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Habitat utilization, diet and reproductive success in the Kestrel in a temporally and spatially heterogeneous environment

Jari Valkama, Erkki Korpimäki & Pasi Tolonen

Valkama, J., & Korpimäki, E., Laboratory of Ecological Zoology, Department of Biology, University of Turku, FIN-20500 Turku, Finland
Tolonen, P., Department of Zoology, University of Oulu, Linnanmaa, FIN-90570 Oulu, Finland

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Both habitat selection and foraging theory suggest that animals should choose environments in which their reproductive success is maximized and survival costs are minimized. We examined the habitats selected for foraging by Kestrels *Falco tinnunculus* breeding in western Finland during 1989-1991 and related this to prey availability and the breeding success. Voles (*Microtus epiroticus* and *M. agrestis*) were the main prey of Kestrels in our study area. Voles went through a three year population cycle, with a crash in 1989, a low in 1990 and an increase in 1991. We found considerable variation among years in the use of the main habitat, agricultural fields. Kestrels hunted mainly over fields in 1989 and 1991, whereas in 1990 they hunted mostly over forests and marshland. The proportion of agricultural fields used as hunting habitat remained constant throughout the breeding season, except in 1989 when vole populations crashed and falcons shifted to hunt away from fields. Overall, reproductive success seemed to be better in small farmland areas (size 0.1–10 km^2) than in a large farmland area (100 km^2). We conclude that small farmland areas contained suitable habitats for alternative prey (bank voles, shrews, small birds, lizards, insects, etc.). Small farmland areas are thus probably more stable environments for Kestrels, because even in years of few *Microtus* voles in agricultural fields there are favourable food patches closer to the nests than in the large farmland area.

1. Introduction

In general, mobile predators should hunt in habitat patches that maximize their net rate of energy intake (e.g. Pyke 1984, Stephens and Krebs 1986). Predators should find the most profitable prey patches in their territories and concentrate their hunting effort on these patches. Patch profitability is usually determined by the prey density, but for avian predators locating prey by eyesight, prey availability is also important. Prey availability is affected by the amount and distribution of vegetative cover and weather conditions (e.g. Southern and Lowe 1968, Wakeley 1978, Stinson 1980, Baker and Brooks 1981, Korpimäki 1981, 1986, Bechard 1982, Pettifor 1984). Some studies on birds of prey have shown that prey availability is more important to reproductive success than absolute prey abundance (e.g. Janes 1984, 1985).

The Kestrel *Falco tinnunculus* is a small widespread open-country raptor. In Fennoscandia, where Kestrels are breeding migrants, males arrive at their breeding site from late March to early May, a few days to two weeks earlier than females (Palokangas et al. 1992). Egg-laying starts in late April–late May and the nestling period may continue to late July. In western and northern Europe, Kestrels feed primarily on voles *Microtus* and *Clethrionomys* spp. (Korpimäki 1985 and references therein). Kestrels are capable of using alternative food sources when voles are either scarce or their availability is poor. For example, in northern Europe, where vole numbers fluctuate in 3–4 -year cycles (e.g. Hansson and Henttonen 1985), small birds, shrews, lizards, and insects are the main alternative prey types (Korpimäki 1985, 1986, Itämies and Korpimäki 1987).

Here, we present data on changes in hunting habitats of Kestrels in relation to annual fluctuations in the main prey density, and examine the inter-relationships between habitat utilization, diet and reproductive success. These potential correlations are only rarely considered (but see Janes 1984, Korpimäki 1986), although there is a plethora of studies on the diet composition of avian predators (see Marti et al. 1993 for a review). They show that there are marked seasonal and annual changes in the diet of breeding birds of prey, but it remains to be shown whether these changes are due to differences in the prey density or habitat utilization for hunting. We also discuss the relationship between spring arrival times of Kestrels and their habitat selection. In the Sparrowhawk *Accipiter nisus* (Newton et al. 1979, Newton 1991) and Tengmalm's Owl *Aegolius funereus* (Korpimäki 1988), mean laying dates were earlier on the high-quality territories than on the low-quality ones.

We made the following three predictions. (1) In the same study area, Korpimäki (1986) found that as vole densities in farmland increased, the proportion of agricultural fields that Kestrels hunted over tended to increase. However, his results were based on data from sightings of unmarked falcons (breeding status unknown) and may be biased (see Village 1990: Appendix 2). The present data are from individually marked breeding birds and includes an entire three year vole cycle. We expect that agricultural fields should be used more for hunting in good vole years than in poor ones. (2) The proportion of *Microtus*-voles (*M. epiroticus* and *M. agrestis*) in the diet decreased toward the end of the breeding season (Korpimäki 1986), although voles reproduced at this time. This might be due to the fact that Kestrels shifted from hunting over fields to forested areas, because the vegetative cover increased more rapidly on farmlands than in woodlands. Thus, the proportion of fields as a hunting habitat should decrease in the course of the breeding season both in poor and good vole years. (3) Among others, Orians and Wittenberger (1991) have argued that individuals arriving first should occupy the best breeding habitats. Therefore, we expected that the importance of agricultural fields as a hunting habitat should decrease with arrival dates in at least good vole years.

