

Differences in the diets of resident and non-resident Kestrels in Spain

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The Eurasian Kestrel (*Falco tinnunculus*) is a partial migrant in Spain, i.e. some individuals migrate in autumn, while other ones are sedentary. In this paper the diets of resident and non-resident kestrels were compared during autumn to study whether differences in the diet may account for individual migratory behaviour. Results indicated that kestrels changed their feeding habits during autumn. Resident kestrels substituted grasshoppers, a typical summer prey, for field crickets and/or mammals (typical winter prey), whereas non resident kestrels hunted fewer crickets and mammals, but more mantids and flying ants, which are not available later, during winter. Trophic diversity (H') was larger for non-resident kestrels than for residents, which indicates that profitable substitution prey might be scarce in the territories of non-resident kestrels. Indeed, BPP (Biomass per whole pellet), which may be an indicator of daily energy intake, was lower for non-resident than for resident kestrels. The negative relationship between the date of disappearance and H' on one hand, and the positive relationship between date of departure to BPP for non-resident kestrels on the other, indicates that these kestrels remained at the breeding sites for as long as possible.

1. Introduction

Partial migration is a common phenomenon among birds, which occurs when some individuals of a population migrate while other ones are sedentary (Gauthaux 1982). Resident individuals may improve their reproductive success by remaining in the breeding area (Adriaensen & Dhondt 1990, Village 1990), but they may also increase the risk of starvation during winter because food may become too scarce. Some studies have found that factors such as previous breeding success, age, sex, dominance, food abundance, nest-site availability have some effect on migration (Lundberg 1979, Newton 1979, Ketterson &

Nolan 1983, Village 1985, Smith & Nilsson 1987). Other studies have shown a genetic basis for migratory behaviour (Berthold & Querner 1981, Biebach 1983). However, a genetic basis of migration does not preclude the importance of environmental factors (Adriaensen & Dhondt 1990). Thus, in regions with strong inter-annual environmental variation, the decision to stay or to leave the breeding area may depend on environmental conditions before winter.

The Eurasian Kestrel (*Falco tinnunculus*) is partially migrant in the Iberian Peninsula (Bernis 1966), as it is in the British Isles and Central Europe (Cavé 1968, Cramp & Simmons 1980). Autumnal migratory movements, which are noted

crossing the Strait of Gibraltar, occur from September to early November (Bernis 1980, Cramp & Simmons 1980). I have studied the diet of the Eurasian Kestrel in a population inhabiting an area in central Spain where, coinciding with that period, a half of adult kestrels abandon their territories. In this paper, I compare the diet of resident and non-resident kestrels in order to investigate whether the diet may account for the decision of migrating or not in this population.

2. Study area, materials and methods

The study area is located in an agricultural (>70% cultivated) plain in central Spain (40°8'N, 2°18'W). Summers are dry and warm, while winter is cold (frequently below 0°C). Rainfall usually ranges between 300 and 500 mm per year (Allué 1966). In the study period, rainfall and temperatures varied around the mean of a normal year.

In this area most kestrel pairs nest in natural rock cavities (Aparicio 1994), and they roost in low cliffs (< 5 m). To study kestrel diet, I collected pellets in their roosts. These pellets were easily attributed to a particular individual because they usually roost alone. Even both members of a pair normally roosted in separated places. Kestrel's breeding performance and diet have been intensively studied for several years in this area (e.g. Aparicio 1990a,b, 1994, 1999). Thus, each potential nest or roost is well known. The presence of birds in the breeding area was easily checked because of the high roost-fidelity in this population, and because potentially alternative roosters are normally scarce. The disappearance of individual kestrels was inferred from their absence at their usual roost. Moreover, I checked that individuals which apparently had departed were not in other roosts within a radius of approximately one kilometre. In autumn, all roosts were checked every 7–15 days to determine the presence/absence of kestrels.

