

Consistent differences in feeding habits between neighbouring breeding kestrels

David Costantini^{1,2)}, Stefania Casagrande³⁾, Giuseppe Di Lieto¹⁾,
Alberto Fanfani¹⁾ & Giacomo Dell’Omo⁴⁾

(¹ Dipartimento di Biologia Animale e dell’Uomo, Università La Sapienza, Viale dell’Università 32, 00185 Roma, Italia; ³ Dipartimento di Biologia Evolutiva e Funzionale, Università di Parma, Parco Area delle Scienze 11, 43100 Parma, Italia; ⁴ Division of Neuroanatomy and Behaviour, Anatomy Institute, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland)

(Accepted: 30 March 2005)

Summary

In this study, we analysed the diet of breeding kestrels (*Falco tinnunculus*) in a Mediterranean area with the aim to evaluate the relative importance of both hunting area and individual feeding behaviour as factors affecting prey selection. Differently from the populations from middle and northern Europe which primarily feed on voles, the kestrels breeding in the Mediterranean region showed a wider diet composition. As expected, hunting area features influenced the diet composition and, in general, the kestrels were feeding on what was locally more abundant. However, we detected consistent differences in the diet composition between neighbouring breeding pairs which were also maintained in subsequent years. Since the neighbouring birds were sharing the same hunting grounds, the differences observed were likely to reflect individual preferences or capabilities in catching some prey type regardless of their actual availability. The presence of differences in diet composition between neighbouring pairs and their temporal consistency suggests that the hunting skills, and in general the feeding behaviour of kestrels, is likely to represent a trait characterising a behavioural type.

Keywords: *Falco tinnunculus*, diet, feeding behaviour, personality, behavioural syndrome, predator-prey, Mediterranean region.

2) Corresponding author’s e-mail address: david.costantini@uniroma1.it.

Introduction

From an adaptive perspective, individuals adjust their behaviour to local conditions in order to maximize their fitness. For example, generalist predators catch on the most common or easy preys occurring in their hunting area. The Eurasian kestrel (*Falco tinnunculus*) is a small raptor widespread in open-countries throughout the Palearctic, Afrotropical, and Oriental regions (Cramp & Simmons, 1980). This raptor is considered to be an opportunistic forager catching on what is locally available (Village, 1990). In northern and central Europe the kestrel is almost exclusively a vole-eater (e.g., Davies, 1975; Korpimäki, 1985a; Masman et al., 1986; Kochanek, 1990), other prey species occurring in its diet only when the availability of voles decreases (Village, 1982; Korpimäki, 1985b, 1986). In southern regions, such as in the Mediterranean basin, lizards, birds, and particularly insects, represent the main component of its diet (Gil-Delgado et al., 1995; Fattorini et al., 1999; Baziz et al., 2001).

In addition to this large-scale geographical (latitudinal) variation, the relative occurrence of the preys in the diet can vary also at a smaller scale. Local differences in diet composition can be related to the hunting area. In fact, the preys vary in type and abundance according to the type and structure of the (micro-) habitat. For example, in western Finland, shrews and birds were more frequently preyed in small fields (<10 km²) whereas voles in medium-sized (10-50 km²) and large fields (>50 km²; Korpimäki, 1985a). Urbanisation seems to affect the diet with a shift towards the birds (see Quere, 1990). For example, in Warsaw 80% of the preys were sparrows (*Passer domesticus*, Rejt et al., 2000) and in Manchester, like in other British towns, kestrels were feeding largely on birds (Yalden, 1980; Yalden & Yalden, 1985). In central Italy also Piattella et al. (1999) found that birds were mostly preyed by kestrels hunting in the city of Rome and in suburban areas, whereas rodents and reptiles were more preyed in rural areas (Salvati et al., 1999). However, the diet composition of different individuals sometimes could vary also in the same hunting area. This could emerge when comparing the diet of birds nesting in close proximity, particularly in the case of kestrels in which the hunting areas overlap widely (e.g., Cavé, 1968; Village, 1990).

To our knowledge, the occurrence of differences in diet composition between individuals sharing the same feeding ground has not received much attention. Therefore, in the present study, we compared the diet of neighbouring breeding kestrel pairs of a Mediterranean population with the aim to

evaluate the relative importance of both hunting area and individual feeding behaviour as factors affecting prey selection. The fidelity of kestrels to their nest site, particularly of males (Village, 1990), allowed us to carry out a longitudinal study on the feeding behaviour of the neighbouring pairs. For these pairs, in the absence of differences in individual feeding habits, we expected a similar occurrence of the various preys in the diet.

