Diet variation, hunting habitat and reproductive output of the Kestrel *Falco tinnunculus* in the light of the optimal diet theory

Erkki Korpimäki

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Field data were collected in western Finland on the diet, hunting habitats and breeding of the Kestrel *Falco tinnunculus*, and on the density of its main prey. These records were used to study the variation in the diet and the extent to which it fulfilled three qualitative predictions of the optimal diet theory (ODT). The relationship between diet and reproductive output was also examined.

The annual densities of the preferred prey (*Microtus* voles) correlated positively with its proportion in the diet and with reproductive output. As predicted by ODT, only the abundance of the preferred prey was important in determining the diet composition. The observations and predictions were in agreement as regards the annual variation in the diet; the diet expanded with decreasing abundance of *Microtus* spp. This widening was not caused by changes in the hunting habitats.

Diet width did not decrease with the increasing density of voles during the breeding season. This was inconsistent with ODT and was probably due to the increasing density of the vegetation cover, which may reduce the availability of the voles to the raptors. In disagreement with ODT but in agreement with most field studies, the Kestrels gradually changed their diet as the abundance of *Microtus* spp. decreased.

The reasons for the relatively high success of ODT in predicting the variation in the diet may be: (1) the low number of available prey types and the uniformity of their nutrient contents, (2) a low degree of satiation during the rearing of the young, (3) sequential encounter of prey and (4) low vulnerability to predation of hunting Kestrels. Since the changes in the diet are gradual, a convex fitness set seems to be applicable, which explains why Kestrels are inefficient as predators of birds and insects.

Erkki Korpimäki, kp. 4, SF-62200 Kauhava, Finland

Introduction

The Kestrel *Falco tinnunculus* is adapted both morphologically (relatively broad wing span and fairly long tail) and behaviourally (wind hovering) to catching small mammals. The importance of voles in its diet has been shown by several investigators in Central and West Europe (e.g. Tinbergen 1940, Cavé 1968, Village 1982), where microtine populations do not show pronounced annual fluctuations (e.g. Hansson & Henttonen 1985). The most frequent alternative prey types are shrews (Village 1982), mice (Fairley & MacLean 1965), birds (Yalden 1980), insects (Yalden & Warburton 1979) and earthworms (Village 1982). In contrast, the food of this species has only rarely been studied in North Europe, where vole cycles are pronounced (but see Korpimäki 1985a).

The idea that foraging behaviour should be optimized by natural selection has produced many theoretical studies (e.g. Emlen 1966, MacArthur & Pianka 1966, Schoener 1971, Charnov 1976, Stenseth & Hansson 1979), but as remarked by Krebs (1978), the predictions have seldom been tested against field data. Most field studies have been carried out with herbivorous or insectivorous animals (see Krebs et al. 1983) and the optimal foraging of avian and mammalian predators has only rarely been examined (but see e.g. Erlinge 1981). The aim of the present paper is to study the variation in the diet of the Kestrel in the light of the following qualitative predictions of the optimal diet theory, which is a category of the general optimal foraging theory (for a review, see e.g. Pyke et al. 1977, Pyke 1984): (1) Only the absolute abundance of the preferred prey is important for the optimal diet; the relative abundances of the non-preferred prey types are unimportant (see also Pulliam 1974). (2) The diet of the predator should expand when the abundance of the preferred prey decreases (see also Emlen 1966, Schoener 1971). (3) At fixed food densities, a prey type is either included in the diet or completely excluded — predators should never exhibit "partial preferences".

Since it is important to know whether variation in the diet reflects changes in prey choice or habitat use (Krebs et al. 1983), data on the hunting habitats of the species are also presented. Finally, the relationship between diet and reproductive output is investigated. This is an important subject which has frequently been discussed in theory (e.g. Pianka 1976), but rarely studied in the field (but see Erlinge 1981).

Material and methods

Study area. The study area was about 63 km^2 of level cultivated fields at Alajoki, western Finland (63°05'N, 22°55'E), broken only by small islands of trees and bushes, large ditches and two rivers. Mainly oats, barley and hay were cultivated (for details, see Korpimäki 1984). Kestrels most often arrived in the area at the beginning of April and left in September (Korpimäki unpubl.). They bred in open twig nests or in nest-boxes (Korpimäki 1983).