Diet was studied during three periods: from August to September (summer), from October to the first week of November (autumn, when some kestrels abandoned the area), and from the last three weeks of November until end of February (winter). The study of the diet is based on the analyses of pellets, which were collected at the

roosts within maximum intervals of fifteen days. Pellets were dried and preserved in boxes containing naphthalene before analysis. I analysed 236 pellets belonging to 20 individual kestrels (6 resident males and 4 resident females, 5 non-resident males and 5 non-resident females). Each of these 20 birds had bred during the previous spring. The analysed pellets include a sample of 18 and 15 pellets collected in summer of resident and non-resident kestrels respectively, 120 in autumn (six pellets for each individual), and 83 in winter. These pellets were randomly selected for each period and individual. A total of 7 097 prey items (622 in summer, 3 909 in autumn and 2 566 in winter) were found. In autumn, 206 ± 65 S.D. (range: 110–301), and 185 ± 56 S.D. prey items (range: 131–307) were identified on average for each resident and non-resident kestrel respectively.

I used a binocular microscope (20×) for the analyses of pellets. For identification of prey, I used collections of hard parts from previously determined specimens. A number of invertebrates were identified by their exoskeleton. To estimate their masses, several specimens were caught in the study area and immediately weighted with portable balance. Number and size of lizards were estimated by number and length, respectively, of parietal and frontal scales, which appeared normally in the pellets and are easy to identify. The equations to estimate mass of lizards were obtained by measuring specimens from museum collections. Birds were recognised by the presence of feathers. Teeth and hairs were used to identify mammals. The biomass of birds and mammals was calculated from regression functions which related feather and hair mass of pellet remains to biomass (Table 1). These functions were experimentally estimated with captive kestrels which were principally fed with *Mus* and *Microtus*, and also with four House Sparrows (Aparicio 1990a; see also Crichton 1977, Yalden & Yalden 1985). To estimate the number of birds and mammals appearing in a pellet, first I estimated the biomass from the mass of feathers or hair, and then, biomass was divided by the standard mass of the prey item (17 g for birds, 19 g for *Microtus duodecimcostatus*, 12 g for *Mus musculus*; these standard values were the mean amount consumed when kestrels took these prey), and rounding up

the quotient (Yalden & Yalden 1985).

Because the importance of each prey type for kestrels' diet may be given by the portion of biomass (or energy) rather than the number of prey items, I used the proportion of biomass of each prey type to calculate diet composition. By contrast, trophic diversity was calculated using the number of each prey type because the number of prey reflects the frequency of attack decisions for each prey type (Stephens & Krebs 1986). It is, therefore, a better expression of diet selection. Shannon's Diversity Index (H') was used to calculate trophic diversity, applying the natural logarithm:

$$H' = -\sum_{i=1}^n p_i \ln p_i \quad (1)$$

where P_i is the frequency of prey 'i'. I used taxonomic 'family' for invertebrates and species for vertebrates as prey category.

I used the statistical package SPSS for analyses. I verified that data adjusted to normal distributions when a parametric test was realised. All statistical tests were two-tailed and the level of significance 5%.

3. Results

3.1. Seasonal variation in the diet composition

Mammals and Orthopterans constituted 75% of biomass intake by kestrels. However, the composition of the prey varied largely seasonally (Fig. 1). Crickets (*Gryllus campestris*) and mammals increased in the diet from summer to winter, while grasshoppers (Acrididae and Tettigoniidae) decreased in number. Grasshoppers also decreased in size from summer to autumn (mean size in summer \pm S.E.: 0.51 ± 0.02 , autumn: 0.28 ± 0.01 , paired t-test: $t_{17} = 14.1$, $P < 0.0001$), but not from autumn

Table 1: Equations to estimate biomass consumed of each prey type.

