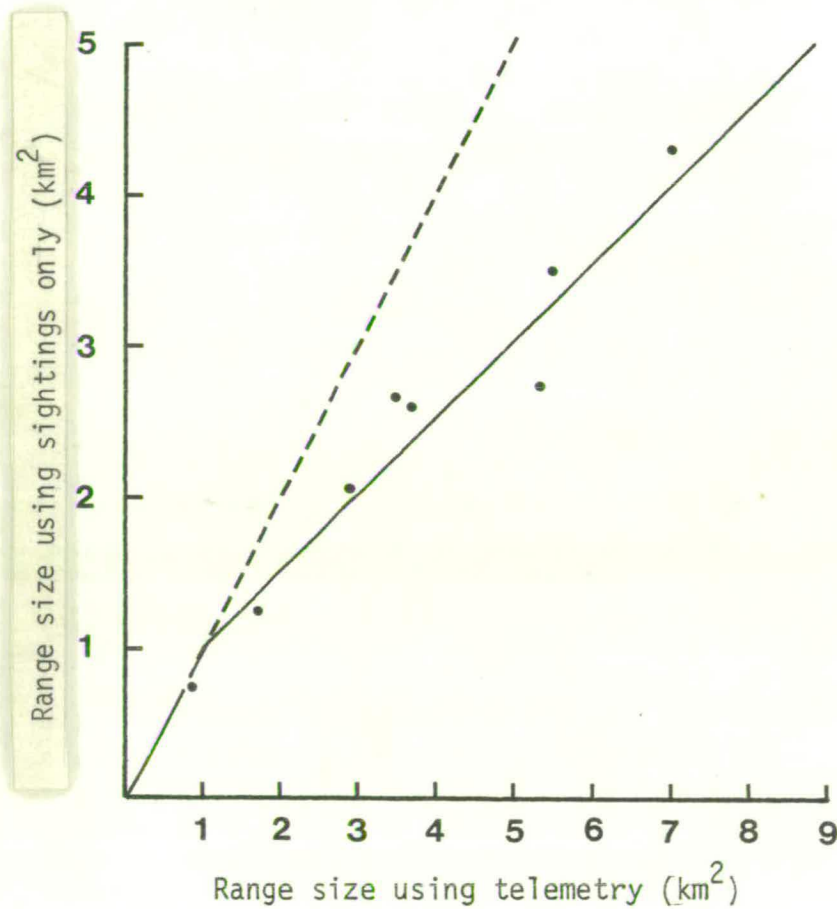
Data are maximum ploygon areas for 8 individuals followed by
sight alone and radio-tracked over the same period. Solid line is
fitted regression:

    Y = 0.52X + 0.49

    (r = 0.9667, P < 0.001)

Dotted line is the fit expected if both methods gave identical
estimates.

have reflected the actual utilization of the range by its owner. Such blind spots were largely removed with telemetry because the bird could be located regardless of where it was. Furthermore, the way in which data were collected meant that the points were probably a random sample reflecting the use made of the range by the bird.

Unfortunately, it was difficult to compare telemetry observations and sightings directly because only a few birds had sufficient observations from both methods and because locations had to be compared over the same period as their distribution changed through the season. The results which were available differed between individuals. In some cases the distribution of sightings, although based on smaller in numbers, was similar to the distribution of telemetry observations, whereas in others the two distributions were noticeably different (Table 5.6). Birds were seldom seen in outlying parts of their range that they rarely visited, thereby reducing range size when compared with telemetry observations. The effect of blind spots varied between individuals depending on where there were obstructions in the range. Thus, while the distribution of sightings of any individual may have been affected by visibility, the bias was not consistent between the ranges of different birds, and the combined distributions of several birds gave a reasonable estimate of average range utilization relative to the range centre.

Table 5.6 Distributions of sightings and telemetry

observations for two radio-tracked birds.

Data for both birds were collected April-July 1978.

(a) Adult male EF90418.

Distance from the nest (km).	0.0-0.5	0.5-1.0	1.0+
Number of sightings.	4	23	19
Number of telemetry observations.	44	60	35

Chi-squared= 10.5   df=2   P<0.01>0.001

(b) Yearling male EF90650.

Distance from the nest (km).	0.0-0.5	0.5-1.0	1.0+
Number of sightings.	39	35	3
Number of telemetry observations.	67	55	11

Chi-squared= 1.59   df=2   NS

In summary, the sightings maximum polygon area (MPA) index seemed to be the most useful measure of range size, but it was necessary to correct for small sample size bias (the 'R15' correction) and to allow for the problems of assessing ranges by sight rather than by telemetry. The resulting index (the TMPA) seemed free from sample bias and was used in preference to the ellipse area because it made fewer assumptions about the distribution of the data. Territory size was taken as the amount of the MPA not overlapped with that of other birds. Range utilization was assumed to be reflected in the distribution of sightings within the range, provided results were summed over several individuals to reduce the bias due to blind spots in each range.

SEASONAL CHANGES IN HOME RANGE.

Home Range Size.

There was considerable variation in range size between periods, the largest mean range size (5.69 km^2 in summer 1977) being five times the smallest (1.14 km^2 in autumn 1975), Table 5.7. Although range size varied between years, seasonal changes followed a similar pattern from year to year (Fig. 5.8a). In autumn, ranges were usually $1\text{-}2 \text{ km}^2$, but increased to $2\text{-}5 \text{ km}^2$ in winter as the density of birds fell (see chapter 4) and those remaining expanded into the gaps left by individuals that either moved away or died. This was borne out by observation on a several occasions when birds suddenly occupied the previously exclusive area of a neighbour that was not seen again (or, in two instances, found dead some time later). Whether the remaining bird caused the other to disappear, or whether it had passively expanded into the empty range, was hard to tell. However, I never saw the 'intruders' use another range while the original occupant was still there, so they probably moved in only after the range was vacated. Birds that did this usually continued to use their previous range as well, hence the increase in range size in winter.

In the breeding season, ranges were used by pairs rather than by individuals. Some pairs were present in autumn, but most had split by late December and none was definitely known to have

Table 5.7 Comparison of range size indices for each period, 1975-78.

Period	Year	TMPA	CR	ELLIPSE	n
Autumn	1975	1.14 (0.69)	2.34 (1.27)	1.63 (0.74)	6
	1976	2.12 (1.06)	4.00 (1.01)	2.71 (1.23)	10
	1977	1.22 (0.71)	2.04 (1.08)	1.93 (1.08)	16
Winter	1975	2.06 (1.39)	2.58 (1.35)	2.23 (1.26)	7
	1976	4.87 (1.64)	6.70 (1.47)	4.92 (1.21)	5
	1977	2.55 (1.28)	4.04 (2.35)	3.05 (1.38)	10
Summer	1976	3.11 (0.75)	3.90 (0.82)	3.43 (0.73)	9
	1977	5.69 (1.89)	7.29 (2.22)	6.18 (1.57)	19
	1978	4.08 (0.95)	5.23 (1.10)	4.39 (0.86)	21

Size given is the mean estimate in km^2.

Figures in parentheses are 2 S.E.

Summer results refer to male ranges only.

TMPA= Telemetry corrected maximum polygon area (see text).

CR= Capture Radius index.

ELLIPSE= Ellipse Area index.

n= number of ranges.

Figure 5.8   Seasonal changes in home range parameters.

(a)   Home range size.

     Points are telemetry-corrected MPA (see text page 153), confidence
limits are + 2S.E.

(b)   Territory size.

     Points are mean exclusive areas of the MPA, confidence limits
are + 2S.E.

(c)   Range overlap.

     Points are the mean % of the MPA overlapped with that of other
individuals, confidence limits are + 2S.E. %

A = autumn, W = winter, S = summer. For definition of seasons,
see text page 132.

(a)

(b)

(c)
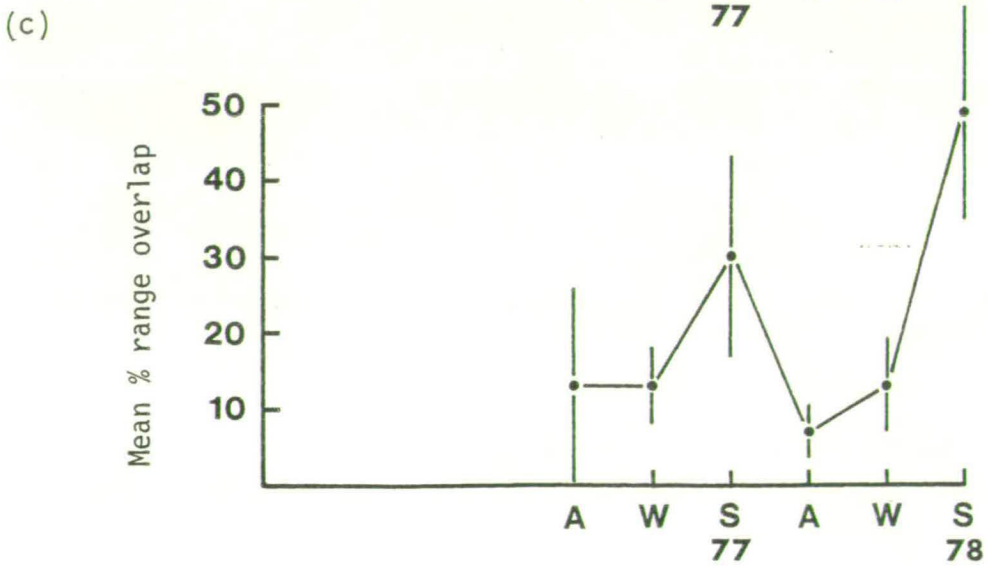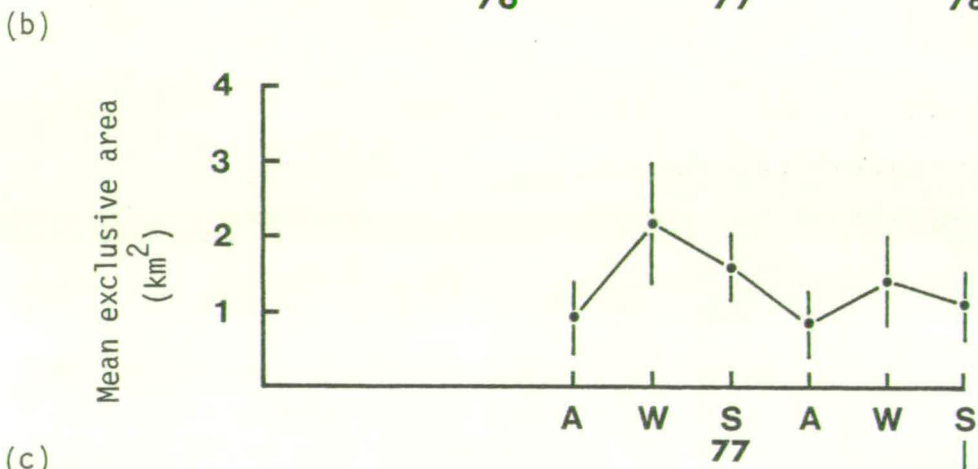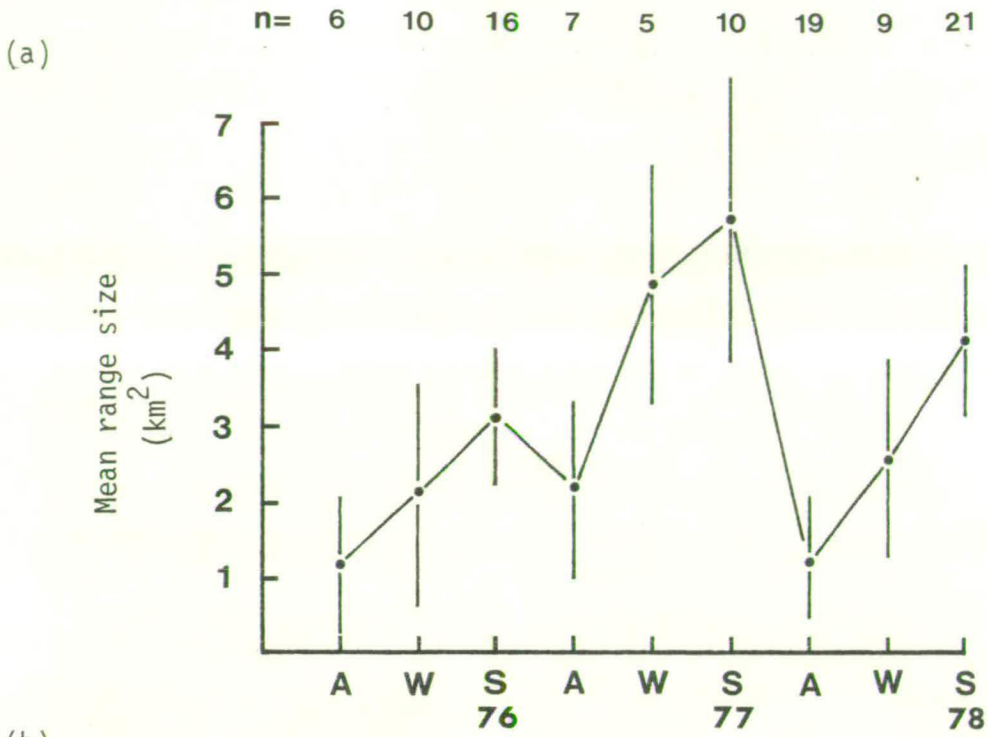
remained together all winter. Shared ranges in summer were usually larger than individual ranges of the previous winter, averaging 3-6 km^2.

Overlap and Exclusive Area.

The overlap of ranges occurred in a variety of circumstances which, although not always distinct, fell into four main categories.

(a) Edge Overlap. In places where range boundaries were not well defined (such as open hill ground) birds sometimes shared the edges of their range with neighbours. This was usually the result of one bird hunting into the range of another when the other was absent. When neighbours met in such areas the owner usually dived at the intruder and chased it away. However, these displays were seldom violent and sometimes not obvious as individuals merely flew together briefly before separating only a short distance. This was the usual type of overlap in autumn and winter and was most frequent when ranges were large. When ranges were small, or where boundaries were well defined (such as those along electricity pylon lines), overlap was unusual and intruders were sometimes violently attacked by the range occupiers (on five such occasions I saw birds fall to the ground and grapple with their talons).

(b) Hunting Intrusions. These differed from the above in that overlap was not confined to the edge of the range, or to between neighbours. Birds were occasionally seen hunting near the range

centre of other birds, though this was only recorded once outside the breeding season. In summer, intruders near the nest were usually chased away by the owners, though some were seen hunting unmolested, apparently because the owner was absent at the time.

(c) Display Intrusions. These were confined to the breeding season when overlap was often caused by birds (usually males) fighting near the nest of another bird. Such fights involved chasing, soaring and 'rocking displays' where the birds flew with rapid wing beats while rocking from side to side. Fights were usually between neighbours (27 out of 33 fights between tagged birds), but sometimes involved intruders that were apparently unpaired and not breeding. Display intrusions generally started when one bird, displaying near its nest, was joined by one or more neighbouring birds, though I twice saw males initiate fights by making long flights to neighbouring nests.

(d) Shared Hunting Ranges. This type of overlap was again confined to the breeding season. It was distinct from edge overlap in that the areas were shared by several birds which were not necessarily neighbours. Shared areas were away from occupied nests, usually on open hill ground, and were often used by birds nesting at high density in low ground valleys. Thus birds with little hunting area around their nest tended to fly to open hill ground to hunt, sometimes up to 5 km away. Areas consistently shared were hills with steep slopes facing in several directions, and birds may have gone to these areas to utilize windward slopes when

flight-hunting (see chapter 3). Although members of up to five pairs used some areas, they were rarely seen hunting close together and would usually dive at one another and separate if they met, in a similar manner to birds with edge overlap.

Outside the breeding season, overlap was less than 20% of range size on average and exclusive area size followed a similar trend to range size, increasing from autumn to winter (Fig. 5.8b-c). In summer both population density and range size increased, so that overlap was over 30% on average and territory size decreased. This corresponded to birds defending mainly an area around the nest and to some birds sharing hunting ranges.

Home Range in Early Spring.

From the end of February to mid-April there was a rapid increase in the number of birds in the study area and a major upheaval of the range system. The speed of the change made it difficult to follow precisely the changes in range at this time, so I had to generalize from scattered and incomplete records.

Birds arriving in early spring settled in areas previously occupied by winter residents, and I saw a number of prolonged fights between incomers and residents at this time. Newcomers seemed to settle eventually because of their persistence and would establish territories in between earlier settling birds. As more birds arrived, those present would gradually reduce their ranges

until all the nesting areas used that year were occupied. I could not tell whether birds arrived as pairs or arrived separately and paired later. However, as I rarely saw an unmated bird defending a nesting area, pairing must have occurred fairly soon after arrival.

The settling of pairs in one area (the Esk Valley) was followed fairly closely in 1977 and is illustrated in Figs. 5.9a-e, which show pair ranges identified by the occupying males only. There were only few records for some pairs, so the boundaries shown probably represent the centre of activity, rather than the whole range. In February, the area was occupied by two adult males, PP and GO (Fig. 5.9a). Two pairs of birds (males DG and OPr) settled between these males and were seen using the area shown in Fig. 5.9b from 8-24 March. On 25 March another pair (male BR) settled and the DG pair shifted their range south to around the nest they eventually used (Fig. 5.9c). The final pair to settle was first seen on 13 April and established to the north of the BR pair (Fig. 5.9d). The male of this pair (GG) had little exclusive area left around the nest and had an unusually large range (16 km^2). This bird was chased away when it tried to hunt near the nests of other pairs and it may have had a large range because it was forced to fly over other ranges to find unoccupied hunting areas. When the BR pair failed in their breeding attempt at the end of May, their vacated range was quickly filled by adjacent pairs (Fig. 5.9e).

During the establishment of pairs in March and April, birds seemed to spend a large amount of time around their nest and less

Figure 5.9   Changes in home ranges in part of the Esk Valley from
             March to July 1978 (for explanation see text page 164).

KEY:

        ●   =   nest used during 1977 by one of the 6 males
                illustrated.

                1   =   PP
                2   =   OPr
                3   =   GG
                4   =   BR
                5   =   DG
                6   =   GO

        ■   =   other nests occupied in 1977.