Materials and methods

The field study was carried out in a 1200 km² area around Rome characterized by cereals and cultivated fields, set-asides, pasturelands, woody patches, and man-made structures. Many nest boxes installed on the utility lines of two local electric power companies (ENEL and ACEA) were used by kestrels for breeding. Every year from 1999 to 2004, during the breeding season, the boxes were checked for assessing the occupation and for collecting reproductive data. During this time, pellets and prey remains were also collected in representative zones of the study area. These were located in three main environment types: type-1 characterised by cereal and cultivated fields rich of granivorous birds (mostly sparrows) and rodents; type-2 pasturelands interspersed with set-asides where insects and rodents were more common; and type-3 open fields with bushes and woody patches characterised by the presence of many lizards.

Only vertebrate preys were considered in counting procedures. This was because pellets containing invertebrate remains flake more quickly than pellets including hairs or feathers, and so many insect remains could get lost. Moreover, only larger species with hard chitinous parts were more likely to be found. To avoid the underestimation of invertebrates we decided to consider only their presence into the nest. Therefore, insect remains were considered only for taxonomic identification either at the family and order level or, when possible, at species level.

After an initial assessment of the invertebrate and vertebrate prey species found in all the nests checked, in a first analysis we evaluated the effects of the hunting area on the occurrence of the three main vertebrate prey species (*Lacerta bilineata*, *Passer italiae*, and *Microtus savii*) in the diet by a contingency table chi-square test applied to the number of specimens of each prey species collected from the three main environment types. Table 2 shows the percent frequency for each species.

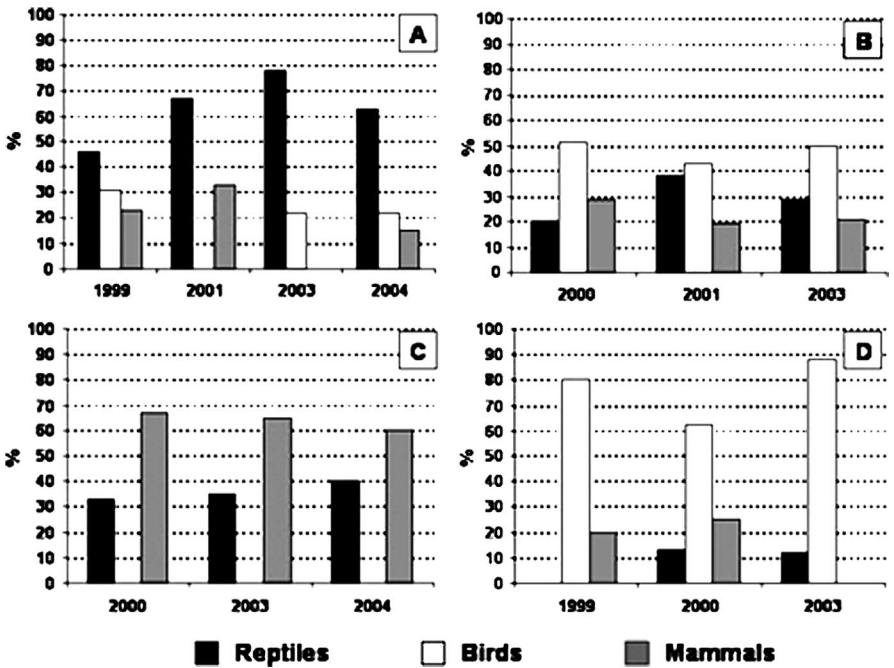


Figure 1. The diet differences between neighbouring breeding kestrels were constant year by year. Reptiles were always the main prey in the nest A, the mammals in the nest C, and the birds in the nests B and D. The nests A and B were sited near woody patches while the nests C and D in cereal fields.