Prey	Equation	R ² %	n	P
Acrididae	$M = 0.014LJ^{3.022}$	81	24	< 0.0001
Tettigoniidae	$M = 0.006LJ^{3.924}$	83	21	< 0.0001
Gryllidae	$M = -0.31 + 0.25LJ$	65	22	< 0.0001
Coleoptera	$M = -0.62 + 0.22LF$	96	27	< 0.0001
Mammals	$BI = 40.08HM^{0.736}$	86	14	< 0.0001
Birds	$BI = 35.57FM (SE \pm 0.33)$		4	
Lizards:				
<i>Acanth. erytrurus</i>	$M = 0.09PS^{3.56}$	89	23	< 0.0001
	$M = 0.013FS^{4.34}$	82	23	< 0.0001
<i>Psamm. algirus</i>	$M = 0.069PS^{2.94}$	93	13	< 0.0001
	$M = 0.0078FS^{4.63}$	91	13	< 0.0001
<i>Psamm. hispanicus</i>	$M = 0.145PS^{2.25}$	44	19	< 0.01
	$M = 0.085FS^{2.73}$	45	19	< 0.01
<i>Lacerta lepida</i>	$M = 0.095PS^{2.67}$	96	14	< 0.0001
	$M = 0.00075FS^{5.73}$	85	14	< 0.0001
<i>Podarc. hispanica</i>	$M = 0.098PS^{2.57}$	80	18	< 0.0001
	$M = 0.038FS^{3.54}$	84	18	< 0.0001
Other prey:				
<i>Forficula</i> sp.	0.1 g	<i>Lycosa</i> sp.		0.5 g
Caterpillars	0.35 g	Soliphuga		0.2 g
Flying ants (fem.)	0.075 g	Other spiders		0.1 g
Flying ants (male)	0.015 g	<i>Julus</i> sp.		1.0 g
<i>Mantis</i> sp.	1.2 g	<i>Scolopendra</i> sp.		1.0 g

M: mass (g); BI: biomass intake (g); LJ: length of jaw (mm); LF: length of femur (mm); HM: hair mass contained in the pellet (g); FM: feather mass contained in the pellet (g); PS: length of parietal scale (mm); FS: length of frontal scale (mm).

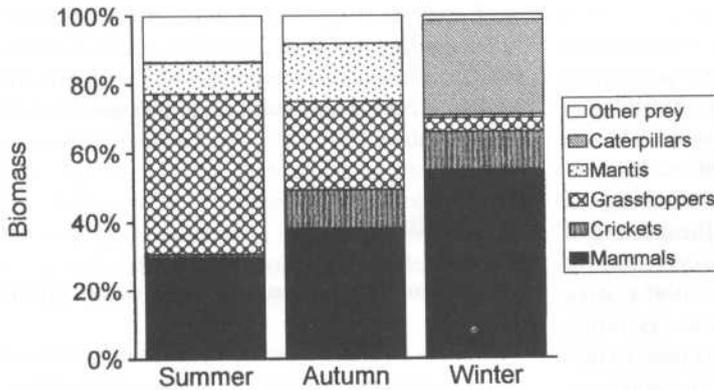


Fig. 1. Seasonal variation in kestrel diet by biomass. "Other prey" includes birds, reptiles and the other invertebrates listed in Table 1.

to winter (mean in winter 0.26 ± 0.02 ; paired t-test: $t_9 = 0.66$, $P = 0.6$). Mantids (*Mantis religiosa*) were only caught in summer and autumn, and caterpillars were taken at the end of winter (January and February).

3.2. Differences in diet between resident and non-resident kestrels

During autumn, I compared the diet of resident and non-resident individuals (Fig. 2). Trophic diversity by number of prey items (see methods), was significantly larger in non-residents (mean \pm SE: 1.42 ± 0.12 , $n = 10$) than for residents (1.07 ± 0.08 , $n = 10$; Mann-Whitney U-test: $U = 20.5$, $P = 0.02$). According to the 'Optimal Foraging Theory', trophic diversity (H') increases when the availability of profitable prey decreases (Stephens & Krebs 1986). In both, resident and non-resident kestrels, trophic diversity was negatively related with the proportion of biomass of grasshoppers ($r_s = -0.73$, $n = 10$, $P < 0.016$ for residents and $r_s = -0.77$, $n = 10$, $P = 0.01$ for non-residents, Spearman's rank correlation). Thus, grasshoppers may be the most profitable prey for these kestrels. However grasshopper density decreases after summer, and therefore, kestrels need to vary their diets.