(a) 1.3.77
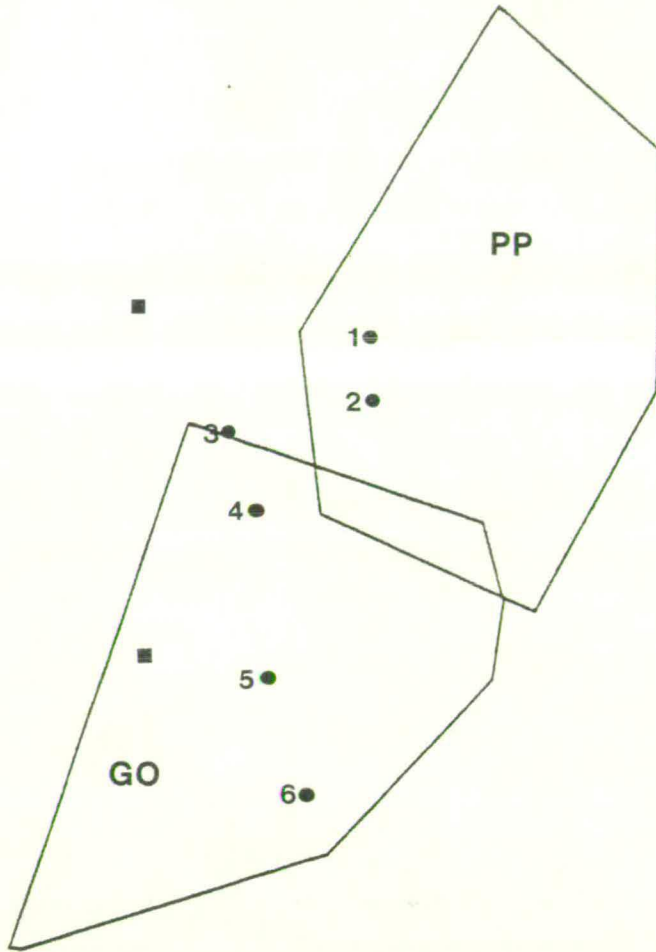
(b) 8.3.77 to 24.3.77
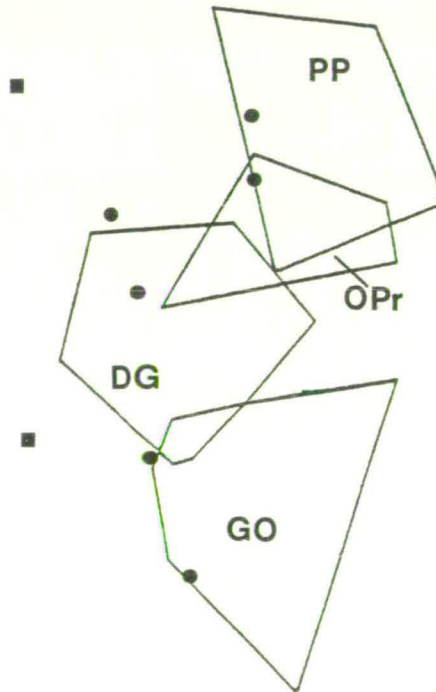
(c) 25.3.77 to 12.4.77
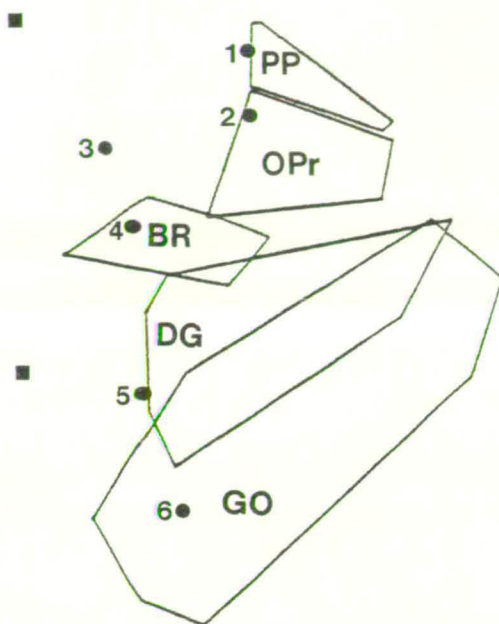
(d) 13.4.77 to 30.5.77
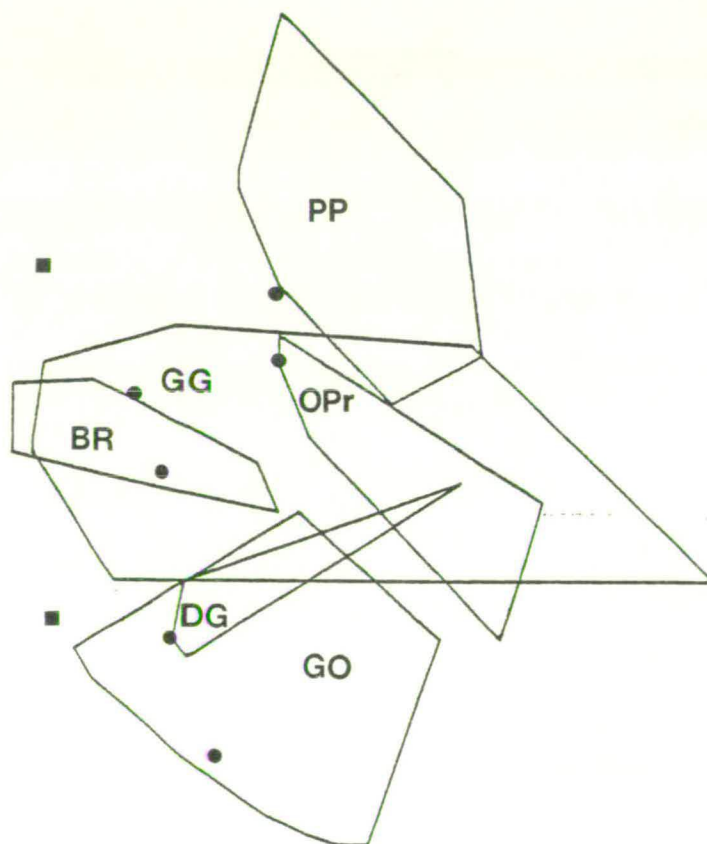
(e) <u>31.5.77 to 31.7.77</u>
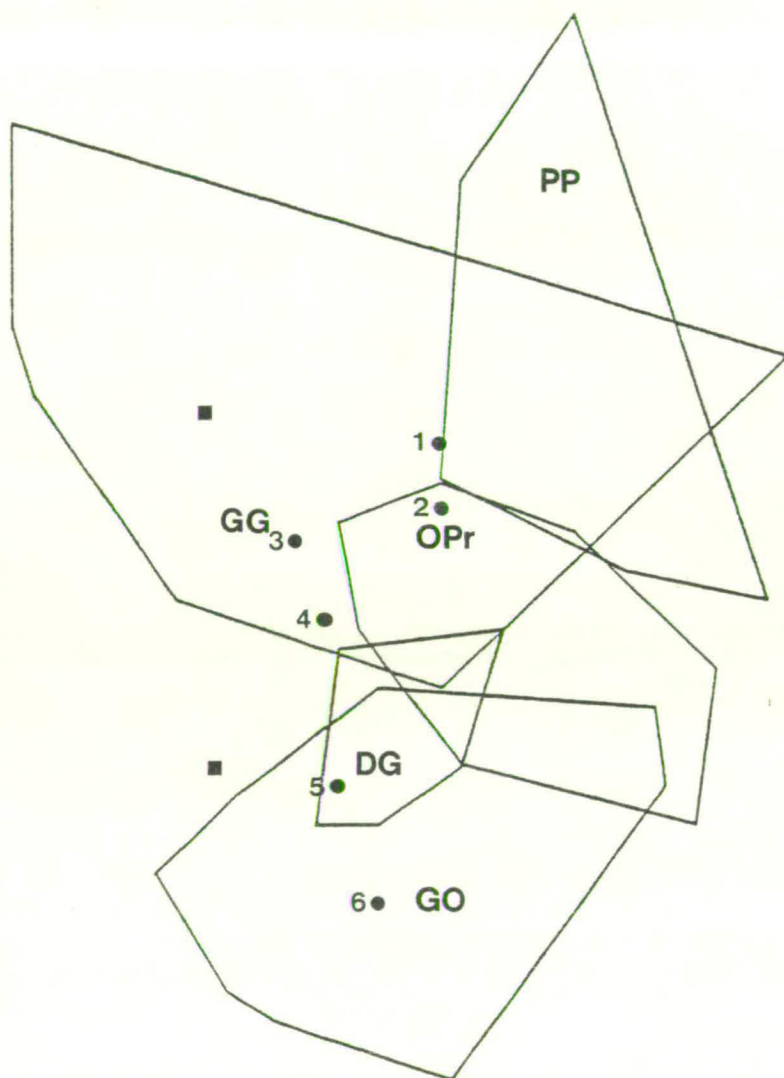
in parts of the range that were some distance away. This was less so later in the season when birds were feeding young. To measure the change in distribution between early spring and summer, a large number of observations was needed from individuals throughout the breeding season. With sightings this was rarely possible, but in 1978 three birds were radio-tracked from March to July, enabling comparison of observations as the season progressed. The period was divided into three parts (March, April and May-July) and the frequency of observations at distances of less than or greater than 0.75 km from the nest was compared (Table 5.8). There was a significant trend for a higher proportion of points to be away from the nest as the season progressed. Males may have spent more time around the nest early in the season in order to ward off intruders, a possibility supported by the following observation made in April 1978.

A radio-tracked adult male was located at least 0.5 km from his nest on 10 out of 14 occasions from 20-26 April. On 26 April I visited the nest and again the male was nowhere in the vicinity; however, his wing-tagged partner was being courted and mated by a yearling male that was displaying vigorously over the nest. Within 10 minutes of my arrival the radio-tagged male flew into the area and began fighting with the intruding male, behaviour that lasted several hours and was apparently resumed on the next day. Of the 8 locations made of this male in the week after this incident, 7 were within 0.5 km of the nest, a significant change (P= 0.025, Fisher

Table 5.8 Changes in the distibution of observations relative to the nest for three radio-tracked males in 1978.

Number of locations:

	within 0.75 km of the nest	over 0.75 km from the nest	Total
March	89	30	119
April	58	27	85
May/July	79	85	164
Total	226	142	368

Chi-squared= 22.8   df=2   P<0.001

exact test).

The seasonal changes in home range were well illustrated by a yearling male which was radio-tracked from 2 December 1977 until 7 April 1978, when its transmitter failed. A second transmitter was attached on 23 May (when his female was still incubating) and this lasted until mid July. Fig. 5.10 shows the increase in range following the disappearance of its neighbour in late December, the subsequent reduction of range in March and April, and the final increase during the nestling period.

Thus the large, exclusive ranges of overwintering birds were reduced in size in spring, both by incoming individuals establishing territories and because birds spent most of their time around the nest. Males that spent too long away from the nest in early spring may have been in danger of being replaced (or having their partners fertilized) by intruders that had no partner or nest. Later in the summer, when adults were feeding young, they more often hunted further from the nest, usually sharing the outer parts of their range with other birds, a behaviour noticed elsewhere in Kestrels (Tinbergen 1940 and Cave´ 1968) and in Sparrowhawks (Newton 1979). At this time there was little danger of replacement by intruders and the heavier food demands on the males may have made it necessary to travel further from the nest to find food.

Figure 5.10   Changes in the range of a radio-tracked male Kestrel,
              October 1977 to July 1978.

(a)   Autumn

              14.10.77 to 19.12.77
              MPA = 1.70 km^2
              Number of observations = 121

(b)   Winter

              20.12.77 to 14.3.78
              MPA = 5.47 km^2
              Number of observations = 84

(c)   Spring

              15.3.78 to 28.4.78
              MPA = 1.08 km^2
              Number of observations = 45

(d)   Summer

              1.5.78 to 31.7.78
              MPA = 2.70 km^2
              Number of observations = 59

Range in spring and summer was a paired range, shared with female.

      ● = position of nest used in 1978.

Each cross shows the position of the bird when first located by
sight or by telemetry.

(a) Autumn.
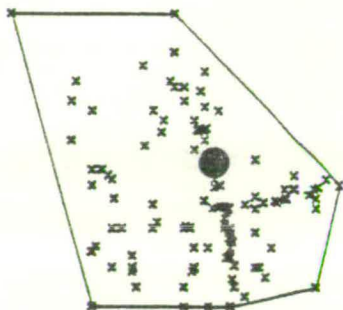
(b) Winter.

(c) Spring.
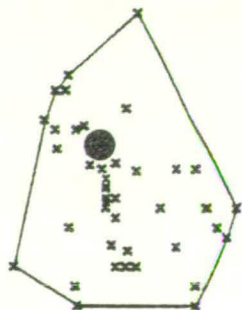
(d) Summer.
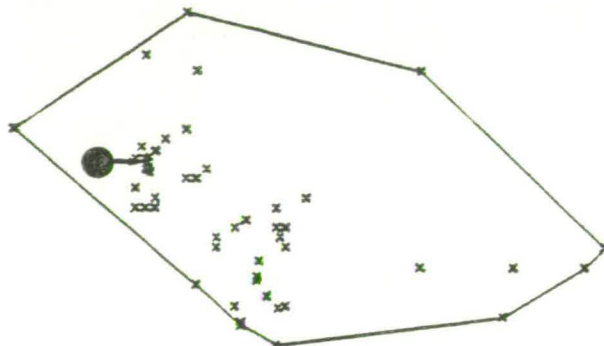
INDIVIDUAL DIFFERENCES IN HOME RANGE.

As well as seasonal differences, there was also some variation in the home range of individuals at any one time. In this section I shall consider three factors which might have contributed to this variation, namely the position of the nest and the age or sex of the bird.

1. The position of the nest.

In each year, some nests were a long way from their neighbours, while others, such as those in the valleys, were much closer. In assessing the relationship of nest spacing to home range, five factors were considered.

(a) The size of the home range.

(b) The size of the exclusive area.

(c) The distance from a nest to its nearest occupied neighbour.

(d) The nearest neighbour distance of the GMC of adjacent male ranges. If all home ranges were centred on the nest, this index was the same as the one above.

(e) The position of the nest within the range. This was measured as the distance between the nest and the GMC of the male home range, divided by the area of the range. The index was zero if the nest was at the GMC of the range and larger if the nest was

near the edge.

The above parameters were obtained for male ranges in summer 1977 and 1978 which were based on at least 10 sightings. Size, overlap, exclusive area and positon of the nest in the range were then related to nest and home range nearest neighbour distances, using simple linear regression (Table 5.9). Although some points were widely scattered, and not all the relationships may have been linear, the following, tentative conclusions emerged.

(a) The size of male summer ranges was independent of the proximity of either other nests or of other male home ranges.

(b) In 1977, males whose nests were close together shared a higher proportion of their ranges than did neighbouring males at isolated nests, which, as a consequence, had larger exclusive areas.

(c) In 1978 there was no relationship between nest nearest neighbour distance and either range overlap or exclusive area, but males with close neighbours had nests nearer the edge of their ranges than males at isolated nests.

2. The age and sex of the bird.

Sufficient data to allow comparisons between male and females or adults and juveniles were available only from autumn 1977 to summer 1978 (Table 5.10). These showed the following trends.

Table 5.9 Relationship of nest and home range spacing

to home range parameters.

For explanation see text, page 172.

DEPENDENT VARIABLE	INDEPENDENT VARIABLE			
	1977		1978	
	NN Nest	NN Range	NN Nest	NN Range
Range size.	NS	NS	NS	NS
% Range overlap.	- 1%	- 0.1%	NS	NS
Exclusive area.	+ 5%	+ 0.1%	NS	+ 5%
Position of the nest in the range.	NS	NS	- 1%	NS

Table shows the results of linear regressions

between dependent and independent variables.

NS= not significant.

- = variables negatively correlated.

+ = variables positively correlated

Percentages are significance levels for the regression.

NN Nest= distance of nest to its nearest neighbour.

NN range= distance from centre of male range to its

nearest neighbour.

Table 5.10 Home range size in relation to the age
and sex of the bird.

(a) Autumn 1977.	Mean size	n	'U'	P
Adult males	2.62	4	1	0.02
Juvenile males	0.68	4	16	
Juvenile males	0.68	4	21	NS
Juvenile females	0.79	8	11	

(b) Winter 1977.				
Adult males	3.62	4	2	NS
Juvenile males	1.63	3	10	
Juvenile males	1.63	3	3	NS
Juvenile females	2.05	3	3	

(c) Summer 1978.				
Adult males	4.25	15	28	NS
Yearling males	3.65	6	62	
Adult males	4.25	15	38	0.05
Adult females	2.73	9	97	
Adult females	2.73	9	18	NS
Yearling Females	2.94	4	18	
Yearling males	3.65	6	10	NS
Yearling females	2.94	4	14	

Size given is telemetry corrected MPA (in km^2),

see text page 153.

Differences between the means tested by the

Mann-Whitney 'U' test.

(a) In autumn and winter there was no difference between the range sizes of juvenile males and juvenile females, but adult males had significantly larger ranges than juvenile males. (There were no estimates of range size for adult females during these periods.) In 20 out of 25 cases, adults had autumn ranges that included at least one nesting area; the proportion in juveniles (8 out of 22) was significantly lower ($X2= 11.11$, $P<0.001$). This difference was unlikely to have arisen purely because of the larger size of adult ranges as the density of nesting areas was greater in adult than juvenile ranges. For example, in autumn 1978 the mean density of nesting areas per range was $3.51/km^2$ in adults ($n=9$) and $1.31/km^2$ in juveniles ($n=13$). The difference in the means was significant at the 2% level when tested by the Mann-Whitney 'U' test.

(b) In summer there was no difference in range size between adults and yearlings, but ranges were larger in males than in females, as mentioned earlier.

Discussion.

The difference between 1977 and 1978 in the relationship of nest spacing to range overlap seems to have been due to the ranges of males occupying closely adjacent nests. In 1978, a few pairs nested less than 200 m apart and their ranges would have overlapped considerably, had they been centred around the nest (Fig. 5.11b). Instead, the nests of close neighbours were at the edge of their ranges and this largely reduced overlap (Fig. 5.11a). This may

Figure 5.11 Illustration of the effects on range overlap of
having the nest near the edge of the range or of
having ranges centred on the nest, for males with
closely adjacent nests.

(a) Nests near the edge of the range.
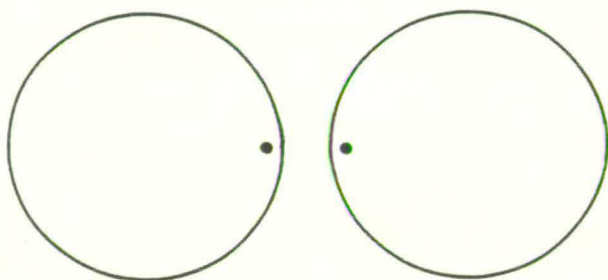
(b) Ranges centred on the nest.
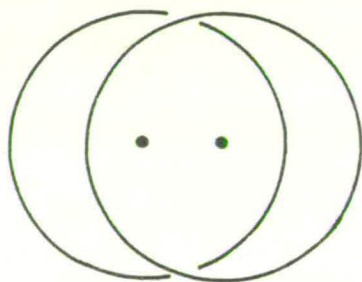
● = position of nest. Lines are hypothetical range boundaries.

occur only when nests are close together, which was not the case in 1977. It is possible that by this means pairs can use nests which are close together without interfering with each others hunting activity.

Why juveniles had smaller ranges than adults outside the breeding season was not clear. They may have been less skilled at defence and their ranges therefore more easily compressed. Alternatively, ranges may have been smaller because nearly all the juveniles at this time were in an area that had a higher vole density than the areas used by the adults. The reason for this separation was unknown, but it seemed that the adults were centering their ranges on particular nesting areas and preferred to remain on a range that was likely to supply a nest the following summer, despite the lower vole densities.

The lack of any marked difference between adults and yearlings in summer may have been because they were less segregated into areas of different vole density or because only better quality yearlings bred and these, given the same food conditions, required similar sized ranges. The difference between sexes at this time was because females spent much more time on or near the nest than did the males. A number of females were seen at some distance from the nest, but all were feeding fairly well grown young at the time.

HOME RANGE, KESTREL NUMBERS AND VOLE DENSITY.

Mean range size, exclusive area and Kestrel numbers for each period were regressed against vole density. In autumn and winter 1977, voles were more abundant in the north of the study area and this area was treated separately to increase the range of vole densities over which Kestrel home range was measured. Kestrel numbers were measured by simple counts (chapter 4), independently from the number of ranges in the area. Kestrel numbers may have been related to vole density irrespective of the size and number of ranges as there was considerable range overlap at some times of year and ranges were occupied by pairs in summer and individuals in winter.

Results.

(a) Kestrel numbers. When all periods were treated together, there was no significant correlation between Kestrel numbers and vole densities. (r= 0.1991, P>0.5). This was mainly because of the difference between the breeding season and the rest of the year. When treated separately, at both times of year Kestrel numbers were significantly related to vole density, being greater when vole density was high than when it was low (Fig. 5.12, autumn and winter: r= 0.8573, P<0.05, summer: r= 0.9987, P<0.05). The summer

Figure 5.12   Kestrel numbers in relation to vole density.