In a second analysis, we evaluated the relative importance of habitat- and pair-related diet composition. We selected 14 neighbouring nests for which we collected more than 30 preys during a period of 3-5 years. The preys were considered as a pool for each nest, the diet being constant year by year (see example in Figure 1). Five groups of neighbouring nests were included in the analysis: two groups in type-1 habitat included three nests from one area in the north of Rome and two nests in the south; two groups in type-2 habitat, one in the north-west and the other in the south of Rome, consisted of three nests each; finally, a group of three nests was in type-3 habitat. The distances between neighbouring nests in the same habitat were less than 1-2 km. Since we could not measure the movements of our birds, we assumed that their hunting range was similar to that determined by Village (1990) and Shrubbs (1993), i.e., up to 10 km². Therefore, because in each group the nests selected were all within this range we assumed that the neighbouring kestrels were hunting on the same ground. This is also supported by literature

data showing that hunting ranges in kestrels overlap (e.g., Village, 1990). By consequence, in our analysis we did not consider the local availability of different prey species because we compared pairs feeding on the same area. Then, we quantified the diet overlap among pairs by the Pianka's index (1973) using the following function $\sum p_{ij}q_{ik} / \sqrt{(\sum p_{ij}^2 \sum q_{ik}^2)}$ where p_{ij} is the relative occurrence of the taxon i in the diet of pair j and q_{ik} is the relative occurrence of the same taxon in the diet of pair k . The index was calculated without considering the insects, but using only the relative occurrence of reptiles, birds, and mammals considered as groups without any reference to the species level. The data set was analysed through a clustering technique, the Unweighted Pair-Group Method with arithmetic average (UPGMA), by the STATISTICA package (Version 5.1, StatSoft, Padova, Italy).

Results

We collected 1066 vertebrate preys from 138 nests for a total of about 30 199 g biomass. We identified 6 reptiles, 26 birds, and 9 mammals species, which represented 43.25, 30.96, and 25.14% of the preys by number and 33.41, 44.15, and 21.97% by weight, respectively (Table 1). Insect preys included 36 species. Beetles (33 species and 16 families identified) and grasshoppers (mostly *Anacridium aegyptium*) represented the most consistent part of the diet, resulting in some cases dominant. *Pentodon bidens* and *Bubas bison* represented the most common beetle species occurring in 46% and 18% of the nests inspected, respectively. Also, *Anacridium aegyptium* was very common being recorded in 26% of the nests.

a) Effect of hunting area

Insects were found in almost all nests inspected (Coleoptera occurred in the 69.3% of nests while Orthoptera in the 37.2% of nests). Lizards, voles, and small birds were the main vertebrate groups preyed on by kestrels (22.8, 14.2, and 9.3%, respectively, by number). Overall, the hunting area influenced generally the occurrence of preys in the diet: most of the lizard's remains (particularly the green lizard *Lacerta bilineata*) were collected from nest boxes in areas characterized by bushes and woody patches, while small birds (mostly sparrows *Passer italiae*) and rodents (particularly *Microtus savii*) were collected from nests located in cereal and cultivated fields (Table 2).

Table 1. Number (*N*), percent frequency by number (*N%*) and by weight (*B%*) of all the vertebrate species identified in the diet.

	<i>N</i>	<i>N%</i>	<i>B%</i>
<i>Rana bergeri</i>	7	0.66	0.46
<i>Lacerta bilineata</i>	243	22.80	20.17
<i>Podarcis muralis/sicula</i>	116	10.88	6.93
<i>Chalcides chalcides</i>	17	1.59	0.85
<i>Anguis fragilis</i>	3	0.28	0.15
<i>Tarentola mauritanica</i>	8	0.75	0.40
Lacertidae und.	74	6.94	4.91
<i>Melopsittacus undulatus</i>	8	0.75	0.53
<i>Coturnix coturnix</i>	3	0.28	1.00
<i>Columba livia</i>	6	0.56	5.98
<i>Apus apus</i>	18	1.69	2.45
<i>Merops apiaster</i>	2	0.19	0.37
<i>Upupa epops</i>	1	0.09	0.22
<i>Jinx torquilla</i>	1	0.09	0.11
<i>Picoides major</i>	1	0.09	0.25
<i>Pica pica</i>	1	0.09	0.66
<i>Alauda arvensis</i>	3	0.28	0.40
<i>Motacilla alba</i>	2	0.19	0.12
<i>Motacilla cinerea</i>	1	0.09	0.06
<i>Sturnus vulgaris</i>	21	1.98	5.89
<i>Oriolus oriolus</i>	1	0.09	0.27
<i>Troglodytes troglodytes</i>	1	0.09	0.03
<i>Turdus merula</i>	10	0.94	3.32
<i>Turdus philomelos</i>	4	0.38	1.01
<i>Phoenicurus ochruros</i>	2	0.19	0.11
<i>Luscinia megarhynchos</i>	1	0.09	0.07
<i>Carduelis carduelis</i>	34	3.19	1.58
<i>Carduelis chloris</i>	22	2.08	1.90
<i>Fringilla coelebs</i>	1	0.09	0.08
<i>Parus caeruleus</i>	1	0.09	0.04
<i>Passer italiae</i>	99	9.29	9.86
<i>Passer montanus</i>	6	0.56	0.45
<i>Passer</i> sp.	40	3.76	3.45
<i>Emberiza cirius</i>	3	0.28	0.24
Passeriformes und.	37	3.47	3.69
<i>Microtus savii</i>	151	14.17	10.03
<i>Apodemus sylvaticus/flavicollis</i>	45	4.22	3.96
<i>Clethrionomys glareolus</i>	18	1.69	1.61
<i>Mus domesticus</i>	1	0.09	0.06
<i>Rattus rattus</i>	3	0.28	1.89
<i>Muscardinus avellanarius</i>	3	0.28	0.27