Diet. Between 1977 and 1983, prey remains and pellets were collected during the breeding season (from 1 May to 31 July) at 72 nest sites. After drying, the food samples were carefully examined and all bones, feathers, scales and parts of insects were separated. Mammals were identified by diagnostic features according to Siivonen (1974) and the numbers of individuals were estimated by counting the mandibles. Most birds were identified by comparing the humeri with reference material from museum collections. Details of the methods for determining insects are given elsewhere (Itämies & Korpimäki 1986). The total number of identified prey items was 2118 (for additional details of the collecting methods and determination of prey species, see Korpimäki 1985a).

Pellets collected near the nests provided information on the food brought to the females and young by the male. This tended to be larger items (Korpimäki unpubl.), because the males did not carry small prey animals long distances. In the breeding season male Kestrels frequently ate the head of larger prey items. Since they often dropped their pellets some distance from the nest, these prey animals were not found, when food samples were collected. Studies of captive birds (e.g. Yalden & Yalden 1985) have shown that the pellets of the Kestrel may contain identifiable remains of only about 60 % of the ingested prey. For small animals, such as shrews and insects, the bias could be even larger, so that they would be underestimated in the recorded diet. Since these sources of error acted in the same way during the whole study period, however, they did not influence comparison of food between years or within seasons.

Availability of small mammals. Small mammals were snap-trapped in May and early June (spring catches) and in late August and early September (autumn catches), in four sample plots (in cultivated field, abandoned field, pine forest and spruce forest) each year (a total of 10844 trap nights). In each plot, 50–60 traps were set in small mammal runs at intervals of 10 m for 3–4 days and were checked once a day (see Korpimäki 1981, 1984, 1986 for further details).

Snap-traps may catch various small mammal species with different probability. For example, pitfall traps are more effective than snap-traps for collecting shrews (e.g. Pankakoski 1979). Although the Finnish snap-trap of galvanized metal is a relatively efficient model (Henttonen 1985), it is slightly too robust for the smaller species of shrews (e.g. for the Lesser Shrew *Sorex minutus* L.). However, Korpimäki (1981) showed that the trappability of the Common Shrew *Sorex araneus* with snap-traps was as high as that of *Microtus* voles (the Common Vole *M. epiroticus* and Field Vole *M. agrestis*) and Bank Vole *Clethrionomys glareolus*. Since in the present study area the Common Shrew made up 80 % of all shrews in pitfall trappings also (Korpimäki & Norrdahl unpubl.) and 96 % of all shrews in the diet of the Kestrel (Korpimäki 1985a), my snap-trapping data can be considered to illustrate the annual population fluctuations of the different small mammals.

Hunting habitats. Data on the foraging habitats of the Kestrels in Alajoki were collected by following hunting individuals with binoculars or telescopes and recording only the habitats where they were first seen to hunt. Thus, the observations were independent of each other. Five habitat categories were separated and their proportions at Alajoki were calculated from landscape maps (scale 1:20 000) and personal records.

The recorded frequency of hunting Kestrels in different habitats may have been affected by variation in my efforts to watch the birds; I observed hunting falcons when searching for nests of birds of prey and collecting breeding and food data. However, as the same methods were used during the whole study period (see Korpimäki 1984), the data can be used to compare the choice of hunting habitats between years.

Breeding performance was measured by the number of breeding pairs, mean clutch size and mean production of young per pair (for details of the methods, see Korpimäki 1984).

Results

Annual variation in diet. The annual percentage of *Microtus* voles (the most important prey group) in the diet correlated positively with their relative abundance in the traps (Fig. 1), but significant correlations were not observed for Bank Vole ($r = 0.25$) or shrews ($r = 0.19$). The diet width correlated negatively with the spring-trap index of *Microtus* spp. (Fig. 2). Details of the diet composition were given in earlier papers (Korpimäki 1985a, Itämies & Korpimäki 1986).

Seasonal changes in diet. The diet width indices for three periods in the breeding season were: 3.26 for 1 May–15 June, 4.46 for 16–30 June and 4.90 for 1–31 July (data from Korpimäki 1985a: Table 4). Thus, during the first period, the diet was more restricted than later in the season, *Microtus* spp. being the most important prey (for further details, see Korpimäki 1985a).