Each point represents an estimate for one period, autumn
1975 to summer 1978   Vole densities are 'short-term' values,
calculated from the solid line Fig. 2.1a.
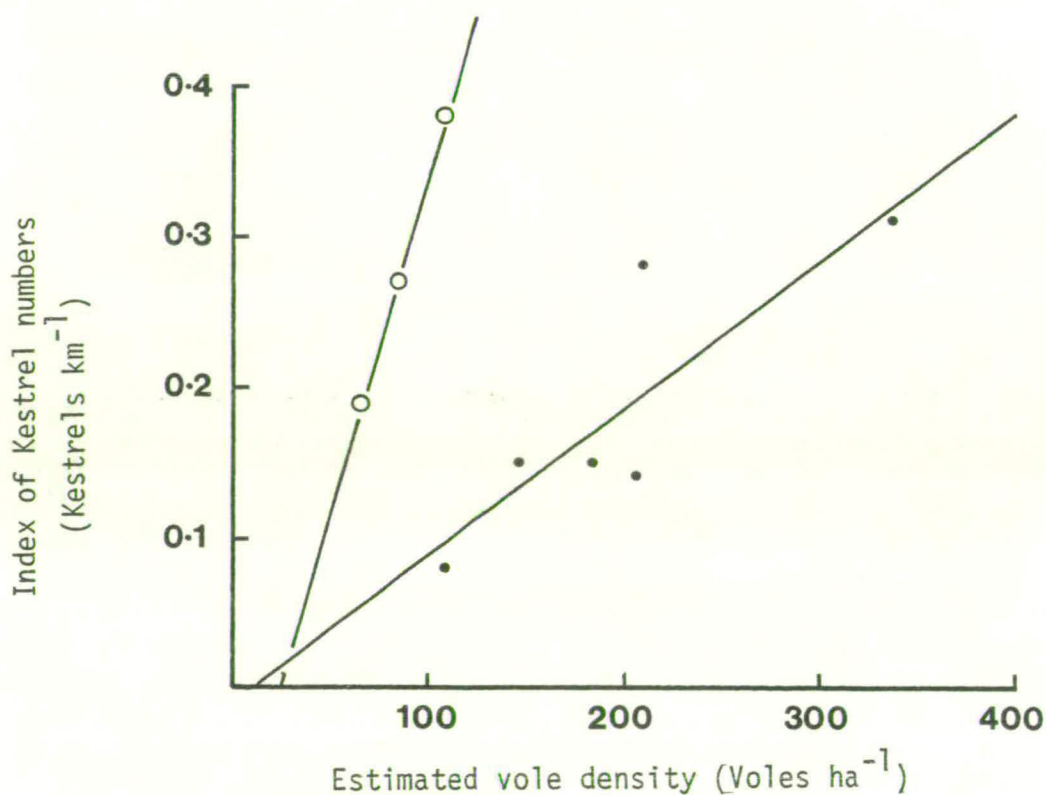
Kestrel numbers estimated from counts made while driving (see
chapter 4).   Lines are fitted regressions for summer (O) and autumn
plus winter (●).

Summer: Y = 0.004X - 0.114 (S.E. b=0.0002, P < 0.05)
Autumn plus winter: Y = 0.001X - 0.012 (S.E. b=0.0003, P < 0.05)

Kestrel densities were approximately twice those expected for the same vole density outside the breeding season.

(b) Home range size. As vole density increased, range size decreased, though the relationship was not linear. The best straight line was obtained by fitting log range size to vole density and this relationship was highly significant ($r=$ -0.9490, $P<0.001$). This regression was used to fit the line in Fig. 5.13a, which shows that the relationship may have been less precise below vole densities of about 100 voles/ha. Summer range size, unlike Kestrel numbers, seemed to follow the same relationship as in the rest of the year, even though ranges were occupied by pairs in summer and single birds in winter.

(c) Exclusive area. Outside the breeding season, exclusive area followed a similar trend to home range, and the best fit was log exclusive area against vole density (Fig. 5.13b, $r=$ -0.9686, $P<0.02$). The two summer values suggested that territory size was still dependent on vole numbers but, for any given vole density, there was a smaller exclusive area than expected outside the breeding season.

Figure 5.13 Home range and territory size in relation to vole density.

(a) Home range size.

Each point is the mean TMPA* for each period, autumn 1975 to
summer 1978. Line is fitted using the regression equation of Log range
size vs. vole density:

Log Y = -1.09X + 2.75
   (S.E. b=0.0003, P < 0.001)

(b) Territory size.

Each point is the mean exclusive area of MPA ranges for each
period, autumn 1976 to summer 1978. Line is fitted using the regression
equation of Log range size on vole density, fitted to autumn and winter
values only:

Log Y = -0.002X + 0.522
   (S.E. b=0.0003, P < 0.02)

O = summer,   • = autumn and winter.

*Telemetry - corrected. Maximum Polygon Area - see text page 153.

(a) Home range size.
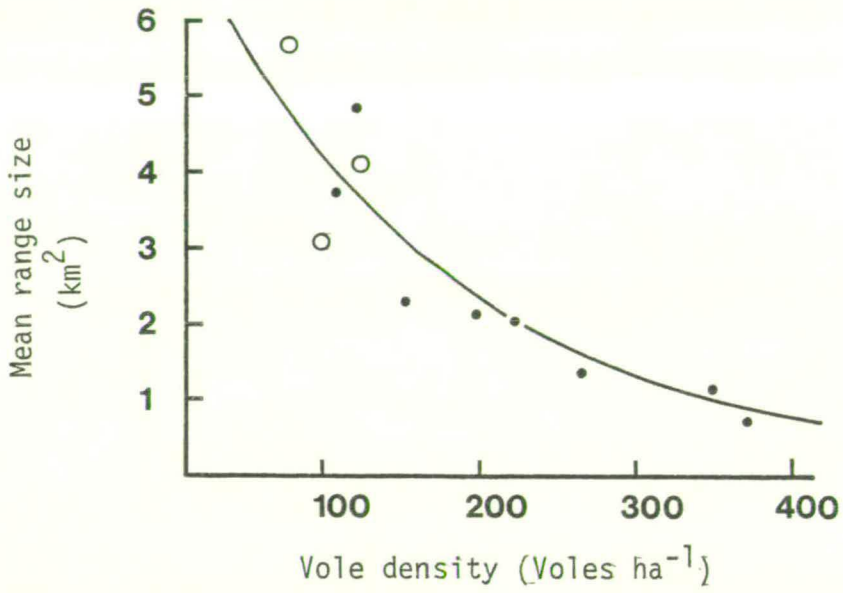
(b) Territory size.
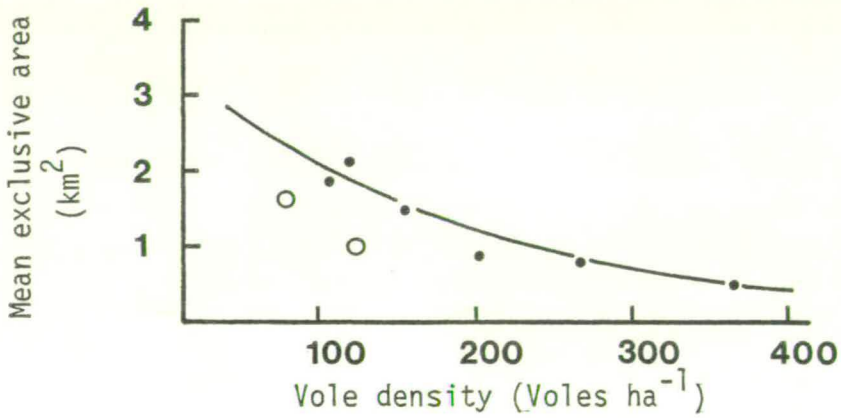
Discussion.

1. Factors influencing range size.

From the above results, it appeared that range size was influenced largely by vole density, regardless of the time of year and whether the range was held by one or two birds. Schoener (1968), in reviewing the sizes of bird feeding territories, found that they were generally independent of the number of birds engaged in defence. This may have applied to summer ranges in Kestrels, particularly as the females tended to do little hunting and remained at the nest.

Range size may have been related to vole density for several reasons:

(a) Range size might have been limited by the territorial behaviour of other birds preventing range expansion. The number of birds able to settle may in turn have been related to vole density, hence the relationship of range size to vole density. This is partly supported by the fact that individuals often expanded into gaps left when their neighbours disappeared, but may not have held in summer when there was considerable range overlap.

(b) The size of the range may have been determined by how far the owner travelled when hunting; this in turn being related to the time taken to make a kill once hunting commenced. Thus birds might start hunting from near their range centre and gradually move

outwards until they capture food. When food is short this may take some time and a large area is covered, whereas when food is plentiful birds capture fairly quickly and need not travel far. In this way, provided successive hunts do not reduce the chance of capture near the range centre, range size may be determined by vole density irrespective of the food demand on the owners.

This may explain why ranges were no larger in summer than at other times of year with similar vole densities, even though they were then occupied by pairs. On the other hand, food supply in summer may have been better at any given vole density than at other times of year because vegetation cover was still low, the number of young voles was increasing and alternative food sources became available (see chapter 2). In this case, range size in summer may have been the product of two conflicting factors, namely the better food supply for a given vole density (which would make ranges smaller) and an increased food demand because of the greater number of occupants (which would make ranges larger). The similarity of summer range sizes to those at other times of the year with similar vole densities may thus have been incidental.

2. Factors limiting Kestrel numbers.

Kestrel numbers bore a different relationship to vole density during the breeding season than at other times of year, so these two periods will be discussed separately.

(a) Outside the breeding season, ranges were mainly exclusive

and home range and territory size showed similar relationships to vole density. Range overlap was higher in winter than in autumn, possibly because ranges were larger then and therefore more difficult to defend (Schoener 1968). When vole numbers were high, territories were small and Kestrel numbers were high, whereas when vole numbers were low, territory size was larger and Kestrel numbers were low. This implied that food supply was ultimately limiting Kestrel numbers in the area, but did not prove that Kestrel numbers were limited by territoriality as territory size may have beeen determined by the number of individuals settling in the area (Lack 1954).

Cave´ (1968) suggested that Kestrels in winter may show no territorial behaviour if food supply is very good. In this study, they seemed to be territorial at the highest vole densities at which exclusive areas were reliably estimated. At this time some ranges were less than 1 km^2 and it seems unlikely that they could become much smaller in such a mobile animal. If vole numbers increase beyond this point there are several possible responses:

(i) The ranges remain the same size and a further increase in Kestrel numbers is prevented by the territorial behaviour of the birds already present.

(ii) Kestrel numbers continue to increase as birds start to share ranges and territorial behaviour ceases.

(iii) Birds start to used previously unused marginal habitats, which provide enough food only when vole numbers are high.

(iv) A combination of these responses.

Unfortunately I had no data to decide between these possibilties as high vole numbers were only experienced at the beginning of the study, when few birds were marked and range estmates were imprecise. No removals were tried in autumn, when densities were at their highest, but where birds disappeared naturally (either by death or emigration) from October to February, they were replaced by neighbouring birds that expanded into the vacated area. Although this might suggest that territory size was determined by local Kestrel numbers and that territory was not limiting Kestrel density, food supply declined over this period so the situation was not stable. Furthermore, it is unlikely that there was a surplus of transient birds, capable of occupying vacant territories, in the area at this time. It is more probable that the number of birds settling in the area after the breeding season in August and September was dependent on food supply, either directly, because only those birds settled which could catch sufficient food, or indirectly, because food supply affected the persistence of incomers and/or the aggression of residents. At this time territoriality may have prevented some birds from settling, but once the main movement of birds was over, territorial behaviour could have affected the dispersion of birds already there, rather than the density of birds as a whole. More work is needed in early autumn to see if Kestrel numbers are limited by territorial behaviour.

(b) Kestrel numbers during the breeding season were also related to vole numbers, being higher in good vole years. However, there were about twice as many Kestrels present in the breeding season than expected at similar vole densities at other times of year. This seemed to be due partly to a doubling in the number of occupants per range, and partly to an increase in the number of ranges. Food supply was better in summer (for reasons outlined above), which may explain why the area was able to support more birds than other times of year with the same vole density.

Territories in summer were smaller than expected at the same vole density outside the breeding season, but again it was hard to tell whether this was caused by the higher Kestrel numbers or vice versa. My impression was that territory size was dependent, at least in part, on how many other birds attempted to settle. Males seemed unable to exclude others from all of their range in the breeding season because there were many more birds in the area and ranges were still large. Perhaps the most important priority was to defend the nest and female until breeding was sufficiently advanced to make this unnecessary. Once this was so, birds could more easily leave their territories and hunt in areas used by several other pairs. Males may have defended as much area around the nest as possible in early spring, but have been compressed if there were large numbers of birds in the area without nests but capable of breeding. Although only two years data were available, exclusive

range size in summer was smaller in 1978, when vole density was high, than in 1977, when vole density was low. Food supply may thus have influenced (i) the number of birds attempting to settle in the area, (ii) their persistence in compressing residents and (iii) the extent to which territory holders would permit themselves to be compressed. This is discussed further in the following chapters.

CHAPTER 6.

BREEDING DENSITY AND PERFORMANCE.

INTRODUCTION.

This chapter examines the breeding biology of Kestrels at Eskdalemuir. There was considerable variation in the number of breeding pairs and their performance, both between years and in different parts of the study area. My aims were to examine such variation in relation to:

(a) Differences in food supply and weather between years.

(b) The age and experience of breeding birds.

(c) Differences in the quality of the habitat surrounding nests.

(d) The availability of nest sites.

With this information I hoped to find which factors, if any, were limiting to breeding production, whether breeding density was regulated according to the food supply and, if so, by what mechanism.

Kestrels use a variety of sites for nesting, including ledges on cliffs or buildings, holes in trees and the disused stick nests of some other bird species. Ground nesting is frequent on Orkney, where it is associated with a lack of natural mammalian predators

(Balfour 1955), and has occasionally been recorded elsewhere (Riddle 1979). In common with other falcons, Kestrels show little nest building behaviour, apart from scraping the substrate prior to laying (Newton 1979). In Britain, most clutches are started between mid April and the end of May. Within clutches, eggs are laid on alternate days and incubation usually starts with the laying of the third egg. Mean clutch size declines through the season (Cave´ 1968), early clutches usually consisting of six or seven eggs but later ones only three or four. Incubation is mainly by the female and lasts for about 28 days. During this time (and while she broods the young), the female is fed by the male, who will often cover the eggs while the female eats the food he has brought. The young are in the nest for about four weeks; the female broods them for the first 10-14 days, but thereafter does an increasing amount of hunting so that, prior to independence, the young are fed by both parents (Tinbergen 1940).

At Eskdalemuir, 90% of the natural nests used by Kestrels were old crow nests in trees, 7% were on the ledges of cliffs or old buildings and 3% were in tree holes (n=60). As is usual in raptors (Newton 1979), pairs tended to nest in the same restricted areas from year to year (e.g. the same small wood or the same part of a larger wood). Newton (1976) suggested the term 'nesting territories' for such areas because no more than one pair bred in them at one time, and their occupants defended them against other pairs. In this study, some nesting territories, defended by a

single pair in most years, were occupied by two separate pairs in other years. As such pairs nested close together (sometimes less than 20 m), it was hard to delimit clear cut territories and, in order to avoid the assumptions associated with this term, a different term, 'nesting area', was used to describe any area that was known to have supported a breeding pair during the three years of study. The boundaries of close nesting areas were not clearly defined, so pairs could be assigned to them only at the time of settling. Thus a small wood, or part of a large wood, might consist of a number of 'potential nesting areas' given by the maximum number of breeding pairs recorded there during my study. The 'primary' nesting area was occupied in every year in which at least one pair was present, additional nesting areas being used only if more than one nest was occupied at any one time, the later settling pair(s) being assigned to the additional nesting area(s), whichever nest they used. Most nesting areas were easier to define as they had only a single pair present at any one time and it was unusual to have simultaneously occupied nests within 200 m of one another.

With practice it was possible to tell which nests were in good enough condition to be used by Kestrels and therefore which nesting areas had available nests in any particular year. Thus, in this study, the NESTING AREA refers to the area around the NEST, which is the stick nest, ledge or tree hole within the nesting area that is laid in or, in the case of non-breeding pairs, receives the most

attention. The NEST SITE is the tree or cliff which contains the nest, whereas the NEST POSITION refers to the location of the nest within the tree or on the cliff (i.e. whether it is high or low, exposed or sheltered etc.).

Previous studies of Kestrel breeding biology.

Of the published work on the breeding of the Kestrel, two papers are particularly important. Tinbergen (1940) described in detail the behaviour during the breeding season. He also measured feeding rates and found that they increased gradually through the breeding cycle, reaching a peak when the young were about three weeks old. From feeding rates he calculated the food requirements of the average Kestrel family over the breeding season. The second important paper is that of Cave´ (1968), who investigated the breeding density and performance of Kestrels in Holland. As this last work is especially relevant to my own, I shall describe the main findings in some detail.

All the birds were breeding in nestboxes, erected on a grid system in three separate areas of recently reclaimed polder. Food was considered the major factor affecting breeding and its direct effect on ovarian development was demonstrated by histological examination of the ovaries of captive birds given different amounts of food. The oocytes of well fed birds developed much faster than

those of poorly fed ones, suggesting that nutrition over winter and spring was a major factor affecting laying dates. The main food of wild birds was the Common Vole (<u>Microtus</u> <u>arvalis</u>) and its density was assessed by trapping on the dyke surrounding the polder. The Kestrel breeding population wintered in the vicinity, so both winter and spring food conditions were related to various breeding parameters. Precipitation hindered hunting, thereby lowering food availability, whereas temperature was thought to influence the amount of food needed (and hence body-condition) in early spring.

The relationship of these three factors (vole density, precipitation and temperature) to various breeding parameters was investigated using multiple regression, assuming simple linear models. Low food density, heavy rainfall or cold were all detrimental to breeding, whereas high food density and warm dry weather were beneficial. The results are included in Table 6.2 and discussed in more detail later. The environmental factors were most strongly correlated with breeding at the start of the season. Their influence gradually weakened thereafter, possibly because of (a) an increase in the hunting time available due to longer daylength; (b) an increase in voles and other alternative prey; and (c) failure of the poorer pairs so that, by mid season, only those pairs that could obtain sufficient food under the prevailing conditions remained.

ANNUAL VARIATION IN BREEDING NUMBERS AND PERFORMANCE.

Methods.

In February and March 1976 I made a thorough search of all the woods, trees or crags likely to be used by Kestrels for nesting, in an area of approximately 100 km^2. Some woods contained no old crow nests, while in others all the nests were in poor condition. Crows were heavily controlled in the region and this may have artificially reduced the number of their nests available to Kestrels. To rectify this, and ensure a sample of breeding birds big enough for study, I erected artificial stick nests in trees in some parts of the area (mainly the White Esk valley). Each consisted of a wire basket filled with twigs and lined with grass, moss and finally soil. Such nests had already been tried successfully in other areas (M. Marquiss pers. comm.) and they again proved successful (both for Kestrels and Long-eared Owls, Asio otus), so were used throughout the study to ensure that some nesting areas always had at least one useable nest in them. Some parts of the area had no nest sites but these were left devoid of nests until 1978 (see later).

During the breeding season all woods were visited until either Kestrels were found, or I was satisfied that none was present. I considered a nesting area was occupied if a pair of birds was seen there regularly, even if they failed to lay. Some nests were hidden

in the tops of trees and could be found only by watching birds displaying or bringing food to the nest tree. Nests were visited as often as necessary to ascertain laying date, clutch and brood size, to catch and mark the adults and to ring the young. Laying date of clutches found complete could usually be calculated from hatching date or, less accurately, from the age of young. A few eggs from fully incubated clutches disappeared during incubation; because most of those that failed to hatch remained intact, eggs missing after hatch were assumed to have hatched and the chick to have died. Young were ringed when they were about three weeks old and I assumed that all of them subsequently fledged. Although this may have over-estimated brood survival, I made no visits after this because the young were prone to fly from the nest prematurely. The majority of nests were checked after the young had fledged, but I found evidence at only four of them that one or more young had died after ringing.