Table 1. (Continued).

	<i>N</i>	<i>N</i> %	<i>B</i> %
<i>Crocidura suaveolens</i>	4	0.38	0.11
<i>Talpa romana</i>	5	0.47	1.43
Chiroptera und.	1	0.09	0.03
Rodentia und.	37	3.47	2.58

Table 2. Percent frequency of the main prey species in the diet of breeding kestrels nesting in three main environment types occurring in our study area (central Italy, Rome province). Data were collected from 138 nests during the period 1999-2004 (62 in cereal and cultivated fields, 49 in set-asides and pasturelands, 27 in open fields). The diet composition varied largely between the environment types confirming an effect of the hunting area ($\chi^2 = 74.164$, $df = 4$, $p < 0.001$).

	Cereal and cultivated fields	Set-asides and pasturelands	Open fields with bushes and woody patches
<i>Lacerta bilineata</i>	20.0	30.7	49.3
<i>Passer italiae</i>	62.1	27.3	10.6
<i>Microtus savii</i>	61.0	22.9	16.1

b) Consistent differences in feeding habits

A second analysis was devoted at evaluating the occurrence of habitat- and pair-related differences in diet composition in the subsample of 14 nests. The food preferences recorded in these nests were constant from one year to the other (see example in Figure 1). The UPGMA analysis showed that the among-pairs differences in the diet composition did not depend only on the differences between the environment types as expected, but also on the pair's feeding habits (Figure 2). In fact, the analysis disrupted the original geographical clustering of the nests and re-assigned a new clustering order based on the diet similarities which pooled together pairs from different areas, thereby showing that birds hunting in the same area were feeding on different prey groups. Seven pairs fed primarily on lizards (52 to 73%), three preyed mostly on small birds (48 to 88%), while four pairs did not show any strong food preference for these two vertebrate groups, but had mammals from 30 to 64%.