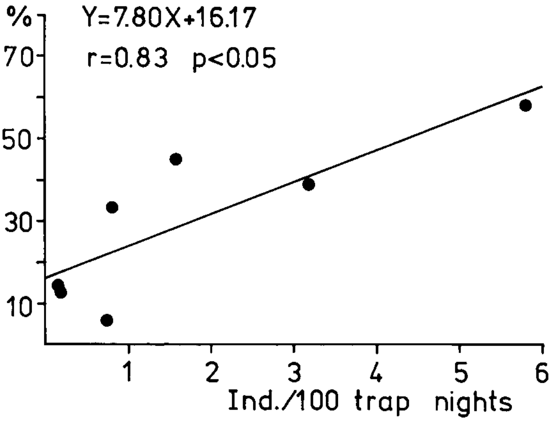

Fig. 1. Correlation between the proportions (%) of the *Microtus* voles in the diet of Kestrels and their relative densities (ind./100 trap nights in spring catches) in the field in 1977–83.

Hunting habitats. The use of the habitats by hunting Kestrels did not differ significantly from the proportions of the habitats in the area (χ^2-test, Table 2), although during the whole study period, the birds tended to hunt more in fields and less in forests than might be expected from the availability of these habitats. There was no significant variation in the use of hunting habitats between consecutive years (χ^2-tests), but Kestrels spent less time hunting in cultivated fields in years when the estimated Common Vole densities were low (Fig. 3). In addition, in those years the width of the hunting habitats seemed to be greater, but the correlation was only indicative ($r = -0.72$, $P < 0.10$).

Diet and reproductive output. The numbers of breeding pairs and average clutch sizes of Kestrels correlated positively with the percentages of *Microtus* spp. in the diet in 1977–83 (Fig. 4). However, there was a gap in the vole index values, and the data were not only consistent with a linear model, but also with a model having a threshold effect on breeding at vole index values of 20–30 %. Further, there was a non-significant positive correlation between the mean numbers of young produced and the proportion of *Microtus* voles in the diet ($r = 0.64$, $0.10 < P < 0.20$). The latter correlation was probably impaired by the irregular variation in the numbers of totally destroyed nests (the main nest robbers being man and the Pine Marten *Martes martes,* Korpimäki 1984). In addition, the mean clutch size correlated positively with the percentage of Bank Voles in the diet ($r = 0.87$, $P < 0.05$), but such relationships were not observed for other small mammal species. There were significant negative correlations between the annual average clutch size and the proportions of birds and insects in the diet (birds: $r = -0.81$, $P < 0.05$, insects: $r = -0.86$, $P < 0.05$; see also Itämies & Korpimäki 1986 for further details regarding insects as alternative prey of Kestrels).

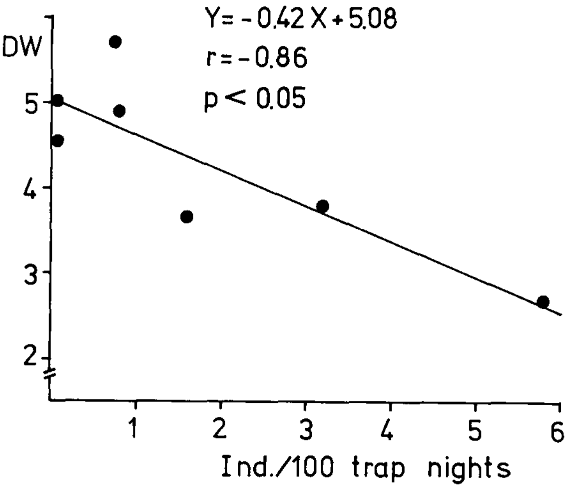

Fig. 2. Diet width (DW) of the Kestrel in relation to estimated *Microtus* vole densities (ind./100 trap nights in spring catches) in 1977–83. The diet width indices were calculated as in Table 1.

Discussion

Annual differences in diet. Energy-maximizing models of the optimal diet theory yield three predictions about diet (see Introduction):

(1) Some investigators claim that prediction 1 is not the general case (Emlen 1966, Rapport 1971, Estabrook & Dunham 1976, Stenseth 1981 among others). Their models predict that the relative densities of non-preferred prey types can also have an effect on the diet, when these food types become relatively more abundant.