Breeding numbers were based on the number of pairs formed, which included those that failed to lay (i.e. 'non-breeding' pairs). A few such pairs remained at nesting areas which apparently encompassed no useable nest (see Table 6.14), but even so, changes in nest availability between years may have affected the number of pairs settling in the area, and hence breeding numbers. To rule out the effects of nest availability on the number of pairs formed, only nesting areas which had a useable nest in all 3 years were included in this analysis.

Results.

A total of 94 pairs were recorded at 40 different nesting areas over the three years. Of these, 86 (92%) laid at least one egg, 63 (67%) hatched at least one young and 59 (63%) fledged at least one young. Performance varied between years, but was generally similar to that reported by Cave´ (1968) (Table 6.1). For comparability with his work, I have expressed results both in terms of failure (the cessation of breeding by the adults before young were fledged) and mortality (which includes the losses due to complete nest failure as well as losses of individuals from otherwise successful nests). Most failures involved clutch desertion and this was the major cause of mortality. The overall mortality in my study was slightly higher than in Cave´'s, due mainly to the poor performance in 1976. The differences between the years can be summarised as follows:

(a) Mean laying date was significantly later in 1977 than the other years, by about 2 weeks (1976: t= 6.03, P<0.001; 1978: t= 5.63, P<0.001).

(b) Clutches were significantly smaller in 1977 than in 1976 (t= 6.83, P<0.01) or 1978 (t= 17.67, P<0.001).

(c) Production (i.e. young produced per occupied nesting area) was low in 1976, due to high failure at all stages, but especially during incubation, when 48% of clutches were deserted (vs. 19% for 1977 and 21% for 1978).

Table 6.1 Breeding performance of Kestrels at Eskdalemuir, 1976-1978, compared with that in Holland, 1960-1964, from Cavé (1968).

| | Eskdalemuir | | | | Holland |
	1976	1977	1978	All Years	1960-64
Number of occupied nesting areas	28	28	38	94	
Number of breeding pairs	21	27	38	86	
Number (%) of nests where:					
(a) young hatched	11 (52%)	22 (82%)	30 (79%)	63 (73%)	
(b) young fledged	8 (38%)	21 (78%)	30 (79%)	59 (69%)	
% of clutches deserted	48%	19%	21%	27%	20%
Mean laying date	28 April ± 3.2d	13 May ±3.9d	29 April ±3.2d	3 May ±2.5d	10 May
Mean clutch size	5.1±0.4	4.7±0.3	5.3±0.2	5.0±0.3	
Number of repeat clutches	2	3	2	7	
Mean brood size at hatch	3.6±1.1	4.2±0.4	4.9±0.3	4.5±0.2	4.9
Mean number of young fledged:					
(a) per successful nest	2.6±0.8	3.6±0.6	4.5±0.5	4.0±0.4	4.1
(b) per clutch started	1.0±0.6	2.8±0.8	3.7±0.7	2.7±0.5	
(c) per occupied nesting area	0.8±0.5	2.7±0.8	3.5±0.7	2.5±0.5	

Table 6.1 (con.)

Total eggs laid	104	126	185	415	
% of fully incubated clutches that:					
(a) failed to hatch	6%	5%	4%	5%	7%
(b) were lost in incubation	2%	3%	2%	2%	
Total (%) eggs that failed to hatch	54 (52%)	35 (28%)	38 (21%)	127 (31%)	
% of nestlings that died	58%	17%	9%	20%	17%
% of dead nestlings that died in the first week	38%	93%	31%	51%	43%
Total (%) mortality (eggs + young)	83 (80%)	50 (40%)	51 (28%)	184 (44%)	

All limits to means are ± 2S.E.

BREEDING, FOOD SUPPLY AND WEATHER.

Methods.

Three factors were considered important to breeding:
vole density, rainfall and temperature. The vole densities
used were means for each period, found by averaging the monthly
estimates given in Figure 2.1. The rate of increase of voles
over the breeding season was calculated from spring and autumn
density estimates, assuming a linear increase between the
trapping periods. Meteorological data were from Eskdalemuir
Observatory, near the centre of the study area. For each regression
I used the mean daily rainfall, or the mean monthly temperature,
during the period in question. The length of periods varied from
2-5 months.

There were no detailed meteorological data for individual
parts of the area, so results for each year had to be treated
together. This gave only three sets of data, which were insufficient
to enable the use of multiple regression to test the effects of each
factor on breeding. Instead, I had to use simple linear regressions,
which did not rule out the possibility of intercorrelations between
variables and therefore limited the conclusions which could be drawn
from the available data.

Results.

The daily rainfall and mean monthly temperatures through the breeding seasons are given in Fig. 6.1a-b. The significance and direction of each relationship tested are shown in Table 6.2, along with similar results from Cave's study.

(a)   Breeding numbers. There was no significant relationship between breeding numbers and winter vole numbers. Although Cave also found this in his study, the low samples in my case were insufficient to rule out such a relationship. Rainfall also showed no relationship to breeding numbers, though there was a possible, but not significant, trend for breeding numbers to be lower following low temperatures in March and April.

(b)   Laying date. There were no significant relationships of laying date to either rainfall, temperature or vole density. There was a trend for laying dates to be later when vole densities were low, which agreed with Cave's result, but this trend was not significant ($P < 0.1 > 0.05$).

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Figure 6.1a Daily rainfall during the breeding season, 1976-1978.
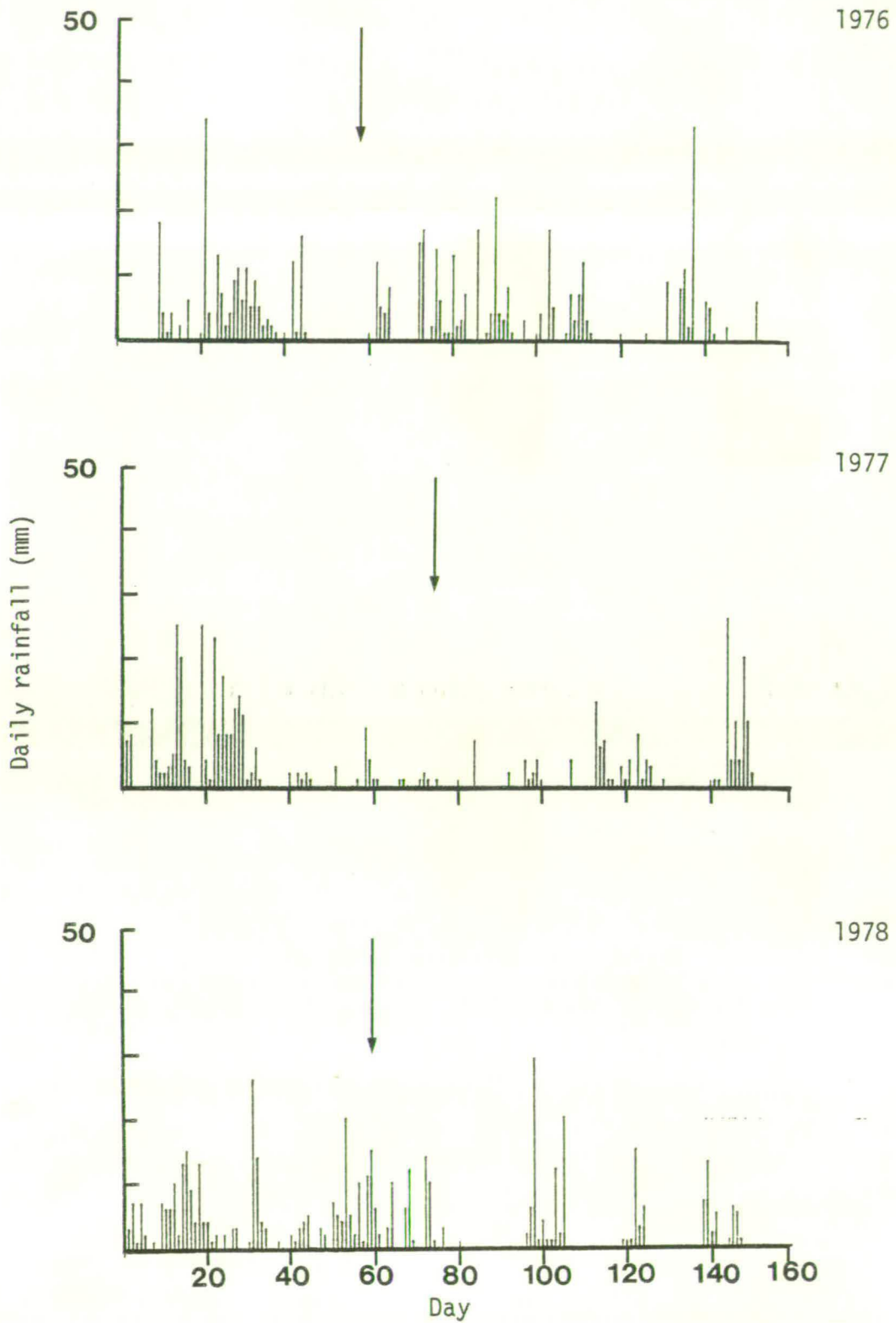
Days numbered from 1 March. Arrows mark the mean laying date for each year.

Figure 6.1b Mean monthly temperature, October 1975 to July 1978.
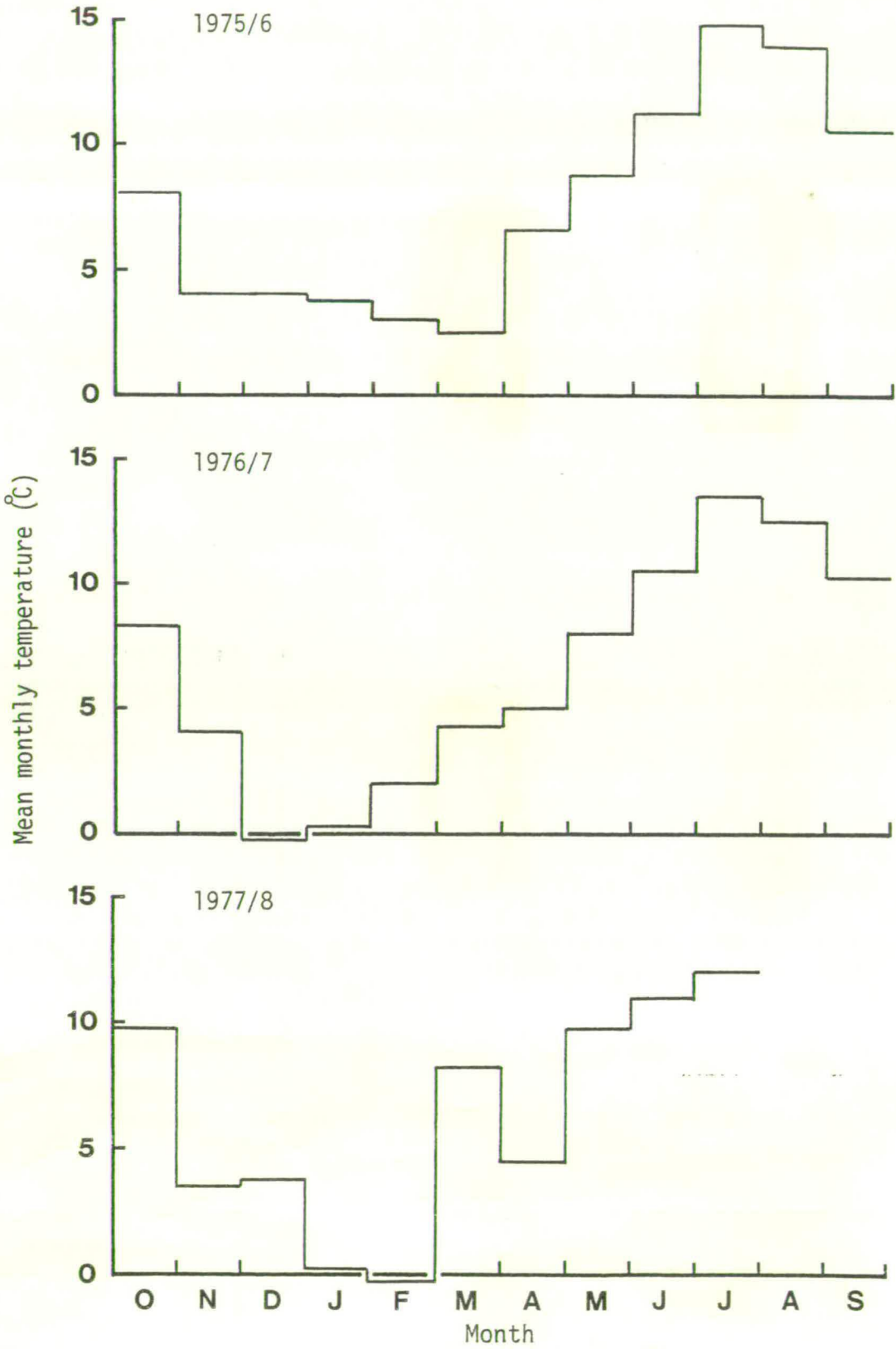
Table 6.2 Relationship of breeding to food supply and weather.

(a) Breeding numbers and laying date.

	Period	Breeding Numbers		Laying Date	
		Eskdalemuir	Holland	Eskdalemuir	Holland
Voles	Dec.-April	+ NS	+ NS	- NS	- 5%
	March+April	+ NS		- NS*	
Rainfall	Dec.-April	+ NS	- 5%	+ NS	+ 5%
	March+April	+ NS		+ NS	
	April+May	- NS		+ NS	
Temperature	March+April	+ NS*	+ 5%	- NS	- 5%

(b) Clutch desertion and brood survival.

	Period	% Clutches Deserted		% Brood Survival	
		Eskdalemuir	Holland	Eskdalemuir	Holland
Voles	April-June	+ NS	- 5%		
	June+July			+0.55	+ NS
Voles(rate of increase)	April-Oct.	- NS		+0.70	
Rainfall	April-June	- NS	+ NS		
	May-July			-0.93	- NS

Results show the direction and significance of relationships tested either by simple linear regression (data from Eskdalemuir) or by multiple regression (data from Holland, after Cave 1968).
+= positive relationship, -= negative relationship, NS= not significant
* relationship not significant but P < 0.1 > 0.05.

(c)   Clutch desertion. There was no evidence of a significant relationship between clutch desertion and either vole numbers, the rate of vole increase or rainfall, though a high proportion of clutches was deserted in the wet May of 1976.

(d)   Brood survival. A similar situation held in the nestling period, with nestling survival showing no significant relationship with vole numbers or rainfall.

Discussion.

Unfortunately, my results were based on too few years to be able to draw any firm conclusions on the factors affecting breeding numbers and performance. My data agree with some of the findings of Cave as there were trends suggesting (a) that high rainfall or low temperatures were associated with low breeding numbers and (b) that laying dates were later when voles were scarce. However, these trends were not significant and more data are needed to confirm them.

Some differences between my results and Cave's may have been expected because of the differing circumstances of the two studies:

(a)   In Eskdalemuir, most breeding birds wintered outside the study area (see chapter 4). Winter food supply in the breeding area may thus have been less important to subsequent breeding than in Holland, where most birds wintered near to where they bred. Once birds arrived at Eskdalemuir in spring, however, the time taken to reach breeding condition (and thus laying date) could have been

affected by local conditions; hence the possible correlation
of spring vole density with mean laying date in my data. Over
the range encountered during the study, vole density did not
seem to affect the number of pairs settling in the area. Most
of the birds arriving in March were adults returning to the
area and they may have formed pairs regardless of the vole
densities or weather. Variation in breeding numbers between
years seemed to depend mainly on whether additional pairs settled
later in the season (see below). Late arriving birds (mainly
yearlings) may have been unable to settle in wet years because
rain hindered their hunting and so reduced their food supply.
This might have been less critical to the adults that arrived
early in the season for two reasons. Firstly, the reduced
competition in finding and maintaining a nesting area as fewer
birds were present at that time, and secondly because, being
adults, they were better able to cope with any difficulty in
obtaining food. Adults may also have shown greater fidelity to
the area if they had previously bred there, and so have been less
inclined to move on in wet weather than were yearlings.

(b)   The main effect of rain was to prevent birds from
hunting, thereby lowering their food intake (see chapter 3). This
was assumed to increase the likelihood of nesting failure by reducing
the amount of food brought to the nest by the males, so causing
their partners to desert their clutches in search of food. Rain may

also have reduced the activity of voles or other prey and so made hunting less successful even if it was possible. Cave found that rainfall was less important after egg-lay, but this may not have been so at Eskdalemuir because of (i) the much heavier rainfall in Eskdalemuir than in Holland and (ii) the difference in nest-sites between the two studies, the nest boxes used in Holland giving better protection than the mainly open sitck-nests used in Eskdalemuir. Soaking by prolonged rain probably caused poqrly fed females in exposed nests to desert, as well as killing any non-brooded young.

VARIATION IN BREEDING PERFORMANCE WITHIN YEARS.

Production at any particular nest was likely to depend partly on the quality of the nesting area and partly on the quality of its occupants. Separation of these two factors was difficult because 'better' quality birds may have occupied only the 'better' quality nesting areas. In this section I shall examine differences between birds and between nesting areas separately, though the two aspects were probably not independent.

Variations Between Birds.

Ultimately, the differences in performance between birds probably related to the ease with which they obtained food. This would have affected the time pairs took to reach breeding condition, as well as their ability to rear young. For any given nesting area (with a particular food supply), birds may have differed widely in their ability to obtain food; two possible causes of the variation will be examined here, the age of the bird and its previous association with the area.

1. Age of the bird.

Once in adult plumage, the age of Kestrels is hard to determine, so the only comparison for which sufficient data were obtained was between yearling and older birds. Yearlings were

breeding for the first time, whereas most older birds would have bred before. In 1976 and 1977, hardly any yearlings were recorded breeding, so only results from 1978 were used for comparison (Fig. 6.2a-b). Because of the strong tendency for assortative mating (see chapter 2) there were few mixed pairs and only one of these was an adult female with a yearling male (this was excluded from the analysis). Adult pairs laid earlier (t= 3.25, P<0.01) and fledged more young per attempt (X2= 4.21, P<0.05>0.01) than yearling pairs; mixed pairs fell between these two. This is in line with other studies which suggest that young birds are less effective breeders than older ones in several bird species (Lack 1966), including some raptors (Cave 1968, Newton 1979).

2. Experience of the breeding area.

Methods.

Knowledge of an area may have enhanced the hunting efficiency of birds by enabling them to learn the best places to obtain food in any given conditions. Thus birds that remained on the same home range all year, or returned to breed in successive springs, may have performed better than newcomers.

In any spring there were three categories in the birds which were present:

(a) birds which were not known to have bred in the study area before;

Figure 6.2 Comparison of the breeding performance of adults and
           yearlings.

(a) Mean laying date.

           Bars are ± 2S.E. of the mean.
           Date is the day number from 1 January.

(b) Number of young fledged per pair.

           Shaded   = observed number fledged per pair.
           Unshaded = expected number fledged per pair (assuming
                        there was an equal chance of rearing young
                        between pairs).

           Calculation of expected values:

	AA	AY	YY	TOTAL
Number of nests	14	7	8	29
Number of young	67	25	24	116
Mean number of young per nest	4.8	3.6	3.0	4.0
Expected number of young	56	28	32	
$(Obs-Ex)^2/Ex$	2.16	0.32	2.0	

           Chi-squared = 4.48 df = 2 NS

Comparison of AA vs. YY only on a similar basis gives:

           Chi-squared = 4.21 df=1 P < 0.05

           Data refer to 1978 only. AA = adult pair, YA = yearling male
           with adult female, AY = adult male with yearling female, YY =
           yearling pair.