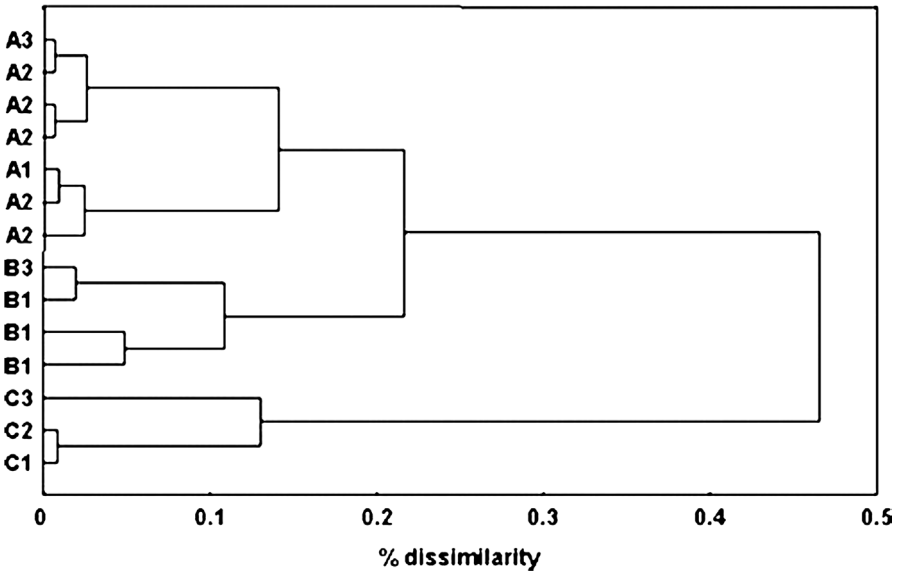


Figure 2. Cluster analysis relating the diet overlap of kestrel pairs calculated by the Pianka's index. Values are reported as percentage of diet dissimilarity. The letters stand for the diet composition: A — mostly reptiles; B — no dominant component; C — mostly small birds. The numbers stand for the hunting habitat: 1 — cereal and cultivated fields; 2 — set-asides and pasturelands; 3 — open fields with bushes and woody patches.

Discussion

Our study confirmed that differently from the populations from middle and northern Europe which primarily feed on voles, breeding kestrels in the Mediterranean region have a wider diet composition. In fact, in our study area the voles accounted only for a small proportion of the preys while insects, lizards, and small birds were predominant.

As expected, the hunting area influenced the diet composition because the species preyed were typical for the three environment types considered. For example, voles and sparrows were preyed mostly in open and cultivated fields, whereas lizards were more frequently caught in areas with bushes and woody patches. Thus, our data support previous observations that kestrels catch on the locally more abundant prey species (Village, 1990), hence implying an opportunistic behaviour and feeding adaptability.

However, in our study we could detect also differences in diet between pairs nesting at short distance. These differences are more likely to depend on the individual feeding behaviour rather than on differences in availability

of the different preys. In fact, the intraspecific competition for preys can be excluded only within the territory, i.e., a small area (in most cases below 50–100 m radius) surrounding the nest, which is defended from intruders (e.g., Cramp & Simmons, 1980; Sommani, 1986). The rest of the home range, i.e., the area in which the birds actively hunt, overlaps widely among pairs, particularly in the case of Eurasian kestrels (Cavé, 1968; Village, 1990).

Several prey species can live in the same area, some more common than others, and different preys require different hunting efforts and skills for kestrels. Therefore, the ability of an individual to detect and catch on a specific prey could be unrelated to the relative species abundance in the hunting habitat. Moreover, observations on some other nests not included in the analysis strengthened further the repeatability of the prey types caught from year to year. For example, we recorded in some cases preys that were rarely found in others nests such as frogs, geckos, and swifts. Specifically, frog and gecko remains were found in nest n. 29 and n. 70 in 2003–2004, whereas swift remains were found in nest n. 23 (1999 to 2003) and n. 121 (2001 to 2004). Frogs, geckos, and swifts were found occasionally also in other nests, but in those listed above they were regularly present. Since it is known that kestrels exploit the same nest site for many years (Village, 1990) it is likely that the birds in our study area were also regularly using the same boxes.

Food preferences in birds have been anecdotically described in the scientific literature. Brown (1969) and Gilraldeau & Lefebvre (1985) reported that individual pigeons selected only few seed types from a mixture of many seeds. Manganaro et al. (1990) observed that two neighbouring pairs of tawny owls in the same urban park had different diets, one pair preying almost exclusively on birds while the other on small rodents. Differences in diet between neighbouring breeding pairs were observed also for the red-footed falcon (*Falco vespertinus*; Purger, 1998) and for the brown goshawk (*Accipiter fasciatus*; Aumann, 1988). In the American kestrel (*Falco sparverius*) free ranging individuals were found to have marked prey preferences (Smallwood, 1989) and in captive individuals were found differences even in the parts of the prey (one-day-old chicks) eaten which were explained in terms of different energy requirements between individuals (Duke et al., 1996). In three North American raptor species, the diet did not reflect the relative abundance of prey types in the environment. Instead, raptors exhibited consistent preferences for certain prey species (Steenhof & Kochert,

1988). Overall, the above-mentioned observations together with our case study suggest that individual food preferences occur in many bird species and do not necessarily rely on the local availability of food types.