At Alajoki the preferred prey of Kestrels was *Microtus* voles, their proportion being twice as great in the diet as in the snap-trapping data (Korpimäki 1985b). In this study I found a positive relation between the snap-trap indices of *Microtus* spp. and their proportions in the diet (Fig. 1), but no correlations for the other small mammals (Bank Vole and

Table 1. Percentages of observations of hunting Kestrels in different habitats at Alajoki in 1977–83 and proportions of habitats in the study area. Habitat width indices calculated as in Table 1.

Habitats	Years							Annual mean	Habitat area as % of study area
	1977	1978	1979	1980	1981	1982	1983		
Cultivated field	85	83	76	69	59	79	71	77	72
Abandoned field	4	4	6	9	15	9	10	7	4
Forest	4	5	9	13	10	6	8	7	18
Marshland	4	7	5	5	8	3	5	5	5
Inhabited area	3	1	4	4	8	3	6	4	2
No. of observations	190	102	79	78	39	148	159	795	
Habitat width	1.37	1.42	1.69	1.97	2.54	1.57	1.89	1.64	

shrews). These results were in agreement with prediction 1, and contrary to the predictions of the other models (e.g. Emlen 1966). Most earlier studies on predatory vertebrates (see Pyke et al. 1977, Krebs 1978) and invertebrates (Charnov 1976) have supported prediction 1 (the Stoat *Mustela erminea* excluded, Erlinge 1981). It is probably more suitable for variation in the diet of predators (see also Pyke 1984), while the other models may better explain the diet of herbivores (Stenseth & Hansson 1979, Stenseth 1981). The difference may be due to the fact that herbivores have much more abundant food supplies (Hairston et al. 1960) with more varied nutrient contents than carnivores. Nutrients affect growth and/or maintenance (see Pyke 1984) and herbivores must take this into account in their food selection. In contrast, the different prey items of carnivores are fairly similar in nutritional value (Ellis et al. 1976) and appear to differ only in their size. Thus, the order of preference in predator diets can correspond to the order of size (e.g. Schoener 1971, Pyke et al. 1977) and/or to the order of vulnerability. This applies in particular to Kestrels living in an area with pronounced between-year fluctuations of microtines and with a low number of alternative prey animals in comparison with the relatively stable food conditions in Central and West Europe.

(2) The present results were in agreement with prediction 2, as the diet width was greatest at the lowest density of *Microtus* spp., the preferred prey (Fig. 2). The success of this prediction in the field does not seem to have been high in other studies (Krebs et al. 1983), and some workers have suggested that this may be due to factors like predation risk, which in the wild may constrain prey selection (e.g. Sih 1980, Gardner 1981). However, this cannot have affected the prey choice of male Kestrels in the breeding season; being swift and skilful fliers, they run little risk of being taken by predators when hunting.

(3) The present results were inconsistent with prediction 3, since the Kestrels showed gradual changes in their diets; when the abundance of *Microtus* spp. decreased, they first shifted to catching more Bank Voles, shrews and Water Voles *Arvicola terrestris,* and then to birds, insects, frogs and lizards (Table 1, see also Korpimäki 1985b). Krebs et al. (1974, 1977) also failed to obtain experimental evidence for prediction 3 (see also Pulliam 1975, Rapport & Turner 1977); rather, they found a gradual change in diet, which is predicted in some models (e.g. Hughes 1979, Stenseth & Hansson 1979). Further, in his recent review of optimal foraging theory, Pyke (1984) concluded that animals in the field regularly show gradual (e.g. partial diet preferences) rather than all-or-none responses. It seems that this should more often be taken into account in the development of foraging theory, especially, in predicting the foraging behaviour of avian predators. At least in northern conditions, with fluctuating food production, birds of prey are dependent on a small number of prey species in the breeding season and are likely to show partial preferences.