2. Material and methods

Our study was conducted in the Kauhava region, western Finland (63°N, 23°E), during 1989–1991. In this area, Kestrels have bred in nest-boxes since the early 1980s. Most of these boxes, numbering between 300 to 320 in each year, were mainly fastened on the gables of barns in the middle of the agricultural fields, but some boxes were placed in trees. The total number of Kestrel nests in the study area was 40 in 1989, 30 in 1990 and 57 in 1991.

The study area was divided into two categories according to the size of farmland areas. (1) The large farmland area (LFA) consisted of a uniform agricultural area covering ca. 100 km^2. (2) The category of small farmland areas (SFA) consists of many separate fields (size 0.1–10.0 km^2) surrounded by coniferous forests. Main crops in the LFA are oats, barley, hay, and potatoes, but there are also small areas which are totally abandoned or are left lying fallow. In the SFA, the proportion of hay and fallow fields is greater than in the LFA (see Korpimäki 1986, 1987 for further details).

The availability of agricultural fields in the vicinity of each nest was estimated along eight 3 km lines directed towards four cardinal and four half-cardinal points of the compass from the nest using detailed landscape maps (scale 1:20 000). The habitat analyses were done as follows: first, we measured the proportions of agricultural fields along each of the eight 3 km lines, and second, we calculated the mean of this habitat for each nest. We chose 3 km long lines because, according to our field observations, in all study years (1989–91) there were at least some male Kestrels that hunted as far as 2.5 kms away from their nests (Table 1). Mean proportions of agricultural fields in both farmland-size categories are shown in Table 2. Forests and marshland (i.e., open peatland area and pine bog developed from the former by drainage) were used as alternative habitats by the Kestrels.

Habitat utilization of Kestrels was studied by making behavioural observations. Each pair was observed using binoculars and a telescope for six hours during the incubation period, eight hours when nestlings were one to two weeks old, and

Table 1. Hunting distances (metres from the nest) of male Kestrels in the incubation, early nestling and late nestling phases of the breeding season. n = no. of males. After log-transformation, differences were tested with 2-way ANOVA.

	Phase					
	Incubation			Early nestling		
Year	Range	Mean	n	Range	Mean	n
1989	200–750	483	3	275–750	482	7
1990	250–2000	864	7	400–1500	996	7
1991	200–2500	881	13	400–1500	854	12

	Phase Late nestling							
Year	Range	Mean	n	Source of variation	Mean square	df	F	P
1989	500–2000	1030	5	Year (Y)	0.44	2	1.07	0.345
1990	250–1300	814	7	Phase (P)	0.16	2	0.40	0.674
1991	85–2400	813	8	Y*P	0.57	4	1.39	0.248
				Error	0.41	60		

Table 2. Proportion (%) of agricultural field in the vicinity (<3 km) of Kestrel nests during 1989-91 in the large (LFA) and small (SFA) farmland areas. n=number of nests. ANOVA was used for statistical comparisons (proportion arcsin-transformed).

	LFA			SFA		
Year	Mean	S.D.	n	Mean	S.D.	n
1989	81.6	9.5	16	53.4	14.9	7
1990	78.1	11.3	16	43.6	17.4	12
1991	79.2	9.9	22	43.5	15.9	20
Pooled	79.6	10.1	54	45.3	16.2	39

Source of variation	Mean square	df	F	P
Year	0.05	2	1.51	0.226
Size	3.99	1	121.52	0.000
Year*size	0.01	2	0.28	0.759
Error	0.03	87		

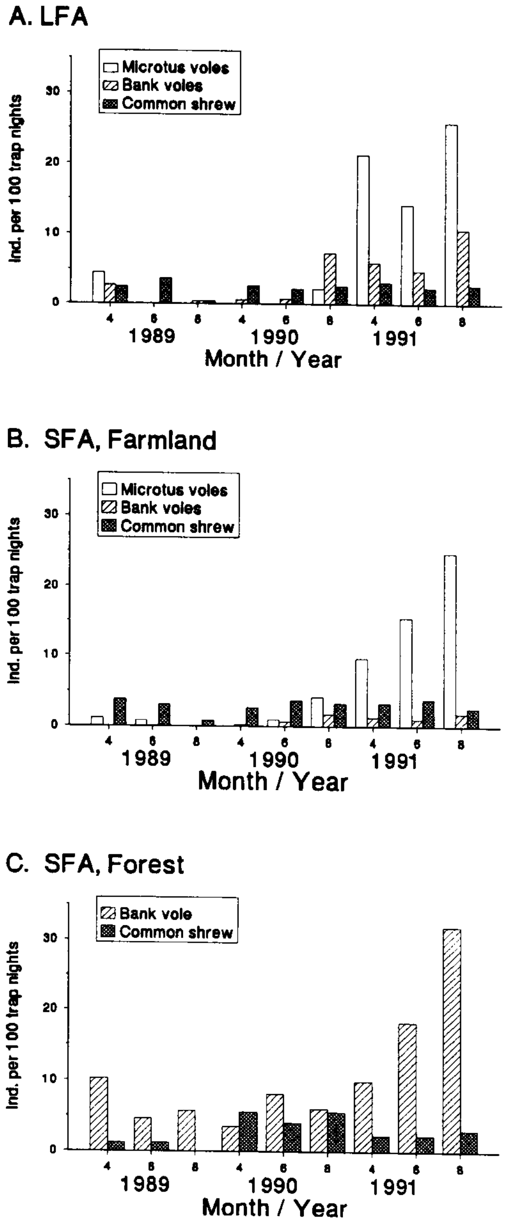

Fig. 1. (a) Density indices (trapped individuals per 100 trap nights) of *Microtus* voles, bank voles and common shrews in the large farmland area from April (4) through June (6) to August (8) in 1989–1991. (b) Density indices of *Microtus* voles, bank voles and common shrews in agricultural fields of the small farmland areas from April to August during 1989–1991. (c) Density indices of bank voles and common shrews in forests of the small farmland areas from April to August during 1989–1991.