During autumn, there was a negative correlation between the percentage of biomass of grasshoppers and the percentage of biomass of crickets plus mammals in the diet of resident kestrels ($r_s = -0.95$, $n = 10$, $P < 0.0001$). This correlation was not found among non-resident individuals ($r_s = -0.20$, $n = 10$, $P = 0.58$). This suggests that resi-

dent kestrels used mammals and crickets to replace grasshoppers, as their abundance is decreasing, whilst non-resident kestrels continued using other prey that later, in winter, will be absent (principally mantids and flying ants [*Messor barbara*]). In fact, non-resident individuals fed relatively more on mantids and flying ants (mean \pm S.E.: 36.6 ± 6.6 , $n = 10$ for non-residents, and 15.4 ± 6.2 , $n = 10$ for residents; $U = 14$, $P < 0.01$), and less on mammals and Orthoptera than resident kestrels (mean \pm S.E.: 60.5 ± 6.4 , $n = 10$ for non-residents, and 81.8 ± 2.8 , $n = 10$ for residents; $U = 16$, $n = 10$, $P < 0.01$).

The number of pellets produced by the kestrel does not change with season, and there is a close correlation between the mean biomass per pellet (BPP) and the mean food intake per day (Aparicio 1990b). Therefore, I used BPP as a reliable indicator of daily biomass intake. In summer, there were no significant differences for BPP between residents and non-residents ($t_{17} = 0.1$, $P = 0.9$), but BPP increased from summer to autumn for resident kestrels (paired t-test: $t_8 = 4.1$, $P = 0.003$), while there was no significant increment for non-residents (paired t-test: $t_8 = 0.93$, $P = 0.38$; see Fig. 3). Thus, resident kestrels ingested more biomass than non-resident ones during autumn as there was differences in mean BPP ($t_{17} = 2.6$, $P = 0.018$). In that period, there was a negative correlation between BPP and H' for non-resident kestrels ($r_s = -0.72$, $n = 9$, $P = 0.03$), but not for residents ($r_s = 0.02$, $n = 10$, $P = 0.96$; see Fig. 4). Taking the date of the last seeing of a kestrel as the date of departure, time of departure was positively correlated with BPP ($r_s = 0.67$, $n = 8$, $P < 0.05$; Fig. 5a) and negatively correlated with

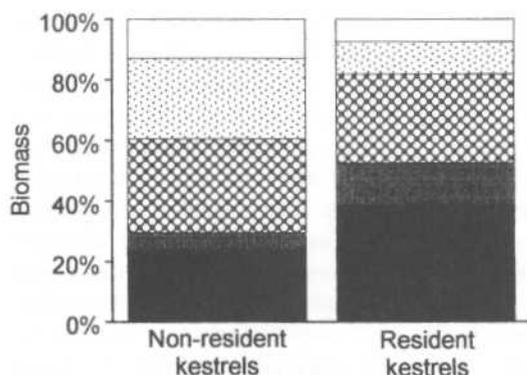


Fig. 2. Diet of non-resident and resident kestrels during autumn. (Symbols as in Fig. 1)

trophic diversity ($r_s = -0.94$, $n = 9$, $P < 0.0001$; Fig. 5b). To see if these correlates were due to an effect of sex differences in both diet and migration behaviour, I compared BPP and trophic diversity between males and females, but no significant difference was found (BPP: mean \pm S.E. 18.6 ± 1.6 for males and 21.4 ± 2.6 for females; $t_7 = 0.98$, $P = 0.36$; H' : 1.45 ± 0.30 for males and 1.38 ± 0.48 for females $U = 11.5$; $n = 5, 5$, $P = 0.84$).