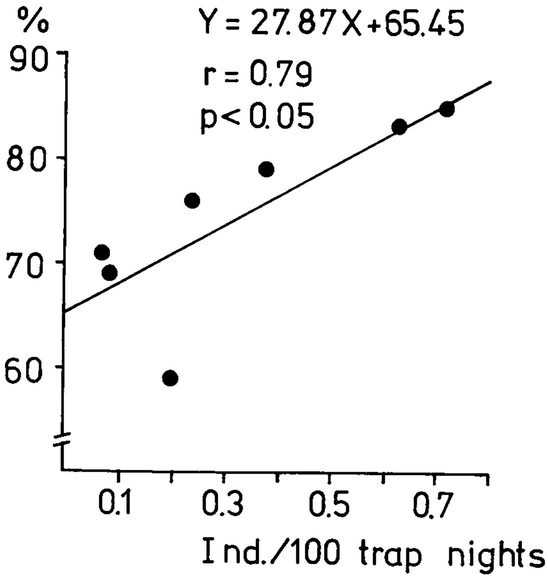

Fig. 3. The proportions (%) of observations of hunting Kestrels in cultivated fields in relation to estimated Common Vole densities in the fields (ind./100 trap nights in spring catches) in 1977–83.

The observed gradual dietary shift cannot have been caused to any great extent by changes in the hunting habitat utilization, since there were no significant annual differences in the proportions of the various hunting habitats (Table 2) like those noted in the diet composition (Table 1). Thus, the year-to-year variation in the diet largely reflected changes in the available prey and also in prey choice, since Korpimäki (1985b) showed that the choice value of the Common Vole, the preferred *Microtus* sp., was negatively related to its snap-trap index. This accorded with the prediction of the foraging theory in the sense that a decrease in overall prey density should not affect the range of habitat utilization as much as the range of prey types selected (MacArthur & Pianka 1966).

Seasonal variation in diet. The optimal diet theory predicts that a predator should widen its food niche, when the preferred prey types become scarce (prediction 2). A widening of the diet with decrease in preferred prey was observed between years, but not between months in the same year (from May to July). On the contrary, the diet width increased as the number of voles in the field increased due to reproduction (Korpimäki 1981, 1984, Korpimäki & Norrdahl unpubl.). In the following I discuss possible

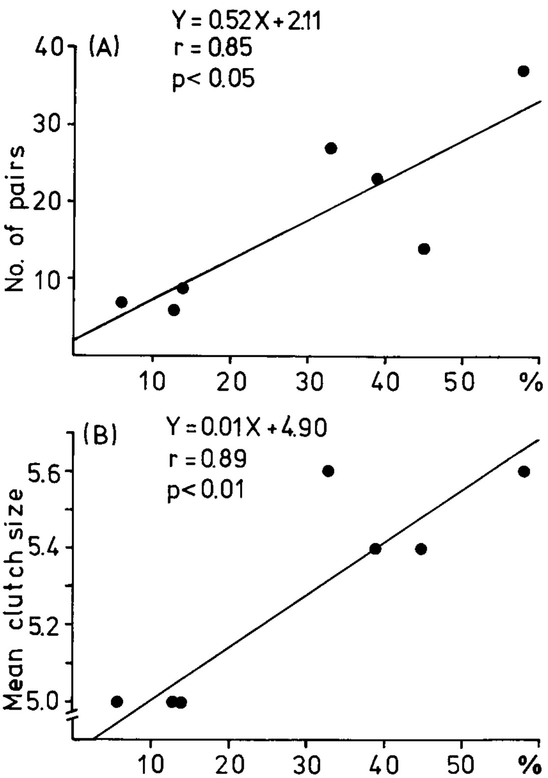

Fig. 4. The correlations of (A) the numbers of breeding Kestrel pairs and (B) their mean clutch sizes with proportions (%) of *Microtus* voles in the Kestrel's diet at Alajoki in 1977–83.

reasons for this disagreement between observation and theory.

During the breeding period the environment in the study area changed markedly (for details of the seasonal variation of the vegetation and snow cover in the study area, see Korpimäki 1985a). The denser vegetation cover in the middle of summer may have decreased the rate at which voles were encountered, thus reducing their vulnerability to attack by the Kestrel (as for Tengmalm's Owl *Aegolius funereus*, Korpimäki 1981). Sparrowe (1972) showed experimentally that the number of successful hunting attempts of the American Kestrel *Falco sparverius* decreased with increasing density of vegetation. Thus both prey abundance and availability (or vulnerability) could be important in studying the diets of predators in the field, since they utilize relatively scarce food resources compared, for example, with herbivores. Krebs et al. (1983) concluded that the difficulty of measuring availability of prey could be a reason for the relatively low success of some predictions of the foraging theory in the field. This difficulty is also encountered in studying Kestrels.