again when nestlings were three to four weeks old. The total observation time was 1042 hours (incubation 330, early nestling period 376 and late nestling period 336 hours). We used a focal sampling-method (Altmann 1974) and continuously recorded behavioural observations (Martin and Bateson 1986). We determined the amount of time (in seconds, later converted to percentage values) that males or females hunted over a certain habitat type. The main hunting modes of Kestrels in the study area were flight-hunting and wind-hovering, which Kestrels used more in our study area than in western Europe (Tolonen 1992), whereas perch-hunting was infrequent and was used much less than in western Europe (Tolonen 1992; see also Pettifor 1983, Village 1983, Masman et al. 1988). Perch-hunting was mostly used by females in the nest vicinity during the early nestling period (see also Village 1983).

We collected pellets and prey remains in the vicinity of all nest-boxes after the breeding season. These samples were dissolved in sodium hydroxide (according to Degn 1978), and bones, feathers, parts of insects, and other matter were separated. Small mammal species were determined according to Siivonen (1974) and birds were identified by comparing the humeri or other larger bones with reference material. Methods for identifying insects are described elsewhere (Itämies and Korpimäki 1987). Numbers of small mammals in the samples were estimated by calculating the number of jawbones (see Korpimäki 1985, 1986 for further details on the method).

Vole abundance was estimated by snap-trapping three times per year (April, June and August). We used a "short line method" (see Norrdahl and Korpimäki 1993), which was modified from the small quadrat method of Myllymäki et al. (1971). Six 3 km^2 sample plots (three in SFA and three in LFA) were chosen from the study area. The lines were randomly placed in ditches inside each plot (8 ditches/trapping occasion per plot in 1989 and 1991, and 10 ditches/trapping occasion per plot in 1990). Ten mouse snap traps and one rat snap trap were set 10 m apart for two nights in each ditch. The total number of trap nights per trapping plot was 160 in 1989 and 1991, and 200 in 1990.

3. Results

3.1. Fluctuations in vole abundance

In 1989 (later called a "crash year"), voles were abundant in early spring, but declined steeply to very low numbers by late summer (Fig. 1). In 1990 ("low year"), vole abundances were low in spring, but started to increase from late summer onwards. In 1991 ("increase year"), vole densities were moderate to high in early spring and reached a high peak in autumn 1991. The bank voles seemed to be more common in the agricultural fields of the LFA than in those of the SFA in 1990–91. In forests in the SFA the bank vole numbers were moderate in 1989 and 1990, but they increased rapidly the next year.

3.2. Seasonal and among-year changes in hunting habitats

In 1989, the proportion of agricultural fields used as a hunting habitat by males in the LFA declined sharply during the breeding season and males increased their time spent hunting over forest and marshland (Fig. 2). This habitat shift was associated with a steep crash in vole abundance in the LFA (Fig. 1). In contrast, in the SFAs the proportion of foraging over fields remained relatively constant (Fig. 2), this probably being due to the fact that the vole crash was not as steep as in the LFA (Fig. 1).

The utilization of fields was lowest in 1990 (Fig. 2) when vole numbers were low in agricultural fields (Fig. 1). In 1991, when vole densities increased both on farmlands and in woodlands (Fig. 1), cultivated fields were the most common hunting habitats both in the LFA and SFA (Fig. 2). The use of fields differed significantly between years during the incubation period both in the LFA (Kruskal-Wallis $\chi^2 = 6.56$, $P = 0.038$) and in the SFA ($\chi^2 = 6.76$, $P = 0.034$). Hunting distances (metres from the nest) of male Kestrels in the LFA did not differ between years or phases of the breeding season (Table 1.).

Utilization of agricultural fields by female Kestrels during the late nestling period is shown in Figure 3. In the LFA, females mostly hunted