4. Discussion

The 'Optimal Foraging Theory' predicts that prey types are added to the diet in order of their profitability. When the most profitable prey type is scarcer the next prey, by order of profitability, is chosen (Stephens & Krebs 1986). Hence, the negative relationship between the proportion of biomass of grasshoppers and trophic diversity suggests that this prey is the most profitable prey for kestrels in Spain. However, the mean size and the abundance of grasshoppers decrease from summer to winter, becoming less profitable for the kestrel. The negative correlation between the biomass of grasshoppers and the biomass of crickets and mammals for resident individuals, indicates that there is a range of substitution in their diets during autumn. When resident kestrels could not hunt grasshoppers, they fed on alternative prey such as crickets and/or mammals. In contrast, non-resident kestrels took more mantids and flying ants. The difference between these two kinds of

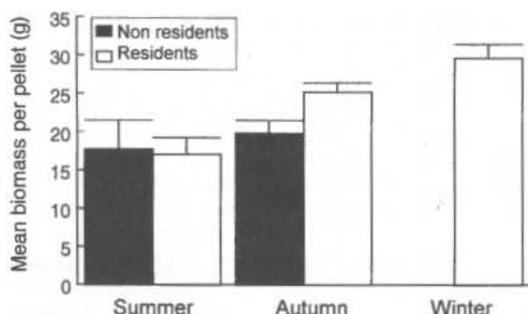


Fig. 3. Seasonal variation of biomass per pellet (BPP [g] mean \pm S.E.).

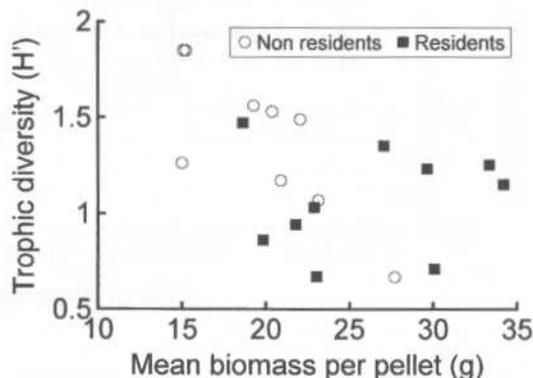


Fig. 4. Relationship between trophic diversity (H') and biomass per pellet (BPP).

prey is that whereas small mammals and crickets persist along winter, mantids and flying ants disappear at the middle of autumn. Therefore non-resident kestrels did not consume as many mammals and/or crickets as resident kestrels probably because they were unable to find enough items of those prey.

The inclusion of crickets and mammals in the diet of resident kestrels produced a slight increase in trophic diversity, however, the maximum values reached by these birds are similar to the minimum values observed in non-resident kestrels. High trophic diversities observed in non-resident ones might be explained by the absence of profitable substitute prey when grasshopper availability decreases. Moreover, the negative correlation between H' and BPP suggests that reduction in prey availability prevents non-resident kestrels from covering their energetic needs, since BPP is larger in resident than non-resident individuals.