The increase in diet width during the breeding period could also have been caused by the increased energy requirements of the nestlings (for the growth curves of the young at Alajoki, see Korpimäki et al. 1979). Schoener (1971) suggested that an increase in energy requirements has the same effect on selectivity as a decrease in food density (i.e. dietary expansion). The greater availability of alternative prey (e.g. fledglings, young Water Voles and insects) might also promote a widening of the diet, since the number of young birds in the food was higher in July than it was in May and June (Korpimäki 1985b).

Diet and reproductive output. The Kestrels showed only small annual variation in mean clutch size (Fig. 4 and Table 3), compared with other small mammal-eating birds of prey (the Long-eared Owl *Asio otus* and the Short-eared Owl *A. flammeus*) in Alajoki (see also Korpimäki 1984, 1985c). Despite this, the abundance of *Microtus* spp. correlated positively with the proportions of these voles in the diet (Fig. 1), so that a positive relationship also existed between the percentage of *Microtus* spp. in the food and the average clutch size (Fig. 4). Birds and insects evidently cannot completely compensate for a lack of voles in the diet, since a negative correlation was observed between annual mean clutch size and the proportion of these alternative prey groups.

The number of breeding Kestrel pairs in Alajoki was positively correlated with the proportion of *Microtus* spp. in the diet (Fig. 4), and with the spring-trap index of these voles (Korpimäki 1985c). The annual variation in pair numbers and breeding success was about as great as in *Asio* spp. (Table 3). This indicated that the numerical response (e.g. Holling 1959) of this falcon to the abundance of *Microtus* voles was similar to that of Long-eared and Short-eared Owls. Thus, in the Kestrel, the adjustment to vole numbers largely occurred before egg-laying, but to some extent also during the nestling period.

Stenseth (1981) suggested that optimal diet models should incorporate a fitness set (for details of the concept of fitness set, see Levins 1968, Pianka 1976), since his model predicted that the shape of the fitness set function is important for predicting foraging performance. For a consumer exploiting food types which require similar catching methods, the function will be convex and for animals hunting different prey types, concave. The former fitness set assumes gradual changes in diet and the latter abrupt variations. When rearing the young, the Kestrels have high food requirements (Korpimäki et al. 1979) and they must restrict hunting to an area around the nest. The gradual annual and seasonal changes in the diet support the conclusion that the Kestrel is adapted to capturing similar prey types (i.e. small mammals), as do also its morphology and hunting behaviour (see Introduction). This indicates that a convex fitness set is suitable. Since the hunting methods used to catch birds and insects (e.g. pursuing and perching) proba-

Table 2. Composition of the diet of the Kestrel during the breeding period at Alajoki in the years 1977–83. The relative importance of the different prey species or groups is shown as their percentages of the total numbers of prey animals in the pellet analyses. The diet width (DW) indices were calculated according to Levins (1968): $DW = 1/\sum p_i^2$, where p_i is the proportion of prey category i in the food.

Prey species or	Years							
groups	1977	1978	1979	1980	1981	1982	1983	Total
Soricidae	6.1	7.6	12.2	15.0	21.2	20.6	5.1	11.8
Microtus spp.	58.4	39.4	32.8	13.4	6.0	45.4	14.3	35.7
Cl. glareolus	10.2	8.6	18.3	4.7	3.8	9.2	4.1	9.0
Ar. terrestris	0.9	0.3	–	0.8	1.6	3.4	4.4	1.8
Microtidae, tot.	69.4	48.3	51.1	18.9	11.4	58.0	22.8	46.5
Muridae	4.6	4.2	8.0	1.6	8.2	7.1	4.1	5.5
Mustela rixosa	–	0.3	–	–	–	–	–	0.1
Mammals, tot.	80.1	60.3	71.4	35.4	40.8	85.8	32.0	63.8
Birds	4.4	3.4	9.2	14.2	13.6	5.5	20.7	8.7
Lizards and frogs	0.5	0.5	0.8	0.8	1.1	0.4	2.4	0.8
Coleopterans	10.2	30.1	17.8	37.6	20.9	6.2	34.2	20.1
Other insects	4.8	5.7	0.9	12.0	23.7	2.1	10.7	6.5
Prey animals	432	383	262	127	184	436	294	2118
No. of nests	22	11	11	5	7	9	7	72
Diet width	2.69	3.77	4.93	4.57	5.71	3.69	5.00	4.88