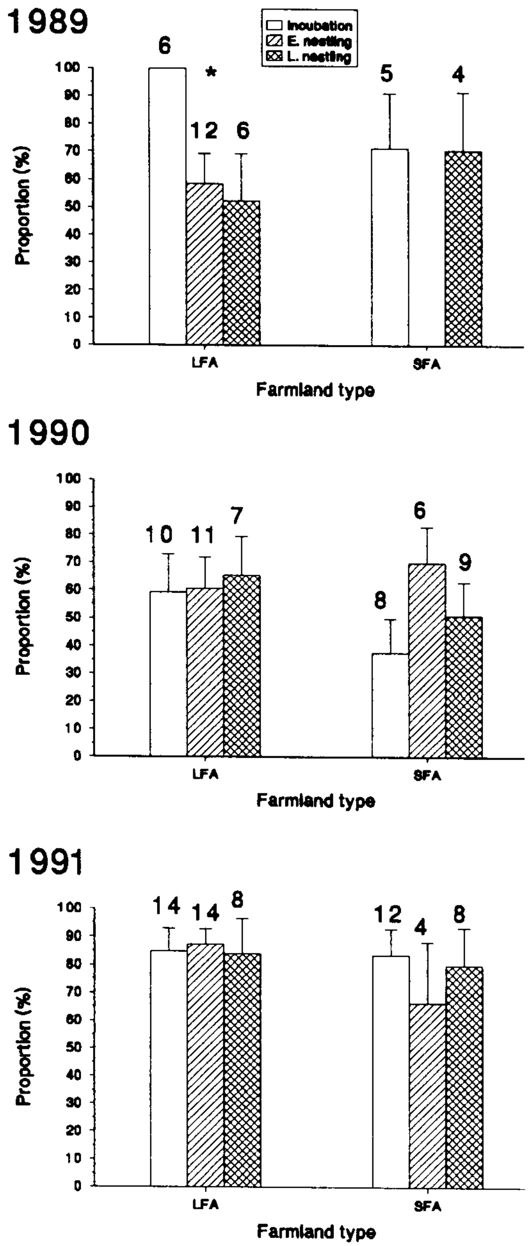

Fig. 2. Mean (+s. e.) proportions of agricultural fields used by male Kestrels for hunting in large (LFA) and small (SFA) farmland areas during 1989–1991. No. of males is presented above the bars. E. and L. nestling = early and late nestling periods. No data were available from early nestling period in SFA in 1989. Kruskal-Wallis test (two-tailed) was used to test differences among periods. * = P < 0.05.

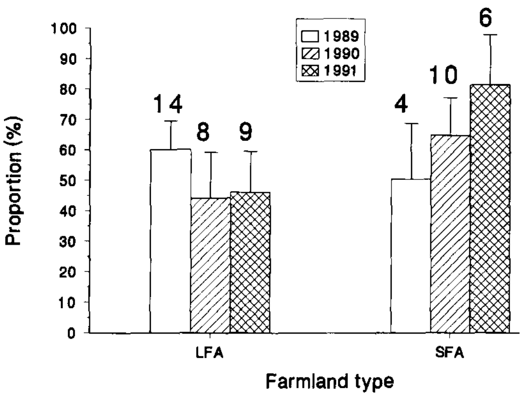

Fig. 3. Mean (+s. e.) proportions of agricultural fields used by female Kestrels for hunting in the large (LFA) and small (SFA) farmland areas during the late nestling period in 1989–1991 (N as in Fig. 2.).

over fields in 1989, though vole numbers were low in June (Fig. 1). In 1990 and 1991, females mostly hunted over forests or marshland, although voles were abundant in agricultural fields in 1991 (Fig. 1). In the SFA, fields were the most common hunting habitat in 1990–91. These results are only partly consistent with the density changes of voles in fields and forests of SFA (Fig. 1). We did not find any significant between-year differences in the habitat utilization of females. When comparing habitat use of males and females during the late nestling period (Fig. 2–3), it seemed that in the LFA in 1991 females used agricultural fields less than males did (Mann-Whitney U-test, $U = 17$, $P = 0.075$). There were no significant intersexual differences in the SFA.

3.3. Utilization and availability of habitats

During the incubation period of 1989, agricultural fields were used significantly more by male Kestrels than what was available in the LFA (Fig. 4). In 1990, males hunted slightly less than expected over fields. In 1991, agricultural fields were used more than their availability indicated in both the LFA and SFA (Fig 4). During the late nestling periods of 1989–90, males in the LFA tended to ignore fields and shifted to hunt over other habitats (marshland or forest, Fig. 5). In 1991, males hunted more than expected over

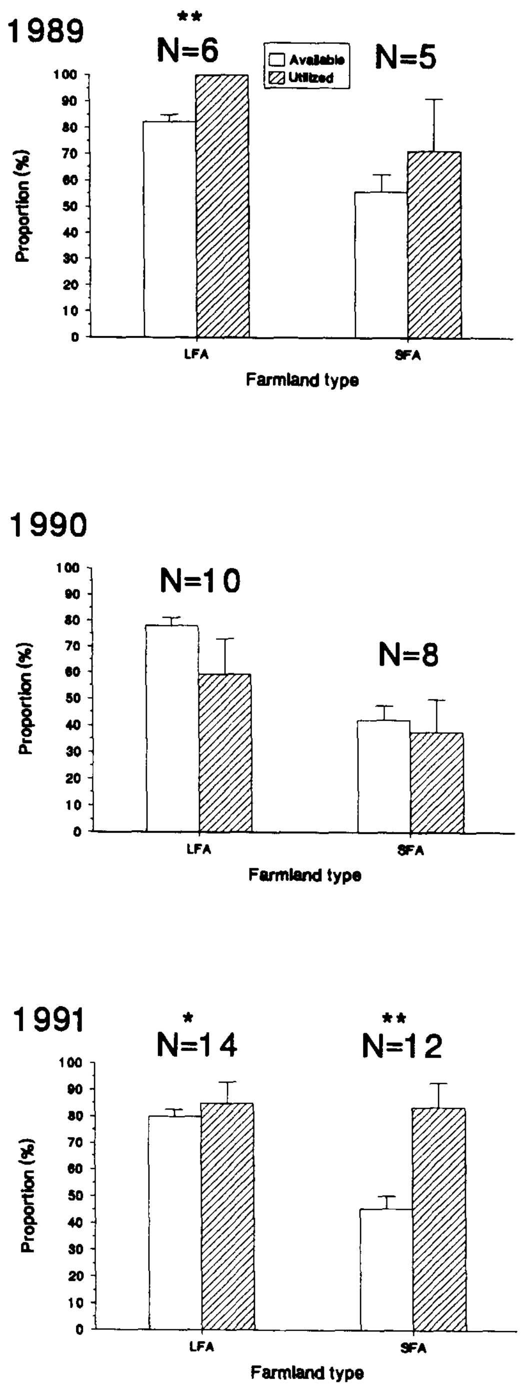

Fig. 4. Availability (means +s. e.), and utilization (means +s. e.) of agricultural fields by male Kestrels during the incubation period in 1989–1991. N = number of males. * = $P < 0.05$, ** = $P < 0.01$.