(a)
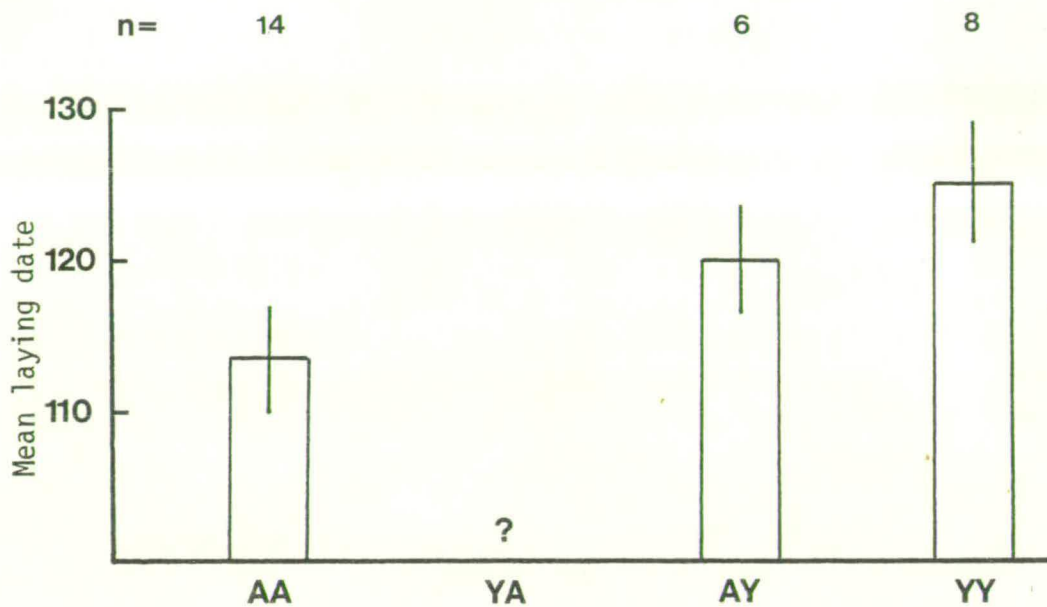
(b)
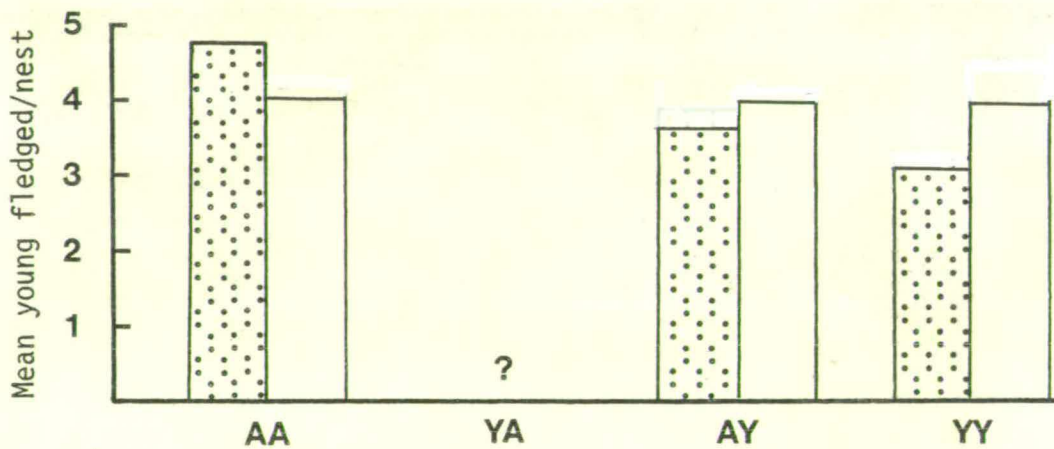
(b) birds which bred in the study area the previous year but at a different nesting area;

(c) birds which bred at the same nesting area the previous year.

The first group could have included birds which had never bred before (e.g. yearlings), birds which had bred in the study area but not been caught, and those that had previously bred elsewhere. Groups (b) and (c) contained both permanent residents and birds that left the study area for the previous winter, but returned to breed. An individual was assumed to have overwintered if it was seen on several occasions from October to February. The few unmarked birds were usually in isolated areas with single roosts. A bird subsequently caught at such a nesting area was considered to have been resident if the roost there had been in continuous occupation throughout the winter. This seemed a reasonable assumption as nearly all the tagged birds which overwintered subsequently bred within their winter range, usually near the winter roost.

I assumed that when a large proportion of the breeding population was caught in one year, any unmarked birds the following year had either not bred the previous breeding season or done so elsewhere. Futhermore, analysis had to be confined to adult birds because yearlings were less successful anyway.

Results.

Sufficient breeding birds were caught in 1977 to allow some comparisons the following year.

(a) Return to the area and subsequent breeding performance. Unfortunately, only 2 of 16 all-adult pairs in 1978 were of unmarked birds (i.e. assumed strangers), so it was impossible to decide if returning to the area was linked with greater breeding success.

(b) Change of nesting area and subsequent breeding performance. If the performance of an individual was affected by its previous knowledge of the terrain, birds breeding at the same nesting area as the year before might have been more successful than those breeding at a different one. Of 24 birds breeding in the area in 1978 for the second successive year, 13 were breeding in the same place and 11 were not. There was no difference in laying dates or production between these two groups, but samples were small (Table 6.3). Females that changed nesting areas laid later than those that did not, but the difference was not statistically significant.

Similar proportions of males (5 out of 13) and females (6 out of 11) changed nesting areas between years. The mean distance moved was less than 2 km and similar in both sexes (males= 1.85 km, range= 0.55-3.75 km; females= 1.93 km, range= 0.55-4.25 km). This only applied to birds that returned to the study area and some may

have bred outside it and so have been missed. There was no evidence that birds increased their chance of pairing with the same partner in the second year by remaining in the the same nesting area (Table 6.4a). However, for birds that changed nesting areas, females were more likely than males to end up with a partner that had not changed nesting area from the previous year (Table 6.4b).

(c) Breeding performance and subsequent return to the study area. Studies on Sparrowhawks have shown that successful birds were more likely to return to the same territory the following year than those that failed (Newton and Marquiss 1976). In this study, 27 out of 49 successful birds (i.e. those that fledged young) were present the following year, whereas only 4 out of 19 birds that failed were recorded again in the area, a highly significant difference (X2= 10.46, P<0.01). Of the 31 birds recorded breeding in the study area for the second successive time, only 5 had failed the previous year; which meant there was insufficient data to test whether successful birds were more likely than failed ones to use the same, rather than a different nesting area within the study area. There was a difference in the sexes in that more males (4 out of 10) returned after failure than females (0 out of 9), (P= 0.054, Fisher exact test). Successful birds showed no such sex difference.

(d) Overwintering and breeding performance. To find whether winter residents differed in breeding performance from other birds, analysis had to be restricted to males because insufficient females overwintered. Conditions varied from year to year, so each was

Table 6.4 Changes of nesting area and of partners in Kestrels
breeding in successive years within the study area.

(a) Change of partner in relation to change of nesting area.

(i) Males

	Male at:	
	Same NA	Different NA
With same partner	2	1
With a different partner	6	4

P= 0.7 (Fisher Exact Test)

(ii) Females

	Female at:	
	Same NA	Different NA
With same partner	2	1
With a different partner	3	0

P= 0.5 (Fisher Exact Test)

(b) Status of new partner.

For birds that changed NA and partner.

	Partner on:	
	Same NA	Different NA
Males	0	4
Females	5	0

P= 0.008 (Fisher Exact Test)

Using all birds recorded breeding in the study area in two
successive years.

NA= nesting area.

treated separately, which meant data from winter 1975-76 were too few to analyse.

The proportion of birds that used the same nesting area between breeding attempts was higher in overwintering birds (11 out of 13) than in others (7 out of 17) (P= 0.019, Fisher exact test). Males resident over the previous winter were more successful (in terms of earlier laying date and number of young fledged) than incomers in 1977 (Table 6.5). Similar differences were apparent in 1978 but, they were not statistically significant (though samples were small). Similarly, males overwintering in 1976-77 had previously reared significantly more young than those that subsequently disappeared (t= 2.49, P<0.05>0.01), though the difference in laying date was not statisically significant (t= 1.60, P<0.1). These trends were not apparent in the limited data for birds overwintering 1977-78, possibly because 1978 was the best year for breeding.

Discussion.

The above results, although based on small samples, suggest that fidelity to the area may have been the result of success, rather than its cause. Thus, while there was no evidence that birds breeding in the area for the second time fared any better than those that were not, successful birds were more likely than failed ones to return the following year. Individuals which did not return

Table 6.5 Breeding performance of male Kestrels in relation to wintering within the study area.

Breeding year	Wintering period	In study area?	n	Laying Date mean	Laying Date 't' value	Laying Date s.l.	Young Fledged mean	Young Fledged 't' value	Young Fledged s.l.
1977	1976/77	Yes	7	127.3	2.33	5%	4.0	2.38	5%
		No	17	135.6			2.3		
1978	1977/78	Yes	5	113.4	0.89	NS	4.8	0.67	NS
		No	14	116.9			4.4		
1976	1976/77	Yes	7	114.1	1.60	NS	2.1	2.49	5%
		No	11	118.6			0.5		
1977	1977/78	Yes	4	137.2	0.28	NS	2.0	0.06	NS
		No	22	133.5			2.9		

Laying dates expressed as day number from 1 January. Data refer to males only.

NA= Nesting Area, s.l.= significance level of difference (NS= Not Significant).

may have bred elsewhere, though it is possible that they suffered greater mortality than successful birds. Breeding failure may be linked with an inability to obtain sufficient food and this may have made such birds more vulnerable to any food shortage the following winter. On the other hand, successful breeders may have suffered greater strain in completing the breeding cycle than those which failed before trying to feed young.

The results obtained would also be expected if variations in performance were due to differences in quality between areas. If such differences were consistent between years, successful birds may have increased their chance of success the following year by returning to the same area, whereas failed birds might do better by going elsewhere. I could not tell if this was true between specific nesting areas, but return to the general area, rather than a particular nest, seemed more likely (a result also found by Cave' 1968). Within the study area, most birds returned to within a few kilometres of their previous nest, and there may have been no particular advantage in choosing the same nest in view of the overlap of home ranges in summer (chapter 5). The exact nesting area chosen probably depended on where there were other unpaired birds of the opposite sex at the time of settling. The difference between the sexes in the status of the partner chosen may have arisen if returning males arrived earlier and tended to go to their previous nesting area, whereas returning females, arriving slightly later, chose a mate rather than a specific nesting area. They would

thus be less likely than males to pair at the same nesting area, but more likely to find a partner that was on the same area as the previous year.

The birds with the best knowledge of a particular nesting area were probably those that remained on it through the winter. These birds did not always breed better than non-residents, but the results varied between years. Males resident in a winter when vole numbers were low (1976-77) bred better, relative to non-residents, the following year. This was not so of males which overwintered during better food conditions (1977-78), possibly because:

(a) Overwintering may have been advantageous to males irrespective of the winter food supply, but this could only be detected in summers when food was scarce. Birds that arrived in a spring when vole numbers were high were not at a disadvantage to residents, but this was not so when food conditions were poor. Thus overwintering may not guarantee a good food supply, but it might enhance success the following summer because birds which overwinter were more likely to occupy the same, familiar nesting area.

(b) An alternative explanation, which does not assume any advantage of overwintering, is that only 'better' birds (i.e. birds which have a higher breeding performance) were present in poor food winters and that these were more likely to show better performance in the following year anyway. In years when food was plentiful more birds were able to stay in the area in winter, including some 'inferior' birds which could not have survived a poor winter. The

high proportion of adult males present in the poor food winter of 1976-77 is consistent with this idea (see chapter 2).

With the data available, I could not decide between these two explanations. Possibly both were true to some extent, in poor winters only better birds were present and any advantage of wintering on the breeding ground was more evident the following breeding season.

In conclusion, there was no firm evidence that experience of a nesting area enhanced breeding performance. Resident birds had better performance than non-residents in some years, but this could have been due to their age and quality rather than any knowledge of the area. Residents may also have occupied better quality nesting areas. To examine this further, I looked at variation in the nesting areas themselves.

Variations Between Nesting Areas.

Young were fledged at a few nesting areas in all three years, whereas at some others young were produced only once, or not at all. Was this because some nesting areas were more likely to be occupied, and offered a better chance of successful breeding, than others, or because birds of a particular quality tended to occupy only certain nesting areas?

Turnover at nesting areas.

Turnover of birds at nesting areas (i.e. changes caused by birds moving or dying) was fairly high: of 27 nesting areas where the identity of the male was known in successive years, it was a different individual in 15 cases (56%), the figures for females being 21 out of 26 (81%). The difference between the sexes was significant at the 5% level ($X2= 3.87$, $P<0.05>0.01$). These results may have underestimated turnover because most birds which remained in the area for some time were eventually tagged and their presence thereafter could be checked easily without trapping. Untagged birds may have been newcomers but had to be caught to confirm this (in case of tag loss), and so birds breeding only once were less likely to be recorded than long term residents. The high overall turnover at nesting areas (at least 68%) suggested that any consistency in performance at them was not entirely due to having the same individuals present there each year. However, this did not show whether consitencies in performance were due to (a) the quality of the nesting area, or (b) the possibility that particular nesting areas were occupied by different individuals of a similar quality from year to year.

Nesting area occupancy.

Kestrels bred at a total of 60 nesting areas over the three

year period. Discounting experimental sites erected only in 1978, and others where useable nests were not present in all years, a total of 40 nesting areas remained which could have been used by Kestrels in all three years. Of these, some were occupied in one year, some in two years and others in all three years. To find out whether these nesting areas were occupied at random, or whether some were used more or less frequently than expected by chance, I calculated the frequencies of occupation expected if all nesting areas had an equal chance of being occupied (Table 6.6), following the method used by Newton and Marquiss (1976) for Sparrowhawks. The difference between the observed values was significant only at the 1% level, but the trend suggested that more nesting areas were occupied in only one year and fewer in two, than might be expected by chance. Without more data, it was impossible to say whether birds showed any real preference or avoidance of nesting areas.

To examine occupancy in more detail, I further divided nesting areas on the basis of winter occupation because birds which overwintered in the area tended to breed at roughly the same nesting areas from year to year. Strictly, it was not possible to say which nesting areas were occupied outside the breeding season because winter ranges overlapped several nesting areas and individuals did not necessarily centre all their activity around one in particular. In practice, overwintering birds nearly always bred within their previous winter home range and the nesting area they used was assumed to have been the one occupied the previous

*Calculation of expected values for Table 6.6, using the method of Newton and Marquiss (1976).

Year	Number of NA occupied	Number of NA unoccupied	Total
1976	29	11	40
1977	28	12	40
1978	33	7	40

(a) Probability of any nesting area being occupied in all 3 years (P_3):

$$\frac{29}{40} \times \frac{28}{40} \times \frac{33}{40} = 0.42$$

Expected number occupied in all 3 years $= 0.42 \times 40$
$$= 16.8$$

(b) Probability of being occupied in 2 years (P_2)- enumerate all possible cases i.e.in years 1+2, 2+3 and 1+3:

$$(\frac{29}{40} \times \frac{28}{40} \times \frac{7}{40}) + (\frac{11}{40} \times \frac{28}{40} \times \frac{33}{40}) + (\frac{29}{40} \times \frac{12}{40} \times \frac{33}{40}) = 0.43$$

Expected number occupied in 2 years $= 0.43 \times 40$
$$= 17.2$$

(c) Probability of being occupied in 1 year (P_1):

$$(\frac{29}{40} \times \frac{12}{40} \times \frac{7}{40}) + (\frac{11}{40} \times \frac{28}{40} \times \frac{7}{40}) + (\frac{11}{40} \times \frac{12}{40} \times \frac{33}{40}) = 0.14$$

Expected number occupied in 1 year $= 0.14 \times 40$
$$= 5.6$$

(d) Probability of being unoccupied P_0: $1 - (P_3 + P_2 + P_1) = 0.01$

Expected number unoccupied $= 0.01 \times 40$

$= 0.4$ - as this cannot be

observed, eliminate the zero case by multiplying all other expected values by 40 / (40-0.4).

Years occupied	Ex_1	Ex_2
3	16.8	17.0
2	17.2	17.4
1	5.6	5.7
0	0.4	
	40.0	40.1

Table 6.6 Comparison of observed and expected frequencies of
nesting area occupancy.

Number of years occupied	1	2	3
Observed frequency of occurrence	10	8	22
Expected frequency	5.7	17.4	17.0
$(Obs-Ex)^2/Ex$	3.24	5.08	1.47

Chi-squared = 9.79   df=2   P< 0.01

For calculation of expected frequencies, see facing page.

Table 6.7 Summer and winter occupancy of nesting areas.

Number of summers occupied	1	2	3
Number of NA x winters	30	24	63
Number of winter occupancies:			
(a) Observed	0	1	20
(b) Expected	5	4	11
$(Obs-Ex)^2/Ex$	5.0	2.3	7.4

Chi-squared= 14.65   df=2   P<0.01>0.001

(Expected values calculated assuming all nesting areas
were equally likely to be occupied in winter.)

NA= Nesting Area.

winter.

Nesting areas were scored according to the number of winters occupied out of the number for which the information was available and grouped by summer occupancy (Table 6.7). Those used in all three summers were more likely to be occupied in winter than the others (X2= 14.65, P<0.01). Nesting areas were then classified according to how they were occupied during the whole study period:

Type 1: occupied for one summer only.

Type 2: occupied for two summers only.

Type 3s: occupied for three summers and no more than one winter.

Type 3w: occupied for three summers and more than one winter.

Thus type 3w nesting areas were occupied more or less continuously during the three years, though not necessarily by the same bird.

Nesting area occupancy and breeding performance.

An obvious question to ask was whether the most used nesting areas offered a better chance of breeding successfully. Two parameters were used to evaluate performance: (a) success (i.e. whether or not young were fledged) and (b) the number of young fledged from all nests in each group. Table 6.8a-b shows the observed frequencies in each nesting area type and the frequencies expected if all had the same chance of success. In both cases the trend was for better performance at the more heavily occupied

Table 6.8 Occupancy and breeding performance at nesting areas.

(a) Success. (Attempt scored 1 if at least one young fledged.)

Occupancy type	1	2	3s	3w
Total attempts	10	16	42	21
Observed successes	5	5	26	20
Expected successes	6	10	26	13
$(Obs-Ex)^2/Ex$	0.2	2.5	0.0	3.8

Chi-squared= 6.4 df=3 P<0.1>0.05 NS

(b) Young fledged per nest.

Occupancy type	1	2	3s	3w
Total attempts	10	16	42	21
Total young fledged	22	19	103	73
(Mean young per attempt	2.2	1.2	2.5	3.5)
Expected young fledged	24	39	102	51
$(Obs-Ex)^2/Ex$	0.2	10.3	0.0	9.5

Chi-squared= 19.9 df=3 P<0.001

(c) Frequency with which nesting area types were used in summer.

Occupancy type	1	2	3s	3w
Number occupied in:				
(a) 1976	3	7	15	7
(b) 1977	0	6	15	7
(c) 1978	7	4	15	7

(Expected values calculated assuming all types had an equal chance of fledging young.)

Calculation of expected values:

$$\text{Expected score of } type_n = \frac{\text{Mean score of all types}}{} \times \text{number of attempts at } type_n$$

nesting areas, though the differences were statistically significant only for the number of young fledged per attempt (X2= 19.9, P<0.001). Type 1 nesting areas did better than the trend suggested, probably because most were used only in 1978, when production was high in general, whereas types 3s and 3w, by definition, were also occupied in poorer years (Table 6.8c). This had the effect of raising the type 1 scores relative to the rest and the performance in these nesting areas would have been lower if this was allowed for. Thus two main points arise from this analysis:

(a) Birds at the most frequently used nesting areas also had the best breeding performance.