A common feature seems to be that all these species are non-social and have a non-specialist diet. Given their consistency with time, the individual differences in feeding habits could likely be assimilated to behavioural types or personalities (Dall et al., 2004; Groothuis & Carere, 2005) or, according with a new term in behavioural ecology, could represent one trait of a 'behavioural syndrome' (Sih et al., 2004). This new concept implies that individuals can show less than optimal plasticity contrasting the common view of an unlimited behavioural plasticity that allows individuals to maximize their fitness in each environment. In our case, the individual feeding behaviour should be considered *sensu* Neff & Sherman (2004) in a more adaptationist view on behavioural flexibility. In fact, the 14 nests monitored during the study period always succeeded in producing viable chicks, thereby suggesting that the peculiar individual feeding habits were not maladaptive. However, the specialization of feeding habits on a particular prey should not be considered necessarily an adaptive behaviour because it could reduce the spectrum of preys thereby resulting in harmful effects under harsh circumstances (i.e., food shortage in winter).

As a possible mechanism which could have caused the development of individual differences in diet and which could be responsible for their maintenance in the population one can call in question the variation of the diet with time during the breeding season (e.g., Village, 1990). Birds breeding earlier or later in the breeding season could specialize on different preys and develop a preference for it. Also, food imprinting could represent a way of transmission from parents to offspring of a familial preference for a specific prey *via* the development of a specific searching image (Tinbergen, 1960; Mueller, 1971), thereby maintaining a 'cultural' propensity to develop individual feeding habits in the population (Stokes, 1971; Allen & Clark, 2005).

Differences in diet between individuals have been for a long time neglected as biologically relevant variations because were considered extremes of population means with only descriptive value. Our study suggests another way to look at these differences by considering the feeding behaviour as a part of a behavioural profile which could be linked to other traits of the avian

personalities (Groothuis & Carere, 2005). Despite its descriptive nature, our data analysis provides an indirect confirmation of the hypothesis tested.

The existence and maintenance of different personalities has been suggested to have important effects on the ecology and evolution of populations, potentially leading to speciation as well (see Sih et al., 2004). Therefore, considering individual feeding preferences could add new hints toward the clarification of the concept of personality in behavioural ecology.

Acknowledgements

Three anonymous reviewers improved the manuscript with their comments and suggestions. A. Vigna Taglianti, E. Piattella, and G. Amori provided a valuable help in the identification of preys. ENEL-TERNA and ACEA allowed the monitoring of nest boxes on their utility lines. Ornithologica, an ornithological scientific association, sponsored part of the field work. D. Costantini was supported by a PhD fellowship from the University of Rome La Sapienza. G. Dell’Omo was supported by the Swiss National Science Foundation and the NCCR ‘Neural Plasticity and Repair’.

References

- Allen, T. & Clarke, J.A. (2005). Social learning of food preferences by white-tailed ptarmigan chicks. — *Anim. Behav.* 70: 305-310.
- Aumann, T. (1988). The diet of the brown goshawk, *Accipiter fasciatus*, in south-eastern Australia. — *Aust. Wildl. Res.* 15: 587-594.
- Baziz, B., Souttu, K., Doumandji, S. & Denys, C. (2001). [Some aspects of the kestrel *Falco tinnunculus* diet in Algery]. — *Alauda* 69: 413-418.
- Brown, R.G.B. (1969). Seed selection of pigeons. — *Behaviour* 34: 115-131.
- Cavé, A.J. (1968). The breeding of the kestrel in the reclaimed area Oostelijk Flevoland. — *Neth. J. Zool.* 18: 313-407.
- Cramp, S. & Simmons, K.E.L. (1980). Handbook of the birds of Europe, the middle east and north Africa. Vol. 2, Hawks to bustards. — Oxford University Press, Oxford.
- Dall, S.R.X., Houston, A.I. & McNamara, J.M. (2004). The behavioural ecology of personality: consistent individual differences from an adaptive perspective. — *Ecol. Lett.* 7: 734-739.
- Davies, T. (1975). Food of the kestrel in the winter and early spring. — *Bird Study* 22: 85-92.
- Duke, G.E., Tererick, A.L., Reynhout, J.K., Bird, D.M. & Place, A.E. (1996). Variability among individual American kestrels (*Falco sparverius*) in parts of day-old chicks eaten, pellet size, and pellet egestion frequency. — *J. Raptor Res.* 30: 213-218.
- Fattorini, S., Manganaro, A., Piattella, E. & Salvati, L. (1999). Role of the beetles in raptor diets from a Mediterranean urban area. — *Fragm. Entomol.* 31: 57-69.
- Gil-Delgado, J.A., Verdejo, J. & Barba, E. (1995). Nestling diet and fledgling production of Eurasian kestrels (*Falco tinnunculus*) in eastern Spain. — *J. Raptor Res.* 29: 240-244.