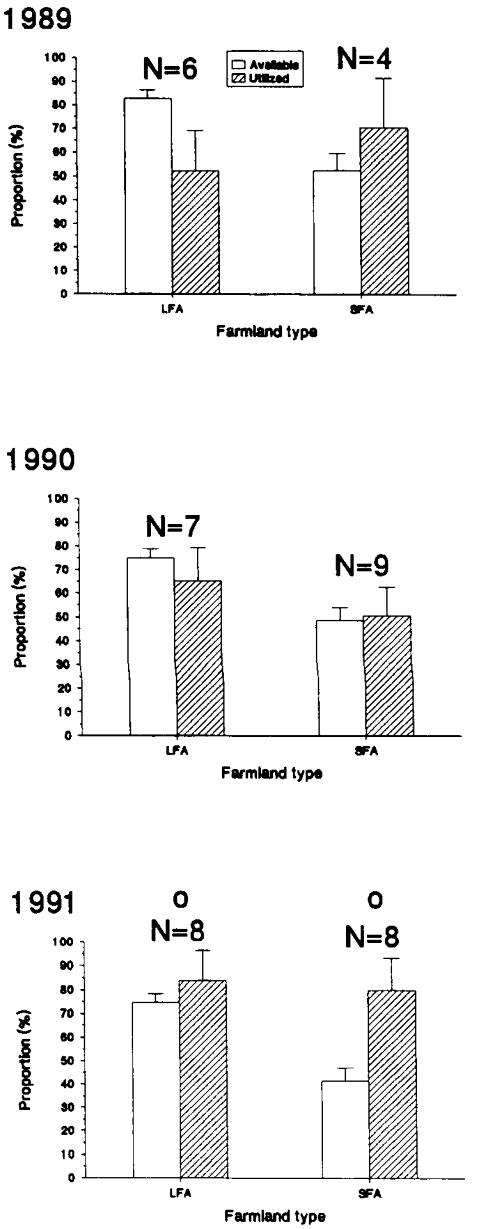

Fig. 5. Availability (means +s. e.), and utilization (means +s. e.) of agricultural fields by male Kestrels during the late nestling period in 1989–1991. N = number of males. o = P < 0.10.

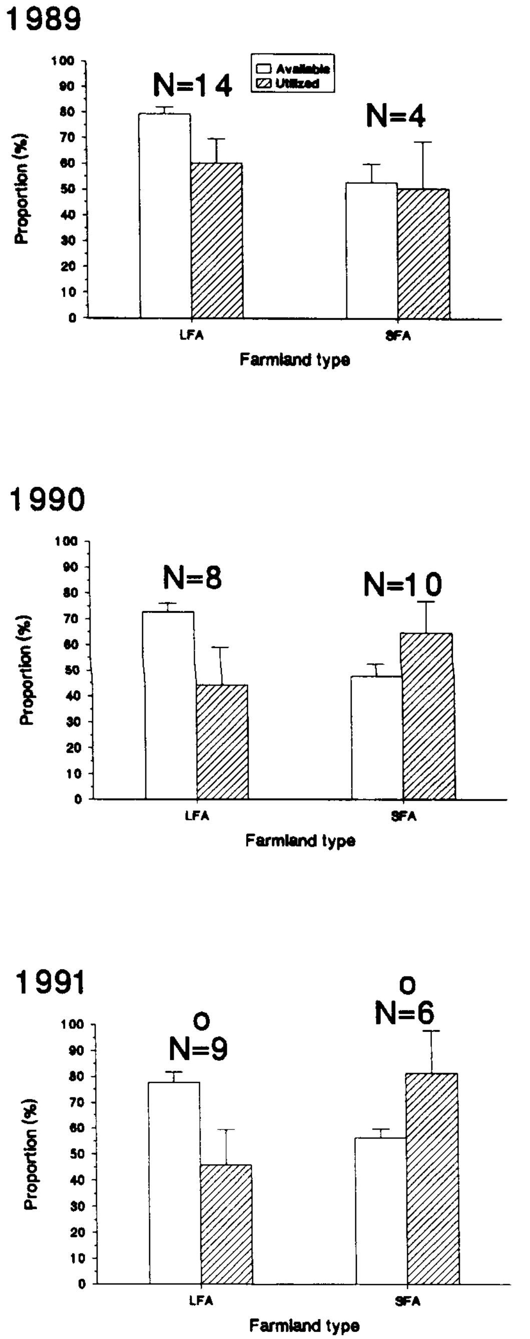

Fig. 6. Availability (means +s. e.), and utilization (means +s. e.) of agricultural fields by female Kestrels during the late nestling period in 1989–1991. N = number of females. o = P < 0.10.

fields in both the LFA and SFA (Fig. 5). In 1989, females seemed to use fields less than their availability allowed (Fig. 6). In 1990–91, females in the LFA avoided fields whereas those in the SFA preferred them (Fig. 6).