(b) Nesting areas of low occupancy (i.e. type 1) were mainly used in a year of high average breeding performance.

Nesting area occupancy and the age of birds.

The above trends may have been due to differences in the quality of birds using the various nesting area types. Adult birds did better than yearlings (see above), so it is possible that types 3s and 3w were more likely to be occupied by older birds than were the less used nesting areas. This was tested by comparing adult to yearling ratios between the nesting area types (Table 6.9). These ratios varied between years, so only 1978 data were used and groups had to be combined because numbers were small. More adults used

Table 6.9 Age ratio of Kestrels breeding at nesting areas

in relation to nesting area occupancy.

For explanation, see text page226. Data refer to 1978 only.

Occupancy type	1	2	3s	3w
(a) Males:				
Number of adults	3	1	11	7
Number of yearlings	4	2	3	0
(b) Females:				
Number of adults	2	1	6	7
Number of Yearlings	3	2	7	0

For both sexes:

Nesting area type:	Adults	Number of: Yearlings
1 + 2	7	11
3s + 3w	31	10

Chi-squared= 6.91 df=1 P<0.01>0.001

higher occupancy nesting areas, and more yearlings used low occupancy nesting areas, than expected by chance (X2= 6.91, P<0.01). This trend was apparent in both sexes, but statistically significant only for males (P= 0.015, Fisher exact test). Thus, to to some extent, variation in the performance at different nesting areas could be explained by the age of birds occupying them; younger, less experienced birds tending to use the nesting areas of lower occupancy. This result meant that the differences noted in the success of yearlings and adults may have been partly due to the nesting areas they occupied. In order to exclude the effects of age, success for adults only should be compared in the different nesting area types; unfortunately I had insufficient data to do this because too few adults used low occupancy nesting areas in any one year. What little there were suggested no significant difference between types. I therefore had no firm evidence that nesting areas differed in the chance they offered for successful breeding. This contrasts with the conclusions of Newton and Marquiss (1976), who did similar analysis on Sparrowhawks.

Differences between nesting areas.

Although the variations in performance at the different nesting area types may have been due to age differences between the occupants, there was still a possibility that the variation in age ratios between the groups was due to differences in site quality. To examine this, I looked more directly at differences between the

nesting areas themselves.

1. The distribution of nesting areas.

Although some nests were found only by watching their occupants, all the woods in Eskdalemuir were small so it is likely that I found most of the nests which could have been used by Kestrels each year. To examine the distribution of these nests relative to one another, and to compare this with the distribution of those nests that were actually laid in by Kestrels, the nearest neighbour distances of all available and of all occupied nests were plotted as frequency histograms for each year (Fig. 6.3). This revealed a number of points:

(a) In each year there were more useable nests than those actually occupied. In the first two years, only about 30% of all nests were used by Kestrels, but this increased to 60% in 1978.

(b) In all years, nests occupied by Kestrels were further apart, on average, than were all available nests. The difference was most striking at distances of less than 200 m: although only a few occupied nests were found this close, about 50% of all nests available in any one year were within this distance of their nearest neighbour. Most of the nests in this class were in woods where the activity of crows over several years had produced a number of nests in a small area. Although all of them seemed suitable for Kestrel breeding, it was rare to find more than one

Figure 6.3 Frequency distributions of nearest neighbour distances of
all nests and those nests occupied by Kestrels.

(a) 1976

(b) 1977

(c) 1978

Classes of nearest neighbour distance are labelled by their upper
limit. Solid line = all useable nesting places (such as disused crow
nests, ledges and tree-holes), broken line = all nests occupied by
Kestrels.

(a)

1976

(b)

1977

(c)

1978

Nearest neighbour distance (km)
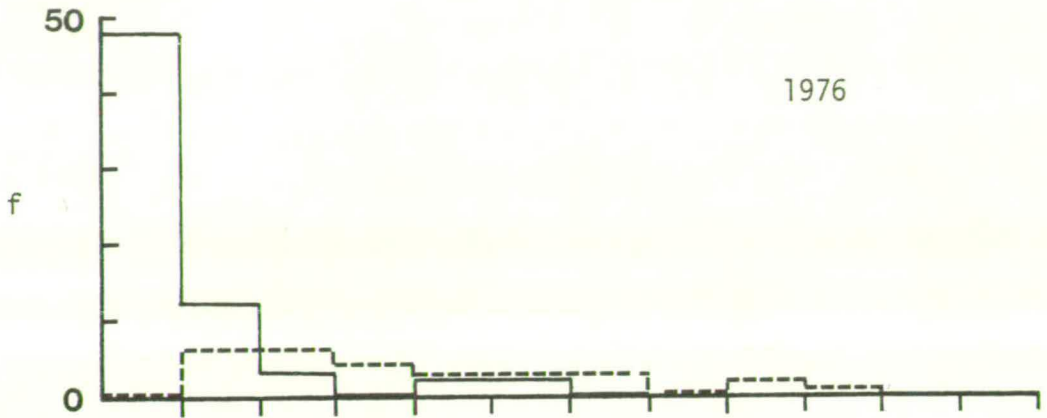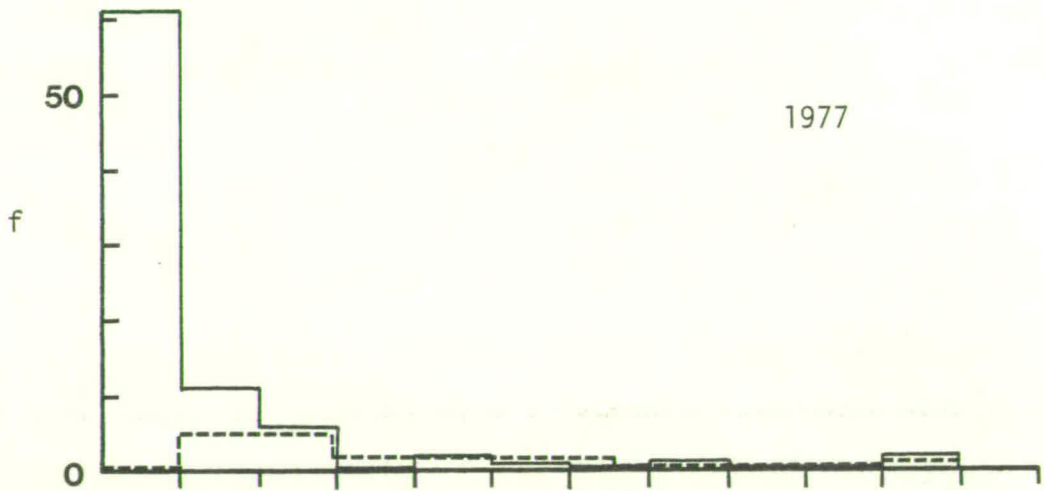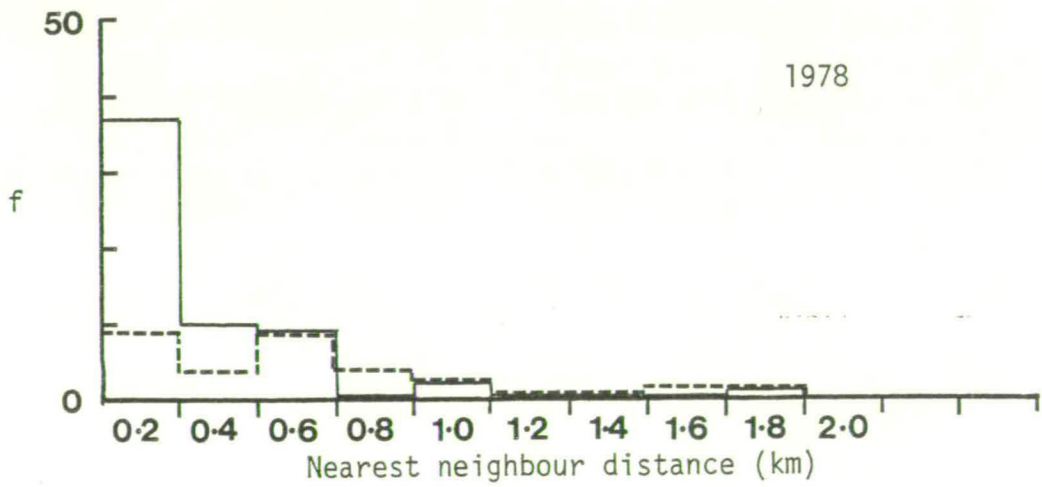
pair per crow nesting territory.

(c) The spacing of all nests was similar from year to year, but the spacing of occupied nests was significantly closer in 1978 than in either of the other two years (Table 6.10). In particular, occupied nests were found closer than 200 m only in 1978, and this was because some crow nesting territories held two separate pairs of Kestrels in that year.

Thus the increase in breeding numbers in 1978 was not due to a sudden occupation of previously unused habitat, but rather to an increase in the density of pairs within already occupied areas. Consequently, nesting areas used in all three years were further apart, on average, than were all nesting areas taken together (Fig. 6.4). This is clear from Fig. 6.5, which shows there was no segregation of type 1 and 2 nesting areas (i.e. those used mainly in 1978 alone) from the rest. Instead they occurred in between, or close to, nesting areas used in all three years.

2. Habitat differences between nesting areas.

The proximity of nesting area types might suggest that they occurred in equal proportions in both sheepwalk and young-plantation. This was tested by looking at the occurrence of major habitats within 0.5 and 1 km of each nesting area. There was a slight, but significant, tendency for nesting areas of lower occupancy to have a higher proportion of young-plantation in their

Table 6.10 Annual variation in the separation of occupied

nesting areas.

Using only occupied nesting areas that had a useable

nest at them in all three years.

| | Year | | |
	1976	1977	1978
Number of occupied NA's	28	28	38
Mean NN distance	0.82	0.94	0.53
Minimum NN distance	0.30	0.40	0.02

Differences in the means tested by the Mann-Whitney 'U' test:

Years	Value of 'z'	P
1976 vs. 1978	2.3851	0.0087
1976 vs. 1977	0.7132	0.2389
1977 vs. 1978	2.9086	0.0018

NN= Nearest Neighbour distance in kilometres.
NA= Nesting Area.

Figure 6.4 Frequency distributions of nearest neighbour distances
for all nesting areas and of those used in all three
years, 1976-78.
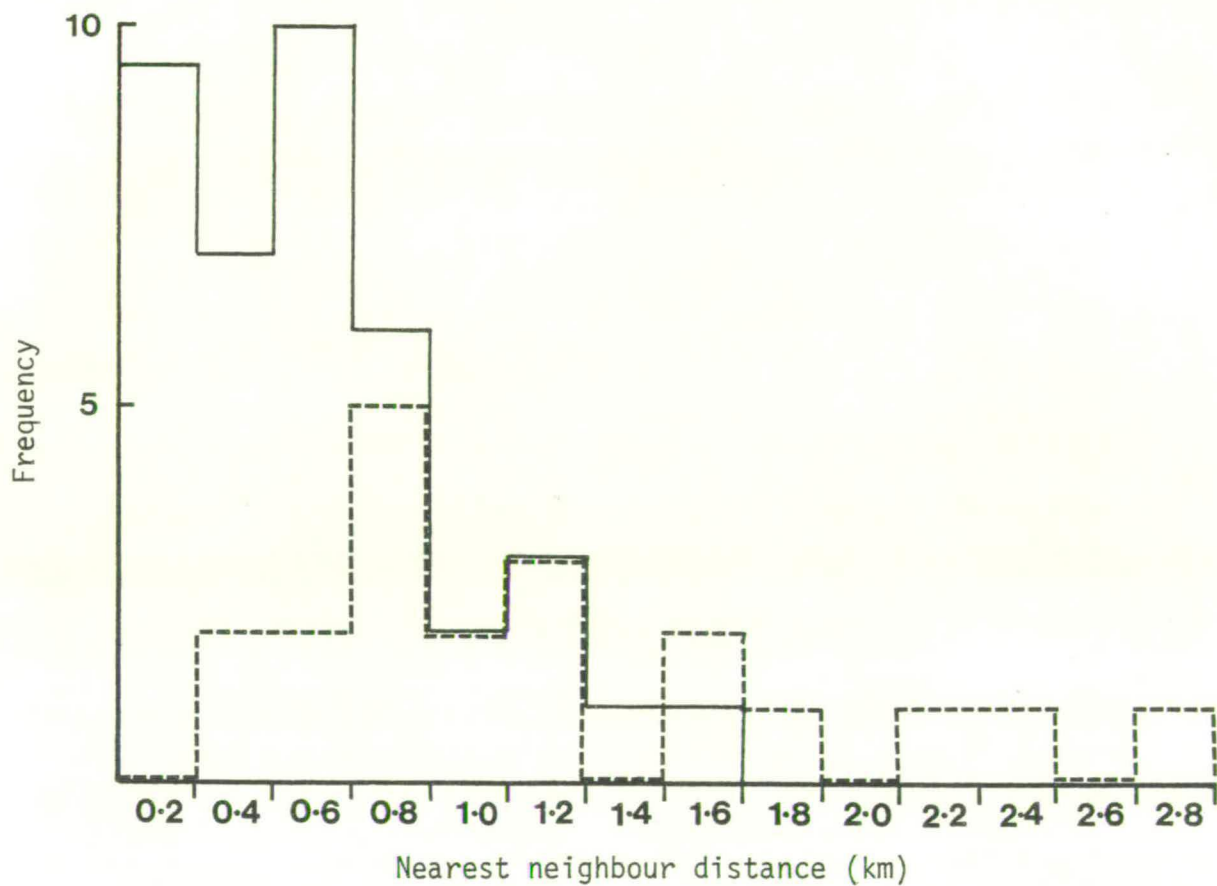
Solid line = all nesting areas, broken line = nesting areas
occupied in every year from 1976 to 1978 (i.e. types 3s and 3w as
defined in text, page 224).

Figure 6.5   Distribution of the different Kestrel nesting area types
             within the study area.
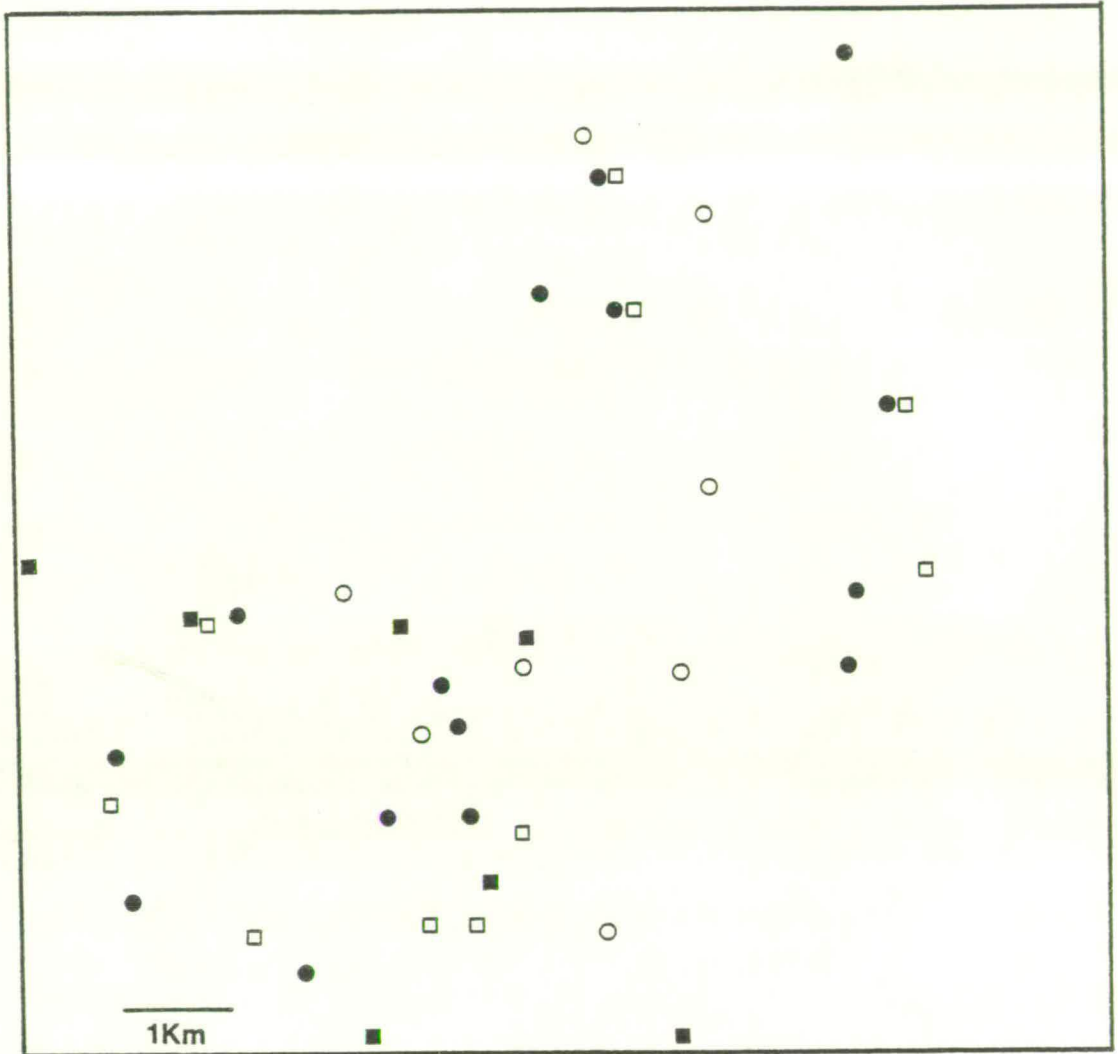
For definition of the nesting area types, see text page 224.

□ =   type 1
O =   type 2
● =   type 3s
■ =   type 3w

surrounding area (Spearman rank correlation coefficent= -1.0, P<0.05). This trend was somewhat unexpected because it implied that frequently used nesting areas (= the preferred nesting areas?) occurred in less forested habitats, which had lower vole densities (see chapter 1). The reason for this is unknown, but there are several possible explanations:

(a) The frequently occupied nesting areas may, in fact, have a better food supply because of better vole availability or the presence of alternative food. This generally better food supply could have allowed pairs to use such nesting areas even in poor vole years, hence the better occupancy of nesting areas on sheepwalk.

(b) The main factor affecting occupancy could have been the likelihood of there being a useable nest at the nesting area. Thus 'traditional' nesting areas (i.e. those occupied in most years) may be in places that are most likely to have nests available every year. Nearly all nests used in Eskdalemuir were crow nests, so this idea was tested by scoring each nesting area by two separate indices of crow nest availability:

(i) The total number of crow nests, of any condition, found around the nesting area over the three years. This included new nests built during the study as well as old nests present when it started (Table 6.11a).

(ii) The number of times crows attempted to breed at the nesting area during the study period. This was probably less

Table 6.11 Frequency with which crows occupied Kestrel nesting areas.

For explanation, see text page 235.

(a) Number of crow nests.

Kestrel occupancy type	1	2	3s	3w
Number of NA's	10	8	15	7
Observed number of crow nests	16	17	37	29
(Number per NA	1.6	2.1	2.5	4.1)
Expected number of nests	25	20	37	17
$(Obs-Ex)^2/Ex$	3.2	0.5	0.0	8.5

Chi-squared= 12.1   df=3   P<0.01>0.001

(b) Crow occupancy.

Kestrel occupancy type	1	2	3s	3w
Number of NA x years for which crow occupancy known	24	18	42	21
Number occupied by crows	2	5	22	15
Expected no. occupied	10	8	18	9
$(Obs-Ex)^2/Ex$	6.4	1.1	0.9	4.0

Chi-squared= 12.4   df=3   P<0.01>0.001

(Expected values calculated assuming all Kestrel nesting areas had an equal chance of containing crow nests or of being used by crows.) NA= nesting area.

accurate as some crows may have been killed by gamekeepers before I noticed them (Table 6.11b).