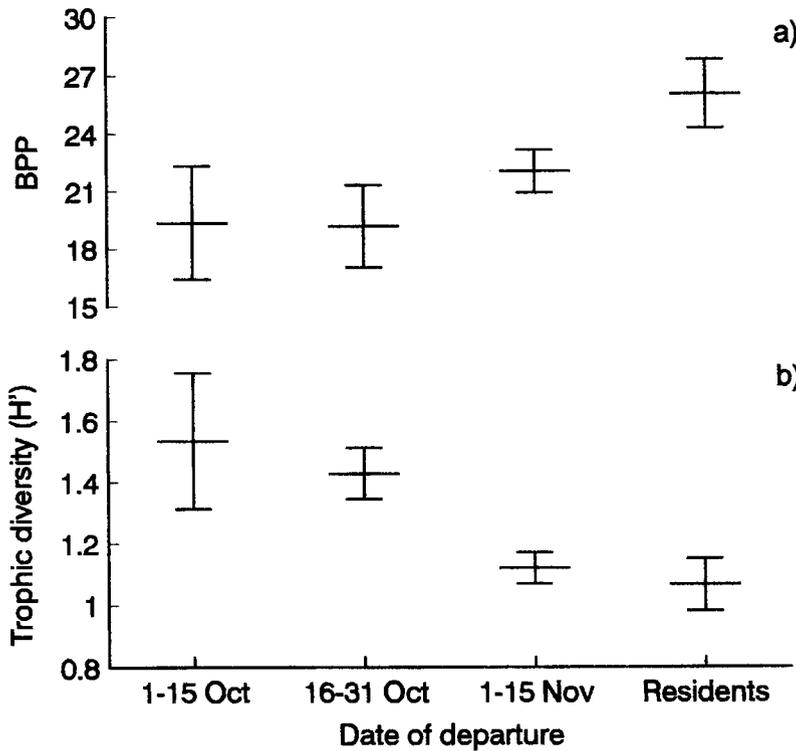


Fig. 5. (a) Biomass per pellet (BPP) and (b) trophic diversity relative to date of departure. Means \pm S.E.

The territories left by non-resident kestrels were not taken by other individuals which suggests that the reduction in prey availability for non-resident kestrels may be caused by prey depletion within their hunting territory, and not the consequence of intraspecific competition, or due to their individual quality.

The correlations between date of departure and BPP, and H' suggest that kestrels remained in the breeding territories as long as possible. This strategy may be more risky than migrating before food becomes scarce as observed by Village (1985) in Scotland, but it may be advantageous in Spain. Assuming that wintering in the breeding territory may have some advantage for subsequent breeding (Kemp 1984, Village 1990), individuals with a higher residential tendency would have an advantage over premature non-resident kestrels in years with mild winters. It is possible that Scottish kestrels migrate prematurely because winters in Scotland are more severe, and thus the possibility of escaping would be lower in case the decision of staying was incorrect.

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Selostus: Paikallisten ja muuttavien tuulihaukkojen ravinto Espanjassa

Tuulihaukka on Espanjassa osittaismuuttaja. Kirjoittajat vertailivat muuttavien ja paikallisten yksilöiden ravinnon käyttöä tarkoituksenaan selvittää ravinnon mahdollisia vaikutuksia muuttostrategian valintaan. Kirjoittajat määrittivät haukkojen ravinnonkäytön oksennuspalloista, joita he keräsivät haukkojen levähdyspaikoilta. Nisäkkäät (Mammalia) ja suorasiipiset (Orthoptera) muodostivat yhteensä 75 % tuulihaukkojen ravintobiomassasta. Saalislajivalikoima vaihteli huomattavasti eri vuodenaikojen välillä (kesä, syksy ja talvi). Kirjoittajat tutkivat yksityiskohtaisemmin haukkojen syksyistä ravintoa. Tulokset osoittavat,

että haukat vaihtoivat ruokailutapojaan syksyllä. Paikalliset tuulihaukat vaihtoivat tyypillisen kesäravintonsa, heinäsiirkat (*Acrididae*) ja hepokatit (*Tettigoniidae*), kenttäsiirkoihin (*Gryllus campestris*) ja/tai nisäkkäisiin (tyypillinen talviravinto). Muuttavat yksilöt käyttivät vähemmän kenttäsiirkoja ja nisäkkäitä sekä enemmän rukoilijasiirkoja (*Mantis religiosa*) ja lentäviä elomuurahaisia (*Messor barbara*), joita ei ole saata- valla myöhemmin talvella. Muuttavien yksilöiden ravinto oli monipuolisempaa kuin paikallisten yksilöiden. Tämä voi olla seurausta siitä, että suosituimpien vaihtoehtoisten saalislajien runsaudet olivat alhaisempia muuttavien yksilöiden territorioilla. Oksennuspallon keskimääräinen biomassa, jota voidaan pitää päivittäisen energian saannin indikaattorina, oli alhaisempi muuttavilla yksilöillä. Muuttavien yksilöiden lähtöajankohdan ja ravinnon monipuolisuuden välinen negatiivinen suhde ja lähtöajankohdan sekä oksennuspallon biomassan välinen positiivinen suhde viittaavat siihen, että linnut pyrkivät viipymään alueella niin pitkään kuin mahdollista. Paikalliset yksilöt voivat parantaa pesimämenestystään jättämällä talvehtimaan hyvälle pesimäalueille, kuitenkin samanaikaisesti talvinen ravintopula voi jotta haukkojen näлкиintymiseen.

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