3.4. Arrival order and habitat choice

Laying dates are good estimates of the order in which Kestrels arrive and form pairs in our study area (Palokangas et al. 1992). To examine whether there was any relationship between the arrival order of Kestrel pairs and breeding habitat choice, we computed Spearman rank correlations between laying dates and the proportion of agricultural fields in the nest vicinity (Table 3). In the LFA, no significant correlations were found, but in the SFA during 1990–91, early arriving pairs selected territories with plenty of agricultural fields, and in 1991 this relationship was also significant in the pooled data.

Table 3. Spearman rank correlations between the start of egg-laying in Kestrel pairs and the proportion of agricultural field in the vicinity (<3 km) of their nests. LFA = large farmland area, SFA = small farmland areas.

Year	Area	r_s	P	n
1989	LFA	0.27	0.305	16
	SFA	0.14	0.789	6
	Pooled	–0.02	0.925	22
1990	LFA	0.04	0.898	14
	SFA	–0.77	0.003	12
	Pooled	–0.07	0.718	26
1991	LFA	0.15	0.514	21
	SFA	–0.49	0.041	18
	Pooled	–0.41	0.010	39

3.5. Hunting habitat and diet composition

The types of prey taken by the Kestrels in the two farmland areas were determined through pellet analyses. Highly significant among-year and between-field size differences emerged in the occurrence of *Microtus-* voles in the diet of Kestrels. The proportion of *Microtus*-voles of prey weight was highest in the LFA in 1989 and in the SFA in 1991, and lowest in both areas in 1990 (Table 4). In 1990, insects were abundant in the food, but their proportion of prey biomass was only 1% to 10%.

We used Spearman rank correlations to examine the relationships between hunting habitat during the late nestling period and diet composition, which here means the proportion of *Microtus*-voles of prey weight in the diet of a pair. In 1989, a positive correlation was found between the proportion of females hunting over fields and proportion of voles in the diet (Table 5). The pooled data from 1989 to 1991 indicated that there tended to be a positive correlation (though not statistically significant) between males hunting over fields and the proportion of *Microtus*-voles in the diet.

3.6. Reproductive success, diet composition and habitat use

Clutches were largest in 1991 in the LFA, and in 1989 in the SFA (Table 6). The mean number of

Table 4. The percentages of *Microtus*-voles of weight in the diet of Kestrels in the large (LFA) and small (SFA) farmland areas. Analysis of variance (percentages arcsin-transformed) was used for statistical comparisons. n = number of nests.

Year	LFA Mean	SFA S.D.	n	Mean	S.D.	n
1989	61.2	13.8	15	35.6	11.5	6
1990	24.6	17.4	16	24.4	14.7	12
1991	51.1	15.5	14	54.0	17.4	15

Source variation	Mean square	df	F	P
Size	0.14	1	4.27	0.043
Year	0.77	2	23.76	0.000
Size*Year	0.17	2	5.27	0.007
Error	0.03	72		

fledglings was generally lower in the LFA than in the SFA. Production of fledglings was highest during 1990–91 in the LFA and in 1991 in the SFA. Clutch size was affected by the study year (phase of the vole cycle) and by the interaction between year and size of the farmland area. The study year affected fledgling production, but there was no interaction between the year and size of the farmland area.

There was a negative correlation between the mean number of fledglings and the proportion of *Microtus*-voles by weight in the diet in the LFA in 1989–1990 (Table 7). The same trend was seen again in the pooled data from the LFA. In the SFA, no significant correlation was detected between these two variables.

Table 5. Spearman rank correlations between the proportion of field used in hunting during the late nestling period and the proportion of *Microtus*-voles of prey weight in the diet of Kestrels. Pooled data from large and small farmland areas.

Year	r_s	P	n
Males			
1989	0.25	0.483	10
1990	0.09	0.732	16
1991	–0.07	0.828	13
Pooled	0.23	0.159	39
Females			
1989	0.64	0.006	17
1990	–0.26	0.292	18
1991	0.03	0.945	10
Pooled	0.16	0.308	45

4. Discussion

4.1. Among-year and within-season changes in hunting habitats

Our main finding was that the use of the main hunting habitat — agricultural field — varied among years and within the breeding season. These changes occurred in both the LFA and SFA, and in both males and females.

The most distinctive hunting habitat shift took place in 1990, when Kestrels spent less time

Table 6. Mean clutch size and number of fledglings in large (LFA) and small (SFA) farmland areas (n = number of nests). Between farmland-size categories and among-year differences were tested with 2-way ANOVA.