Table 3. Reproductive output of the most common birds of prey in Alajoki as indicated by the range of pair numbers, mean clutch sizes and mean numbers of young produced per pair in 1977–83 (for further details, see Korpimäki 1984, 1985c). The coefficient of variation (CV = 100 × (S.D./mean)) describes the amplitudes of the fluctuations in pair numbers in the different species. Total number of observations in parentheses.

	Kestrel		Long-eared Owl		Short-eared Owl	
No. of pairs, range	6–37	(122)	1–22	(68)	2–34	(128)
CV	68.1		84.9		77.5	
Mean clutch size	5.0–5.6	(90)	3.0–6.3	(33)	2.5–7.2	(62)
Mean no. of young produced	0.0–3.9	(103)	0.0–3.5	(62)	0.7–4.1	(81)

bly differ from those required for preying on rodents (flight-hunting and wind hovering), Kestrels presumably cannot catch their alternative prey animals as efficiently as their main prey (for the advantages and disadvantages of the different hunting methods, see Videler et al. (1983) and Village (1983)). Consequently, this specialization on small mammals decreases the Kestrel's reproductive output (as measured by the numbers of young produced per pair) when voles are scarce (Fig. 4 and Table 3).

Concluding remarks. In the present study two of the three predictions of the optimal diet theory were supported by the annual variation in the Kestrel's diet. This might be due to several factors: (1) The Kestrels were dependent on only a few prey types, with uniform nutrient contents, because of the low number of suitable alternative prey animals. (2) When the young were being reared, satiation did not play an important role in prey choice (for details of the role of hunger, see Pyke 1984). (3) The prey was most often encountered sequentially, as predicted by most optimal diet models (Pyke 1984). (4) Avoidance of predators was not an important task for preying Kestrels. On the other hand, the observations did not agree with the predictions as regards the seasonal variation of the diet. Thus, it seems that the diet theory is not suitable for predicting the rapid changes occurring in the foraging behaviour of birds of prey when the environment is undergoing marked changes — as it does in northern areas in the breeding season.

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Selostus: **Tuulihaukan ravinto, saalistushabitaatti ja pesimätulos optimaalisen saalistusteorian valossa**

Etelä-Pohjanmaalta kerättiin vuosina 1977-83 aineistoa tuulihaukan ravinnosta, saalistushabitaateista ja pesinnästä. Ravinnon koostumuksen vuosittaisia ja pesimäkauden sisäisiä vaihteluja suhteessa tarjolla oleviin pikkunisäkkäisiin tarkasteltiin optimaalisen saalistusteorian valossa. Työssä selvitettiin myös ravinnon koostumuksen ja pesimätuloksen välisiä riippuvuuksia.

Suosituimpia saaliita olivat pelto- ja kenttämyyrät. Niiden tiheys maastossa korreloi positiivisesti pesimätulokseen sekä näiden myyrien osuuteen ruokalistalla (kuva 1). Ainoastaan suosituimman saaliin tiheys maastossa vaikutti ruokalistan koostumukseen. Kun pelto- ja kenttämyyrät vähenivät maastossa, ravinto muuttui monipuolisemmaksi (kuva 2), mutta muutokset saalistushabitaateissa eivät lisänneet saalisvalikoiman monipuolisuutta (taul. 2). Kumpikin tulos oli optimaalisen saalistusteorian ennusteiden mukainen.

Pesimäkauden kuluessa ravintovalikoima ei kaventunut, vaikka myyrien tiheys maastossa kasvoi. Tulos oli saalistusteorian ennusteiden vastainen. Todennäköinen syy havaittuun ristiriitaan oli pesimäkauden lopun tiheän ja korkean kasvillisuuden aiheuttama heikompi myyrien saatavuus. Tuulihaukan ravinnon koostumus muuttui vähitellen, kun pelto- ja kenttämyyrien tiheys maastossa laski. Tämä oli ristiriidassa saalistusteorian, mutta sopusoinnussa useimpien muiden maastotutkimusten kanssa.

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