The scores for each type expected by chance were compared with the observed values and in both cases there was a highly significant trend for the most used Kestrel nesting areas to be at places that were most used used by crows. This relationship may have arisen because crows and Kestrels had the same habitat preferences, but this is unlikely in view of their different food requirements. A more likely explanation is that 'traditional' nesting areas were in places which generally offered the best chance of having a useable crow nest in any one year. (N.B. All nesting areas in this analysis had at least one useable nest at them in all three years, so occupancy was not limited by lack of a nest). The trend continued between types 3s and 3w, so it is possible that certain nesting areas may have been consistently associated with overwintering because they were most likely to contain a useable nest the next year.

(c) Type 1 nesting areas may have had higher proportion of surrounding forest because only habitat with a high food supply could support interstial pairs nesting so close to traditional nesting areas. Thus unafforested ground may have been able to support pairs only at well spaced, traditional sites.

NEST AVAILABILITY AND BREEDING NUMBERS.

Raptors are unable to breed if they cannot obtain sufficient food or if they fail to find a suitable nest site (Newton 1979). The evidence presented earlier suggested that food availability may have been the main limit to Kestrel breeding numbers in some years in certain parts of the study area. In this section, I shall examine evidence that, under some circumstances, nest availability also limited breeding in parts of Eskdalemuir.

Variation in Nest Availability Between Years.

Falcons generally show no obvious nest building behaviour and are therefore restricted to nesting in particular situations. Peregrines (F. peregrinus), for example, usually require cliffs or tall buildings, while Merlins (F. columbarius) generally need stands of rank heather or old crow nests in trees (Newton et al. 1978). Although Kestrels show remarkable variation in the position and type of nest used, the location of nesting areas at Eskdalemuir was still determined by the existence of suitable ledges, tree holes or old nests. This resulted in a clumping of nesting areas (Fig. 6.5), which was in sharp contrast to the regular spacing found in some other raptors that build their own nests (e.g. Sparrowhawks, Newton et al. 1977). In Eskdalemuir, the Kestrel nesting areas were concentrated where there were trees suitable for

crows to build in, and therefore tended to be in the valleys. Most of the farmland in the area was also in the valleys, so it was hardly surprising that more nesting areas were found on farmland than would be expected from its area in relation to other habitats (Table 6.12). Thus there were large sections of high ground, both sheepwalk and young-plantation, which were devoid of sites. An obvious question to ask was whether Kestrels used these areas and would they have bred there if nests were available? To test this, I erected artificial nests in some open areas that previously had contained no other nest sites.

Methods.

During the breeding season of 1976, several areas of both sheepwalk and young-plantation were devoid of breeding pairs (Table 6.13). The following year I visited these areas more frequently and found they were used by a number of Kestrels. At Raeburnhead (the place that received most coverage) they were mainly unmarked birds of unknown status, though some were tagged and known to be breeding. Most of the untagged birds seemed to be non-breeding yearlings, and a yearling female caught at Raeburnhead in July showed no signs of having had a brood patch. The few marked individuals were birds nesting nearby that occasionally flew into the area to hunt. It seemed, therefore, that places devoid of nest sites were used by non-breeding yearlings and, around the edges, by breeding pairs from neighbouring ground. Home range data from

Table 6.12 Distribution of nesting areas in different habitats.

	Habitat		
	Farmland	Sheepwalk	YP
Observed score	9.5	7.5	24.0
Expected score	1.6	14.4	24.1
$(Obs-Ex)^2/Ex$	39.0	3.3	0.1

Chi-squared= 42.4 df=2 P<0.001

(Expected values were calculated from the frequency of each habitat in the study area, assuming each was equally likely to contain nesting areas.)

Each habitat scored 1 for each nesting area fully in it.

Nesting areas between habitats scored 0.5 for each habitat.

YP= young-plantion.

radio-tracked birds showed that one area (Glendearg) was used by at least four different breeding males (see chapter 5).

In January/February 1978, 12 nest boxes and 5 artificial stick nests were erected in various locations shown in Table 6.13. (I had no evidence that the two types of nest differed in their suitability for breeding. Although most of the natural nests in the area were crow nests, birds seemed to change freely between stick nests, crags and nest boxes. Five breeding adults were known to have changed nest types between years, and there were 6 cases of birds (4 male and 2 female), reared in one site type, which eventually bred at another.) Initially I selected one sheepwalk area (Clerkhill) and one young-plantation (Raeburnhead) in which to put up as many nests as possible; while using the other areas, devoid of sites, as 'controls'. In practice there were not enough suitable places for nests at Clerkhill, so two had to be put at the edge of the Glendearg area. Some of the boxes at Raeburnhead were in small roadside quarries because no other places were available. As a consequence, a few were low down and may have been unattractive to Kestrels.

Results.

Kestrels laid in experimental nests from both areas, 5 out of 11 in young-plantation and 3 out of 6 in sheepwalk, suggesting no difference in the proportions used in the two habitats (Fisher

Table 6.13 Description of areas in Eskdalemuir devoid of natural breeding sites.

Name of area	Approximate location	Habitat	Position of nests erected	Types of nests
Raeburnhead	East of study area	Young-plantation (5-12 years)	Deer platform	3 Boxes
			Old buildings	1 Box
			Trees	1 Box
			Quarries	6 Boxes
Spotislaw	West of study area	Young-plantation (5-9 years)	None	-
Clerkhill	South of study area	Sheepwalk and farmland	Single trees	1 ASN
			Small woods	3 ASN
Glendearg	North-west of study area	Sheepwalk	Single trees	1 ASN
			Small crag	1 Box

ASN= Artificial Stick Nest (see text page 194).

Exact Test, P>0.05). Nests were occupied during the same period as others in the region, some of them being among the first to have eggs. The proportion of yearlings using these new nests was similar in both sexes (63% yearling males, 67% yearling females) and was higher than the overall figures for the year. The two control areas were searched, but no breeding pairs were found and there was no evidence that ground nesting occurred.

Discussion.

It thus seemed that, at least in some years, breeding in 3 of the 4 areas was prevented by the lack of suitable nests. A number of other studies have also shown that the erection of artificial nesting places can markedly increase the breeding density of Kestrels (Cave' 1968) and other raptors (Hamerstrom et al. 1973, Newton 1979). The high proportion of yearlings I recorded suggests such new nesting areas were more likely to be used by first time breeders than by older birds, possibly because established breeders tended to return to their previous nesting areas. Although this experiment was done only in a good food year, the results from other studies (e.g. Cave' 1968) show that once nests are made available in an area lacking them, some continue to be used even in poor years.

Nest Availability and Non-Breeding.

Introduction.

In the absence of artificial nests, the birds that used them may have moved on and nested elsewhere, so the above experiment did not demonstrate that some Kestrels were prevented from breeding altogether by lack of suitable nests. However, I made several observations which seemed to imply that there were indeed birds present during the breeding season which were not breeding and had no useable nest:

(a) In all years, but especially in 1976 and 1978, I frequently saw birds which did not breed. Some of these were paired and others were not. Of the paired birds, most were at nesting areas which had at least one useable nest. The other pairs either had a nest which may have been unsuitable, or were in thick woods so may possibly have had a nest which I could not find (Table 6.14). The unpaired birds were often in the same place day after day, sometimes hunting close to one another and away from the nesting areas or usual range of known breeding birds. They seemed to roost in small roadside quarries near to where they were seen hunting, but I could not be sure of this. Adults and yearlings of both sexes were among the unpaired non-breeders: of 10 apparently unpaired birds caught, 6 were males, including 4 yearlings, and 4 were females, including 3 yearlings.

Table 6.14 Status of non-breeding pairs recorded in Eskdalemuir 1976-1978.

	Sites where breeding recorded* at least once from 1976-1978			Sites where no breeding recorded from 1976 to 1978		
	Nest available	Nest available probably unsuitable	No nest available	Nest available	Nest available probably unsuitable	No nest available
1976	6	1	0	0	1	0
1977	2	0	0	0	0	1
1978	0	0	1	1	1	1
Tot.	8	0	1	1	1	1

*Breeding is taken as the laying of at least one egg.

(b) On four occasions I noticed that nests occupied by Long-eared Owls early in the season were later used by Kestrels when the Owls failed or fledged young. The Kestrels concerned bred unusually late, suggesting that they had no other nest and may not have laid at all if the Owl nest had not become available. This idea was further strengthened by an observation made at Eskdalemuir before I began: a nest box placed in a quarry was blown down early in the breeding season (before it was used by Kestels) and was not put up again until early June, when it was immediately occupied by a pair of Kestrels which then laid in it (R. Rose pers. comm.).

(c) On 16 May 1977, a female Kestrel with a broken wing was found at an isolated nesting area that contained a scraped nest which had not been laid in. The bird appeared to be in full breeding condition as it laid an egg in its cage within 24 hours of being taken into captivity. The bird was not tagged, but there was no evidence to suggest it was not the female that was previously paired at the nesting area, and no other female was seen there during the removal. However, on 17 May the same tagged male was seen displaying vigorously and was remated with a second female within 3 days, nearly 3 weeks after most of the other pairs settled that year (this pair subsequently reared three young in the original nest).

Methods.

All the above evidence, although circumstantial, strongly implied that there were non-breeding birds in the population, some of which were capable of breeding when nests became available. Such non-breeders included both males and females, so it seemed to be a shortage of nests, not mates, which prevented breeding. I tested this idea with two experiments:

(a) The removal of one member of several pairs of Kestrels known to have commenced breeding. As it was not possible to keep removed birds in captivity over the summer, they had to be killed and so numbers were kept to a minimum, the main concern being whether replacement occurred at all, and not how frequently. It was decided that two trials for each sex would suffice and that only one female removal was necessary in 1978 because the 'natural' removal recorded in 1977 seemed as well controlled as any experimental one. In the event, it was possible to remove only two birds; one adult female caught off an incomplete clutch on 1 May, and an adult male caught off six eggs on 3 May. The respective partners were not caught at this time and their ages were unknown.

(b) The provision of additional, artificial nests late in the season, beyond the laying date of most birds (called 'late nests'). These experiments were done at the same time as the removals in 1978. From 1 May to 13 June, 8 nests were erected in small woods or individual trees which had no useable nest beforehand. In 7 cases

no Kestrels were previously seen at the sites and there was no evidence that pairs were present prior to the experiment. In the other case, two birds were seen in the wood, but showed no signs of displaying so I could not be sure that they were paired. All the sites chosen were at least 200 m from the nearest occupied Kestrel nest as established breeding pairs may have prevented the occupation of nests placed closer than this. Also included in the sample were four sites where the only nest was first used by other birds (three by Long-eared Owls and one by crows) but which became available during the experiment. These 'natural' cases were judged to be equivalent to the experimental ones.

Both experiments were done when it was likely that all the pairs which would naturally breed were already established on their nesting areas. Replacement of removed birds was rapid in early spring; in three cases in March and early April 1978, males removed overnight to affix radio-transmitters had been replaced by the next day. However, these cases were early in the season so the incoming birds might have bred elsewhere had the original male not been removed. It was thus necessary to be as sure as possible that birds replacing removals, or occupying late nests, would not have otherwise bred. This seemed to be a reasonable assumption if experiments were carried out after the date on which all breeding birds were normally paired and on their nesting areas. The evidence from the two previous years suggested that even in 1977, when laying was unusually late, all the birds that subsequently bred

were present on their nesting areas by the end of April; consequently 1 May was taken as the earliest date that these experiments could be started. (In 1978, laying was two weeks earlier, on average, than in 1977.)

Results.

(a) Removals. There was no evidence of re-nesting at the nesting area from which the female was removed, but a second clutch was started at the nesting area from which the male was removed on 16 May. Young were fledged from this nest and both adults were caught on 26 June; the female was an adult and the male a yearling. With the incident in 1977 reported above, these experiments show that both a male and a female removed from nesting areas after the usual time of settling were replaced by birds which then bred.

(b) Late Nests. Five of the eight artificial nests, and all four of the natural ones, were eventually laid in by Kestrels (Fig. 6.6). In two instances the birds failed before laying dates could be established, so the intervals between nest availability and egg lay were only estimates. When these were excluded, the mean interval was 12 days. It is clear that some pairs responded very quickly and one of these (at the Pockleaf 2 nesting area) warrants a more detailed description:

The site consisted of a single spruce tree, containing one disused crow nest, around which a pair of Kestrels were seen

Figure 6.6 Summary of the results of the 'late nest' experiment
            (see text page 247).

Nest number.		DATE					Interval (A-L)
		1	10 May	20	30	40 June 50	
1	A		L				19
2	A		L				18
3	A*?	L					8
4	A					(L)	(41)
5		A			(L)		(24)
6		A	L				11
7		A*	L				5
8				A	L		11
9				A		L	13
10						A	–
11						A	–
				Mean interval			12.1 days

A = date nest made available, L = date first egg laid.
(L) = laying date uncertain, interval excluded from mean.
*Pair present before nest made available.

displaying as early as 8 March. They were frequently involved in prolonged combats with the pair at an adjacent nesting area (Pockleaf 1) some 200 m away, during which the male from Pockleaf 2 seemed to be trying to replace the other male. Fights were centred around Pockleaf 1 with the intruder displaying to the resident female, diving at the nest and being chased for long periods by the resident male. On 20 April I found that a Long-eared Owl had been incubating a clutch in the Pockleaf 2 nest for some time, but in spite of this, the Kestrels continued to display into the nest tree in typical fashion. On 7 May I put a second, artificial nest in the tree and noticed that the Owl eggs had recently hatched but only one chick was still alive. On my return on 13 May, the Kestrels had scraped the new nest, but laid in the Owl nest, which I assumed had failed on 8 May. Thus the interval between the nest becoming available and the laying of the first egg was about 5-6 days. I could not tell if the failure of the Owls was a direct result of the activity of the Kestrels.

In 7 other cases, no birds were seen at the site before the nests were put up and intervals were longer. Of the 18 birds that used late nests, 13 were aged: 4 out of 7 males and 5 out of 6 females were yearlings. Taken with the removal replacements, the proportion of yearlings at experimental nests (11 out of 15), was significantly higher than in the rest of the breeding population that year ($X2= 6.35$, $P<0.02>0.01$). Nonetheless, there were

evidently some adults among the Kestrels which would not otherwise have bred.

Discussion.

Together, these results provide strong evidence for the existence of a non-breeding surplus in the population, which was prevented from breeding by a lack of nesting places. Shortage of suitable nests as such was not necessarily the cause of this surplus as, even in 1978, only 60% of useable nests were occupied (see above). However, the remainder were mainly within 200 m of occupied nests and may have been unavailable because of the territorial behaviour of the resident pair.

The validity of such experiments hinges on the assumption that the birds which came in as replacements (or took up late nests) would not otherwise have bred. Such assumptions may be unwarranted if experiments are done too early in the season, before incoming birds have settled, but even late in the season other explanations of the status of replacement birds are possible:

(a) If there is a preference for particular nesting areas, birds removed from them may be replaced by individuals moving in from nesting areas that are less favoured. Such birds may have bred where they were originally so it is necessary to ensure that there is no movement of neighbouring pairs following a removal. Newton and Marquiss (in prep.) found it necessary to trap not only the

replacement bird during their removal experiments on Sparrowhawks, but also all the birds from as many surrounding nesting areas as possible. In my study, any changes would have been easily noticed because the birds were more readily seen. Although not every surrounding pair was caught and marked, I had no evidence that adjacent pairs were disrupted as a result of either type of experiment. Furthermore, relatively large numbers of late nests were used, so it was unlikely that all the birds involved could have come from previously occupied nesting areas without a noticeable reduction of pairs elsewhere, especially as many individuals at neighbouring sites were marked.

(b) The assumed 'non-breeding pool' may, in fact, have consisted of birds which had failed in a previous breeding attempt that year. If this occurred early enough, pairs could have left their original nests in search of somewhere else to breed. However, I had no evidence to support this and none of the seven pairs which laid repeat clutches did so in a new nesting area. Furthermore, performance was generally high in 1978 so it was unlikely that all the birds that used experimental sites were failed breeders. Even if this was true, it still left open the question why they had not attempted to breed sooner elsewhere. The likeliest explanation was that all the available nesting areas were being used so that no more were vacant.

(c) Even if the two explanations above are incorrect, there is still the problem of knowing whether or not the birds involved

would have bred anyway. Strictly, this could not be tested because I could not tell what would have happened to a bird if the nest it took up had not become available. Some may have moved on until they found an available nest. For example, in 1978 a marked adult male returned early in the season to the nesting area it had occupied the previous year. There was no nest available there, and it later moved and nested elsewhere. Although movements such as this might explain the results of the experiments, the male in the above case moved in mid-April, some time before the experiments were started, and it is likely that birds which could change site did so fairly quickly. The pair at Pockleaf 2 in 1978 remained there even though the nest would not have become available until the end of May had the Owls not failed. It seems unlikely that these birds would have stayed if they could easily have bred elsewhere, but, in the absence of any unoccupied nesting areas, their best chance of breeding may have been to remain where they were until the Owls finished using the nest.

Given the above problems, caution is needed in interpreting the results of removal and late nest experiments. While they strongly suggest that lack of nesting places alone prevented some birds from breeding, other interpretations are possible. Furthermore, the experiments were done in a year when food supply was relatively good and, although a replacement was recorded in 1977, it may be that few would occur in poor food conditions. In

1976 and 1977, some pairs occupied nesting areas that contained nests, but they did not lay in them. No such non-breeding pairs were recorded in 1978, suggesting that a higher proportion of pairs were capable of breeding that year and thus able to use any unoccupied nests.

Assuming that such a surplus did exist, there seems to have been some variation in the status of the birds involved; ranging, on the one hand, from birds that were living unpaired in places devoid of nest sites, to pairs in full breeding condition at nesting areas which had no available nest. This may explain the variation in the time taken to respond to suddenly available nests; those birds which were already paired laid in a matter of days, whereas those that had to find a partner and come into breeding condition took longer. It is interesting that the mean interval recorded (and the usual interval at late nests where no birds were previously seen) was about 12 days- similar to the mean time from pairing to egg-lay reported from studies of captive American Kestrels (Porter and Wiemeyer 1972, 13 days; Bird 1978, 11 days). The shortness of some of the intervals observed in this study suggests that pairing, and possibly the first stages of egg production, had occurred in two females even though no nest was available.

The fact that over 70% of the replacement birds were yearlings implies that this particular age group may have been more

vulnerable to a shortage of nests. They were possibly less able to compete for nests than were adults, or they may have arrived late and found all the available nesting areas already occupied by adults.

The regulation of breeding numbers.

Table 6.15 summarises the main findings in this chapter by listing the likely differences between years of good or poor food supply and/or weather. How these differences come about is not known, but the above results suggest the following mechanism may operate:

A certain number of nesting areas (called here 'traditional nesting areas') are occupied in nearly all years, mainly by adults that winter in the area or return early in spring to breed. These tend to be relatively far apart and, in early spring, the ranges of their occupants include several useable crow nests (especially as these often occur in groups at traditional crow territories). Birds which arrive later in spring are mainly yearlings and these may attempt to use nests that are in between, or close to, the nesting areas already occupied. They seemed to be able to settle only in a year of high food supply or low rainfall, possibly for several reasons:

(a) In a good year the adults arriving first breed early and are therefore further on in their breeding cycle when the other

Table 6.15 Comparison of Kestrel breeding in years of good
and poor food supply and/or weather.

Poor Year	Good Year
Few breeding pairs	More breeding pairs
Few type 1 NA's occupied	Most type 1 NA's occupied
Nests far apart (none closer than 200 m)	Average nest spacing closer (some closer than 200 m)
Few breeding yearlings (mainly females)	More breeding yearlings (including some males)
Small clutches, laid late	Slightly larger clutches, laid earlier
High rate of clutch desertion	Low rate of clutch desertion
Low production of young per territorial pair	High production of young per territorial pair

birds are trying to gain access to nests near them. The level of aggression in birds seemed to diminish as the breeding cycle progressed (see chapter 3), so that late arrivals may have been tolerated near to the nest if the owners are already well on in their breeding attempt.