	1989			1990			1991		
	Mean	S.D.	n	Mean	S.D.	n	Mean	S.D	n
Clutch size									
LFA	5.7	1.0	16	4.9	0.6	15	5.9	0.7	21
SFA	5.8	0.4	6	5.3	0.8	11	5.1	0.8	18
Pooled	5.7	0.8	22	5.0	0.7	26	5.5	0.9	39
Number of fledglings									
LFA	2.1	1.7	16	3.4	1.6	16	3.5	1.6	22
SFA	2.9	2.7	7	3.8	1.3	12	3.9	1.7	20
Pooled	2.3	2.0	23	3.5	1.5	28	3.7	1.6	42

Source of variation	Mean square	df	F	P
Clutch size:				
Size	0.12	1	0.20	0.654
Year	2.72	2	4.61	0.013
Size*Year	3.13	2	5.31	0.007
Error	0.59	81		
No. of fledglings:				
Size	5.52	1	1.90	0.172
Year	10.85	2	3.73	0.028
Size*Year	0.31	2	0.11	0.898
Error	2.91	87		

hunting in agricultural fields, and forests and marshland were preferred. This was obviously due to the poor vole situation on the farmlands (see Fig. 1), and thus supported our first prediction that agricultural fields should be used more for hunting in good vole years than in poor ones.

We detected that the proportion of fields as hunting habitat declined during the breeding season only in the crash year 1989, though the vegetation layer developed similarly during each of the three years of the study. This was inconsistent with the second prediction that the use of fields as hunting habitat should decrease in the course of the breeding season both in poor and good vole years. Thus, Kestrels hunted over agricultural fields whenever there were voles, and the thickness of vegetation cover did not apparently affect habitat use. Therefore, our data on Kestrels appear inconsistent with the idea that areas of dense and high vegetation cover are avoided by hunting raptors, even if there are high prey densities (e.g. Southern and Lowe 1968, Wakeley 1978, Pettifor 1983). However, we have some observations of Kestrels hunting over recently harvested hay fields. These fields are easy for the birds to survey because plant cover is low, and there might also be animals which were injured by harvest machines. This indicates that falcons willingly hunt over patches of low vegetation cover, but they do not necessarily change their main habitat (cultivated field).

Alternatively, changes in habitat use could also reflect energetic demands during years of vole scarcity. It is possible that Kestrels spent more time involved in perch-hunting when voles were scarce, because this is energetically less demanding (Village 1983, Masman et al. 1988). However, in our study area male Kestrels perch-hunted most in the increase year 1991 and flight-hunted most in the crash year 1989 and the low year 1990 (Tolonen, unpublished data).

Table 7. Spearman rank correlations between the mean number of fledglings and the proportion of *Microtus*-voles of prey weight in the diet of Kestrels. LFA = large farmland area, SFA = small farmland areas.

Year		r_s	P	n
1989	LFA	–0.52	0.045	15
	SFA	–0.09	0.868	6
1990	LFA	–0.52	0.038	16
	SFA	–0.25	0.429	12
1991	LFA	0.42	0.135	14
	SFA	0.08	0.764	15
Pooled	LFA	–0.29	0.051	45
	SFA	–0.10	0.593	33

4.2. Arrival times and habitat selection

Our results showed that the earlier in the spring a bird arrives, the greater is the proportion of agricultural fields in the vicinity of the nest it selects, especially in a good vole year (1991). This result was consistent with our third prediction that the importance of agricultural fields as a hunting habitat should decrease with later arrival, particularly in good vole years. Late arriving falcons had to occupy poor habitats with low food supply, because the better habitats were already occupied. This apparently leads to poorer breeding success, as clutch size declines with laying date (e.g. Dijkstra et al. 1982, Palokangas et al. 1992, this study). On the other hand, superior competitors might already have monopolized the richer resource patches. This means that these patches were exploited by fewer individuals than expected, and the occupants thus had higher intake rates than those in poorer patches (see Fretwell and Lucas 1969, Kacelnik et al. 1992).

According to the life-history theory (e.g. Stearns 1992), Kestrels should prefer environments in which their reproductive success is good and survival costs are low. In our study population, the turnover of Kestrel males was 75% and that of females 92% during 1985–1992 (Korpimäki 1988 and unpubl.), which means that most falcons are not faithful to their previous breeding territories. Therefore, when males and females arrive at the study area in spring, most of them do not have any previous experience of the local food conditions. Within a few days of arrival, the birds must decide where to establish territories. This decision, in turn, determines which patches are available for exploitation during the subsequent breeding season.

Viitala et al. (1995) have recently demonstrated in laboratory and field experiments that

Kestrels can see the scent marks of voles that are visible in ultraviolet light. Therefore, when Kestrels are flying over an area, they may easily see patches that include many voles and choose their nest-sites close to these patches. This may explain why Kestrels are able to quickly find local vole patches without prior knowledge of the area.

4.3. Hunting habitat, diet composition and reproductive success

We did not detect direct relationships between the habitats which Kestrels hunted over and their reproductive success, although some trends emerged. Our results suggest that agricultural fields are important, because the main prey of Kestrels (*Microtus*-voles) live there (Korpimäki 1985, 1986). The importance of *Microtus*-voles is further stressed in that Kestrel breeding densities are much higher and reproductive success is better in good vole years than in poor ones (Korpimäki 1984, 1986, Korpimäki and Norrdahl 1991). Also, farmlands include large numbers of birds (especially young ones) that are potentially easier to catch than forest birds, because of the scarcity of refuges. Birds serve as an important alternative prey when the availability of voles is poor. However, forests and marshland are important as alternative hunting habitats, and they are frequently used when voles are scarce on farmlands. Small farmland birds that arrive at the breeding grounds later than Kestrels, and are potential prey species of falcons, also try to avoid settling close to the Kestrel nests, probably because of the high predation risk (Suhonen et al. 1994).