(b) The territoriality of the first settling birds might have been less pronounced in a good year. Although this was not tested for, there was no evidence to suggest that actual nest defence was less if the food supply was better.

(c) Late arriving birds may be more persistent in trying to secure the use of nests close to other pairs in years when the food supply is better. This seems to fit my observations better: in 1978 a number of prolonged fights (lasting many hours and repeated on successive days) were seen between known territory holders and apparent strangers; such fights were shorter and less frequent in other years. Birds may only persist in attempts to intrude into a territory if they are able to obtain food easily when not fighting. Thus food supply may affect the ability of incoming birds to maintain themselves during the prolonged fights necessary to settle near to established pairs.

In conclusion, an area such as Eskdalemuir might consist of a 'framework' of traditional nesting areas, each of which is occupied almost every year and which includes, in its near surrounds, a number of useable nests. By excluding incomers from these nests,

the birds present in early spring may effectively prevent them from breeding, thereby limiting the overall breeding density. Only in years of sufficiently high food supply are late arriving birds able to take up such unused nests near to traditional nesting areas, mainly by being more persistent in their attempts to settle.

CHAPTER 7.

DISCUSSION AND CONCLUSIONS.

1. The response of Kestrels to changing vole density.

Vole density in Eskdalemuir varied (a) between seasons in the same year, (b) between years, and (c) between sheepwalk and young-plantation. The evidence presented in chapters 2-6 suggested that Kestrel populations showed the following characteristics at high vole densities, and the opposite characteristics at low vole densities.

(a) A high proportion of voles in the diet.

(b) The production of relatively heavy all-vole pellets, reflecting a high daily food intake (for individuals eating voles).

(c) A high density of individuals and, possibly, of breeding pairs.

(d) A high proportion of first-year birds in the population at all times of year, and a high proportion of breeding yearlings in summer.

(e) Small home ranges and territories.

(f) Early breeding, low failure and high proportion of young per territorial pair.

Changes in one or more of the above factors were associated with changes in vole density, irrespective of whether the change in

vole density occurred from year to year (i.e. as part of the vole 'cycle') or from season to season. The same changes may have occurred in response to differences in vole density between localities or habitats, but I had evidence that this was so within Eskdalemuir only for diet (Kestrels in sheepwalk had a lower proportion of voles in the diet than those in young plantation). If Kestrels do respond in the same way to changes in vole density, irrespective of whether the changes are in time or space, my results would predict that Kestrels in poor vole habitats (such as arable land) would show the opposite trends to those listed above. This seems to be true for diet and breeding numbers, but evidence for the other factors is lacking and more work needs to be done to investigate this.

Food supply was evidently an important factor affecting the size, age structure and productivity of the Kestrel population. This is in line with studies on a number of raptors, particularly those that are subject to periodic fluctuations in prey density. For example, Newton (1979, table 31), in comparing breeding studies on four raptors that eat rodents (Rough-legged Buzzard, Buteo lagopus, Common Buzzard, B. buteo, Hen Harrier, Circus cyaneus, and Kestrel), found that in each species the response to good food years involved an increase in the number of territorial pairs and in the proportion of pairs producing young. All the species laid earlier in better years (though the strength of this response

varied), but whereas some also showed increased clutch and brood sizes (e.g. Rough-legged Buzzard), others did not (e.g. Kestrels). The general tendency was for greater productivity in good food years, but how this was achieved seemed to vary between species. Similar trends were also found between good and poor food habitats in species whose prey numbers were generally stable from year to year (Newton 1979).

Winter density and range size in various raptors have also been shown to vary with prey density (Craighead and Craighead 1956: Red-shouldered Hawk, B. lineatus, Red-tailed Hawk, B. jamaicensis, Rough-legged Buzzard, American Kestrel, F. sparverius, and Hen Harrier; Enderson 1964: Prairie Falcons, F. mexicanus; Enderson 1960 and Mills 1975: American Kestrel and Cave 1968: European Kestrel). In each case density was higher and ranges were smaller (where they were measured) in good food conditions than in poor ones. My results were similar to these, indicating that Kestrels respond in typical raptor fashion to changes in food supply.

2. Kestrel numbers in relation to the timing of breeding.

One finding which seemed to contradict the idea that Kestrel numbers were directly related to vole density was the timing of the increase in Kestrels from winter to summer. This occurred in February and March, and numbers reached a higher level from April to July than would be predicted from the prevailing vole numbers.

Such a disparity between winter and summer may have arisen for several reasons:

(a) Small raptor species, like most birds, time their breeding so that young are in the nest and are fledged when food is most plentiful (Newton 1979). The timing of breeding in Kestrels may have been linked to the need to fledge young by late summer, when vole and other prey were plentiful, and in Holland Kestrels fledged from early broods survived better than those fledged from later broods (Cave' 1968). This suggests that there was some advantage to Kestrels in arriving at the breeding grounds early in the season, if this facilitated early breeding. However, early arriving individuals faced a possible food shortage until vole numbers increased, so some may have delayed their arrival accordingly. Newton (1979) suggested that the later arrival of some individuals at breeding grounds (especially younger birds) may be because they would probably be ousted from their territories by older birds if they did arrive early, or because they were unable to achieve sufficient body condition to move earlier. In Eskdalemuir, female Kestrels seemed to start coming into breeding condition only after they had settled in the area, rather than arriving already in breeding condition (chapter 3). This implied that the food supply during the pre-lay period was critical to subsequent breeding, which seems to be true for most raptors that have been studied (Cave' 1968, Brown 1976, Newton 1979).

(b) Kestrel numbers may have been higher in summer than

expected from the prevailing vole densities because vole density was not a good index of food supply at that time (chapter 5). If this were so, the timing of arrival in early spring might be explained in two ways.

(i) The period of lowest vole availability may have been in early or mid-winter (i.e. December to January), when there was more vegetation and snow cover than at the end of winter. Kestrel density could have remained at a level corresponding to this availability, even when food supply later improved, because there was little movement in the Kestrel population at this time. Thus, as summer residents arrived, they were able to compress the ranges of the Kestrels already present because winter residents had larger ranges than necessary for the food supply in late winter/early spring.

(ii) Alternatively, Kestrel density at the end of winter may have been the maximum sustainable by the habitat at that time, and summer residents could settle only as the the food supply increased. This implies that food supply increased rapidly from February to April, either through changes in vole availability (because of less vegetation or snow cover?) or by an increase in the abundance of alternative prey. The evidence from vegetation measurements and pellet analysis suggests the former was more likely, because cover was at its lowest and voles were the main prey item during this period.

The gradual compression of home range noticed in early spring

is consistent with (ii) rather than (i), though the two hypotheses would be difficult to distinguish in practice. The main difference between them is that, in the first case, the settling of birds depends on when they arrive from their wintering grounds, whereas in the second case, birds may be continually moving through the area but can only settle if the food supply permits. The two ideas are not mutually exclusive: the fact that a proportion of birds were able to return each year to breed and seemed able to settle as soon as they arrived, suggests that the first argument may hold for early arrivals, but later birds may have been limited in settling by how fast the food supply increased.

(c) Newton (1979) has suggested that raptors are better able to move around in response to changes in food supply outside the breeding season because they are not tied to a nest. This hypothesis predicts a better correlation between vole density and Kestrel numbers in winter than in summer. In my study, Kestrel numbers in successive summers were as well correlated with vole density as in successive winters (chapter 5, Fig. 5.12). However, the measure of Kestrel numbers in summer included unpaired birds, which were presumably freer to move around than breeders, and there was a poor relationship between Kestrel numbers and vole density when only territorial pairs were included (chapter 6).

In conclusion, Kestrel numbers were related to vole density both during and outside the breeding season, but were higher (at

any given vole density) during the breeding season. This was either because Kestrels arrived in the area and started to breed before vole density increased (in order to feed young when voles were abundant), or because vole density was not a good index of overall food supply in summer (as alternative prey were also available).

3. The limitation of Kestrel density.

The factors which might have limited Kestrel numbers in Eskdalemuir fall into two categories, namely, those that limited the population as a whole, and those that limited the number of breeding birds. I shall discuss these separately, though they were probably linked because breeding birds may have had similar limitations as non-breeders, as well as the additional ones related to breeding. A limiting factor, in this context, is a factor that helps to prevent an increase in the number of individuals (or breeding pairs) in an area. A population may be limited by several factors, some of them 'ultimate' and others 'proximate'. Thus, for example, numbers may be prevented from increasing because individuals are dying from disease; if their vulnerability to disease depends on their nutritional condition, food supply could be an ultimate factor limiting population size and disease a proximate one. The most limiting factor may vary according to circumstances, and a factor may act proximately on some occasions and ultimately on others.

(a) Limitation of the population as a whole.

A major ultimate factor limiting the numbers of Kestrels in Eskdalemuir seemed to be the food supply. The evidence for this (discussed in detail in chapter 5) was mainly circumstantial, namely that changes in the abundance of the main prey item (voles) were reflected in corresponding changes in the number of Kestrels. One problem was that vole trapping data may not always have been a good index of food supply. This probably explained the disparity between Kestrel numbers in summer and those at other times of year with similar vole densities, as alternative prey were most abundant (and most frequent in the diet of Kestrels) in summer. Other possible limits to winter or non-breeding raptor populations are the number of suitable roosts or hunting perches in the area (Newton 1979). These may have been important factors in affecting the use and location of ranges, but they did not seem to be limiting numbers during my study. Small quarries or woods which could be used as roosts were fairly numerous and widespread, as were perching places from which to hunt.

How food supply limited Kestrel numbers was difficult to prove. Territory size was also related to vole numbers and this may have been a proximate factor limiting Kestrel density, the aggressive behaviour of some birds preventing others from settling. However, Lack (1954) argued that density itself determined territory size, and without experimental evidence, I could not

decide if this was so. Few Kestrels reared in the area remained there, and their density after the breeding season seemed to depend mainly on the number settling, rather than local breeding production. There was no evidence that breeding performance was lower at high Kestrel densities; rather, birds were most successful when breeding numbers were highest. It therefore seemed unlikely that population levels in the study area were regulated by density-dependent breeding success, but I could not test this, as food supply varied from year to year (breeding performance may have declined had numbers increased and food supply remained constant). I had no data on the mortality of Kestrels in the area, so I could not tell if this was density-dependent (as suggested for some birds by Lack 1954).

(b) The limitation of breeding numbers.

Newton (1979) has argued that the breeding numbers of raptors are limited by the availability of either food or of suitable nest sites, whichever is in shortest supply. Evidence that food supply directly limited the number of pairs able to breed in Eskdalemuir (by preventing birds from settling or reaching breeding condition) was lacking. Furthermore, there was no significant relationship of breeding numbers to vole density and, although this was based on small samples in only 3 years in my study, a similar result has been obtained elsewhere with larger samples (Cave´ 1968). This was possibly because food supply depended mainly on factors such as the weather or the rate of vole increase, rather than on vole numbers

as such. Rainfall showed no relationship to breeding numbers, and its presumed effect of lowering food supply, by preventing hunting, was not proved. Food supply may be more critical in limiting Kestrel breeding numbers in less suitable vole habitats such as arable land, than in upland areas such as Eskdalemuir.

There was stronger evidence that, in one year at least, nest site availability in Eskdalemuir limited breeding numbers. In some areas this was direct, and the erection of nests in places previously devoid of them increased breeding numbers. In other areas the shortage of nests may have been caused by territorial behaviour, in that vacant nests were available, but only very close to other pairs. Watson and Moss (1970) argued that at least three conditions have to be shown to exist before behaviour can be assumed to be limiting breeding numbers:

(i) A substantial part of the population does not breed.

(ii) Such non-breeders are physiologically capable of breeding.

(iii) The breeding animals are not completely using up the relevant resource.

These conditions were shown to exist in 1978 by the removal and late-nest experiments (chapter 6). This implied that territorial behaviour of some breeding Kestrels prevented others from breeding in that year, but whether this limited the population in the long-term was not known.

Behaviour may have been only a proximate factor limiting

breeding numbers because the size of territory seemed in turn to be governed by food supply. The number of territorial individuals able to settle in an area may depend on both the level of aggression of residents and the persistence of individuals in trying to settle (Maynard-Smith 1974). I had no evidence that Kestrels were less aggressive in better food conditions, but incomers did seem to be more persistent in trying to settle in a good vole year than in a poor one. If this was so, food supply may ultimately have decided the number of pairs in an area by affecting the persistence of incomers and hence their ability to settle. Cave´ (1968) suggested that Kestrels were less aggressive when food was plentiful, but this was not carefully tested, and referred to winter rather than to the breeding season. More work needs be done to decide if food supply affects territorial aggression, persistence in settling, or both.

SUMMARY.

(1) Kestrels were studied from October 1975 to July 1978 in an area of young conifer plantation and sheepwalk grassland in the southern uplands of Scotland. Analysis of 1014 pellets and 561 kills showed that Short-tailed voles (Microtus agrestis) were the most important items in the diet; other prey such as shrews, birds, beetles or earthworms were taken according to their abundance relative to voles.

(2) Vole numbers were higher in autumn than in spring, and higher, on average, in 1975/76 and 1977/78 than in 1976/77. Measurements of vegetation structure indicated that seasonal changes in ground cover may have reduced the effects of the annual fluctuation of vole numbers on Kestrels, by increasing the availability of voles when their numbers were low and vice versa. The mean weight of all-vole pellets was positively correlated with vole density, suggesting that Kestrels on all-vole diets had a higher daily food intake when voles were plentiful, than when they were scarce.

(3) Seasonal changes in daily energy expenditure were estimated by the time-budget method, using spot observations to calculate the frequency of different activities in each month. The activities of males and females were similar outside the breeding season, but from April to July females spent most of their time

(when not brooding) inactively perched and did less hunting and flying than males. Estimated daily energy consumption was lowest in winter and highest in summer when young were being fed.

(4) The mean body weight of Kestrels was highest in spring, prior to egg-lay, and lowest in early autumn, after the breeding season. Unlike males, females gained weight rapidly in early spring, during egg production. Seasonal changes in body condition (as measured by breast-muscle size) indicated that weight loss after clutch completion was related to nutritional stress during the incubation and nestling periods.

(5) Kestrels hunted from perches and from the wing, the latter method resulting in a significantly higher capture rate. Capture rates (in terms of number of items per unit time) were higher when invertebrates rather than vertebrates, were hunted. Most hunting was done from perches in winter and from the wing in summer. In autumn and spring, more hunting was done from the wing on windy days than on calm ones, but this was not so in summer. The different capture rates and energy costs of the two hunting methods could have explained their changing frequencies through the year.

(6) Kestrel numbers, as measured by counts made while driving, varied roughly in parallel with vole numbers, decreasing from autumn to winter and increasing rapidly in early spring. Breeding density varied between years from 0.24 to 0.34 pairs/km^2 and was similar to that reported from other upland areas in Britain. Kestrels in the area were partial migrants. Wing-tagging showed

that turnover was highest in autumn and early spring, mainly due to the loss of breeding birds over winter, followed by a return in spring. Males were more likely than females to remain in the area in winter.

(7) There was a a high proportion of first-year birds in the population when voles were plentiful. In both 1977 and 1978 more females bred as yearlings than males, and more yearlings of both sexes bred in 1978 (a good vole year) than in 1977 (a poor vole year).

(8) Ringing recoveries showed a similar trend to that reported elsewhere for northern Britain, i.e. most individuals ringed as pulli were recovered in their first year in a south to south-easterly direction.

(9) Home range size was estimated using observations of wing-tagged individuals and the results were checked by radio-telemetry. Maximum polygon area was found to be the most useful index of range size, but was corrected to allow for inaccuracies when the sample size was small and when range size was large. Examination of range-utilization and the distribution of intruders in the range, showed that the exclusive area of the range was a suitable index of territory size.

(10) Log range-size was inversely correlated with vole density, values for the breeding season lying on the same trend as those at other times of year. Kestrel numbers were higher at any given vole density in the breeding season than at other times of

year. This was because ranges were held by pairs instead of single
individuals, and because there were more ranges in summer than
winter. The large ranges and increased Kestrel numbers in summer
meant that range overlap was higher, and territory size smaller,
than at other times of year with the same vole density. During the
breeding season, pairs defended only a 'core area' around the nest
and shared hunting ranges with other birds.

(11) Within the study area, Kestrels bred mainly in disused
crow nests. With the data available, breeding numbers and performance
showed no significant relationship with either food supply or weather.
However, trends in the data suggested that spring temperatures may
have affected breeding numbers and spring vole numbers laying date.

(12) Breeding performance was examined in relation to the age
and experience of individuals and the quality of nesting areas.
Adults laid earlier, and reared more young, on average, than
yearlings. Familiarity with an area did not seem to enhanced
breeding performance, but breeding success was associated with a
greater likelihood of returning to the study area in subsequent
years. There was no firm evidence that some nesting areas were
preferred to others, but breeding performance was better at those
that were most often occupied. This was probably explained by the

greater proportion of adults, rather than yearlings, breeding at such nesting areas. Infrequently used nesting areas were found alongside those used in all three years, and did not appear to differ in habitat quality.

(13) In each year there were more disused crow nests than were actually used by Kestrels. Most old crow nests were within 200 m of their nearest neighbour, but occupied Kestrel nests were seldom this close. The mean spacing of Kestrel nests was closer in 1978 than in 1977 or 1976. This was associated with some pairs nesting within 200 m of one another and using old crow nests within the same crow nesting-territories.

(14) Evidence from removal experiments and from erecting artificial nest sites late in the breeding season indicated that, at least in 1978, there was a surplus of Kestrels (mainly yearlings) that were physiologically capable of breeding, but prevented from doing so by lack of a suitable nest. Although disused crow nests were present thoughout the season, most were close to occupied Kestrel nests, and seemed to have been unavailable to other Kestrels because of the territorial behaviour the occupying pair.

(15) It is concluded that food supply was the main limiting factor to population density and breeding numbers, though territorial behaviour may have been a proximate factor limiting breeding numbers in some years, by making nests unavailable to some pairs.

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APPENDIX

English and scientific names of birds and mammals mentioned in the text and tables.

BIRDS

English	Scientific
Black-shouldered Kite	*Elanus caeruleus*
Sparrowhawk	*Accipiter nisus*
Rough-legged Buzzard	*Buteo lagopus*
Common Buzzard	*Buteo buteo*
Red-shouldered Hawk	*Buteo lineatus*
Red-tailed Hawk	*Buteo jamaicensis*
Ferruginous Hawk	*Buteo regalis*
Hen Harrier	*Circus cyaneus*
Peregrine	*Falco peregrinus*
Prairie Falcon	*Falco mexicanus*
Merlin	*Falco columbarius*
European Kestrel	*Falco tinnunculus*
American Kestrel	*Falco sparverius*
Lapwing	*Vanellus vanellus*
Long-eared Owl	*Asio otus*
Short-eared Owl	*Asio flammeus*
Tawny Owl	*Strix aluco*
Skylark	*Alauda arvensis*
Meadow Pipit	*Anthus pratensis*
Starling	*Sturnus vulgaris*
Carrion Crow	*Corvus corone*

MAMMALS

English	Scientific
Pygmy Shrew	Sorex minutus
Common Shrew	Sorex araneus
Water Shrew	Neomys fodiens
Mole	Talpa europaea
Rabbit	Oryctolagus cuniculus
Bank Vole	Clethrionomys glareolus
Common Vole	Microtus arvalis
Short-tailed Vole	Microtus agrestis
Harvest Mouse	Micromys minutus
Woodmouse	Apodemus sylvaticus
Brown Rat	Rattus norvegicus
House Mouse	Mus musculus