Prey remains found in the nests mostly accumulated during the late nestling period (Korpimäki 1985). Thus, our analysis of the diet composition probably reflected the hunting habitats used at that time. We conclude that in good vole years agricultural fields are a source of *Microtus*-voles, but in poor years they are probably a source of small birds (especially nestlings) and bank voles that dispersed from nearby forests (see e.g. Hansson 1979, Norrdahl and Korpimäki 1993).

4.4. Breeding success in a spatially and temporally varying environment

Habitats should be considered in terms of their spatial and temporal variability (Southwood 1977). The temporal variability includes two important characteristics: the length and predictability of the favourable period for breeding and the length and predictability of the unfavourable period. Spatially, habitats are outlined by the sizes of favourable and unfavourable patches. The level of resources in a habitat is affected by these traits.

In our study area, the proportion of cultivated fields is much greater in the LFA than in SFA. We consider that in good vole years there are more favourable patches (agricultural fields with *Microtus* voles) in the LFA than elsewhere. But, in poor vole years, the situation tends to reverse: the number of patches with alternative prey is probably higher in the SFA than in LFA, and the length of the unfavourable period is thus shorter there. Therefore, small farmland areas are more stable environments for Kestrels, because, even in poor vole years, there are productive patches closer to the nest than there are in large farmland areas. Kestrels breeding in the SFA seemed to have better overall reproductive success than those breeding in the LFA. This was probably due to better hunting habitats, because the SFA was not so efficiently cultivated as the LFA.

Kestrel populations have declined during the last three decades in Fennoscandia, especially in southern Finland (Kuusela 1983, Saurola 1985, Koskimies 1989) and in southern Sweden (Jessen 1981, Wallin et al. 1983). This decrease might be associated with changes in farming methods. In southern Finland, for example, open ditches have been replaced by subsurface drains, and this reduces suitable habitats for voles. On the other hand, fields in southern Finland are used to produce wheat, barley and sugar beets and this, in turn, means that the proportion of hay and fallow fields favoured by voles is low. All this suggests that further information is badly needed to find out the importance of these habitat changes in the decline of Kestrels. We need data on hunting behaviour of Kestrels breeding in intensively cultivated field areas to detect whether they have to work harder than conspecifics in our study area. Studies made in western Europe show that uncultivated and grassland areas are of great importance to hunting Kestrels (Shrubb 1980, Pettifor 1984).

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Selostus: Tuulihaukan saalistushabitaatin, ravinnon ja pesimistuloksen väliset yhteydet ajallisesti ja alueellisesti vaihtelevassa ympäristössä

Tutkimme tuulihaukkojen saalistushabitaatin valintaa Etelä-Pohjanmaalla vuosina 1989-91. Tuolla alueella lajin ravinto koostuu pääasiassa pelloilla elävistä peltomyyrän suvun myyristä (idänkenttämyyrä, *Microtus epiroticus* ja peltomyyrä, *Microtus agrestis*). Länsi-Suomessa myyräkannat vaihtelevat syklisesti noin kolmen vuoden jaksoissa. Tutkimuksen aikana myyräkannat romahtivat keväällä 1989, olivat pienimmillään 1990 ja kääntyivät voimakkaaseen nousuun 1991.

Tutkimusalue jakautui isojen ja pienten peltojen alueeseen. Isojen peltojen alue koostui Lapuan - Kauhavan Alajoesta, joka on yhtenäinen peltolakeus pinta-alaltaan noin 47 km^2. Pienten peltojen alue muodostui useasta, pinta-alaltaan korkeintaan muutaman neliökilometrin suuruisesta peltoalueesta.

Tuulihaukat saalistivat kolmella habitaatilla: pelloilla, metsissä ja soilla. Tässä tutkimuksessa tarkastelemme tärkeimmän saalistushabitaatin, pellon, osuuden vaihtelua sekä pesintäkauden aikana että vuosien välillä. Myyräkantojen romahdus- ja nousuvuosina haukat saalistivat eniten pelloilla, mutta pohjavuonna 1990 metsien ja soiden osuus saalistusmaastona oli korkea. Pesimäkauden sisäistä vaihtelua saalistushabitaattien osuuksissa ilmeni vain romahdusvuonna 1989, jolloin haukat saalistivat keväällä pelloilla, mutta myyrien kadottua siirtyivät saalistamaan metsien ja soiden ylle.

Etenkin huonona myyrävuonna 1990 haukat käyttivät paljon ravinnokseen päästäisiä ja hyönteisiä (lähinnä kovakuoriaisia).

Pesyekoko vaihteli merkitsevästi vuosien välillä mutta peltoalueen koolla ei ollut vaikutusta. Poikuekoko näytti olevan suurempi pienillä kuin isoilla pelloilla ja sekin vaihteli merkitsevästi vuosien välillä. Poikastuotto oli huonoin myyräkantojen romahdusvuonna 1989 ja paras myyräkantojen nousuvuonna 1991.

Pienet ja väljästi viljellyt peltoalueet saattavat olla tuulihaukoille vakaampi ympäristö kuin tehokkaasti viljellyt isot peltoalueet. Pienet peltoalueet tarjoavat paljon sopivia elinympäristöjä tuulihaukkojen korvaaville ravintokohteille (metsämyyrät, päästäiset, linnut). Siten huonoinakin myyrävuosina pienillä pelloilla on enemmän tuulihaukoille suotuisia ravintolaikkuja lähempänä pesää kuin laajoilla peltolakeuksilla.

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