- Giraldeau, L.-A. & Lefebvre, L. (1985). Individual feeding preferences in feral groups of rock doves. — *Can. J. Zool.* 63: 189-191.
- Groothuis, T.G.G. & Carere, C. (2005). Avian personalities: characterisation and epigenesis. — *Neurosci. Biobehav. Rev.* 29: 137-150.
- Kochanek, H.-M. (1990). [The diet of the kestrel (*Falco tinnunculus*): results of nest content analyses and automatic recording]. — *J. Orn.* 131S: 291-304.
- Korpimäki, E. (1985a). Diet of the kestrel *Falco tinnunculus* in the breeding season. — *Ornis Fennica* 62: 130-137.
- Korpimäki, E. (1985b). Prey choice strategies of the kestrel *Falco tinnunculus* in relation to available small mammals and other Finnish birds of prey. — *Ann. Zool. Fennici* 22: 91-104.
- Korpimäki, E. (1986). Diet variation, hunting habitat and reproductive output of the kestrel *Falco tinnunculus* in the light of the optimal diet theory. — *Ornis Fennica* 63: 84-90.
- Manganaro, A., Ranazzi, L., Ranazzi, R. & Sorace, A. (1990). [The diet of the tawny owl, *Strix aluco*, in the park Villa Doria Pamphili (Rome)]. — *Riv. Ital. Orn.* 60: 37-52.
- Masman, D., Gordijn, M., Daan, S. & Dijkstra, C. (1986). Ecological energetics of the kestrel: field estimates of energy intake throughout the year. — *Ardea* 74: 24-39.
- Mueller, H.C. (1971). Oddity and specific searching image more important than conspicuousness in prey selection. — *Nature* 233: 345-346.
- Neff, B.D. & Sherman, P.W. (2004). Behavioral syndromes versus darwinian algorithms. — *Trends Ecol. Evol.* 19: 621-622.
- Pianka, E.R. (1973). The structure of lizard communities. — *Annu. Rev. Ecol. Syst.* 4: 53-74.
- Piattella, E., Salvati, L., Manganaro, A. & Fattorini S. (1999). Spatial and temporal variations in the diet of the common kestrel (*Falco tinnunculus*) in urban Rome, Italy. — *J. Raptor Res.* 33: 172-175.
- Purger, J.J. (1998). Diet of red-footed falcon *Falco vespertinus* nestlings from hatching to fledging. — *Ornis Fennica* 75: 185-191.
- Quere, J.-P. (1990). [Study of the kestrel's (*Falco tinnunculus*) diet in a urban environment (Paris) during the breeding period]. — *Le Passer* 27: 92-107.
- Rejt, L., Turlejski, K., Bronche, K. & Topczewski, A.M. (2000). Can food caching increase the frequency of chicks' feeding in urban kestrel *Falco tinnunculus*? — *Acta Ornithol.* 35: 217-221.
- Salvati, L., Manganaro, A., Fattorini, S. & Piattella, E. (1999). Population features of kestrels *Falco tinnunculus* in urban, suburban and rural areas in central Italy. — *Acta Ornithol.* 34: 53-58.
- Shrubb, M. (1993). Nest sites in the kestrel *Falco tinnunculus*. — *Bird Study* 40: 63-73.
- Sih, A., Bell, A. & Johnson, J.C. (2004). Behavioral syndromes: an ecological and evolutionary overview. — *Trends Ecol. Evol.* 19: 372-378.
- Smallwood, J.A. (1989). Prey preferences of free-ranging American kestrels, *Falco sparverius*. — *Anim. Behav.* 38: 712-714.
- Sommani, E. (1986). [Notes on the biology of some pairs of kestrels, *Falco tinnunculus*, in Rome]. — *Riv. Ital. Orn.* 56: 40-52.
- Stenhof, K. & Kochert, M.N. (1988). Dietary responses of three raptor species to changing prey densities in a natural environment. — *J. Anim. Ecol.* 57: 37-48.
- Stokes, A.W. (1971). Parental and courtship feeding in the red junglefowl. — *Auk* 88: 21-29.
- Tinbergen, L. (1960). The natural control of insects in pinewoods. 1: Factors influencing the intensity of predation by songbirds. — *Arch. Néer. Zool.* 13: 265-336.

- Village, A. (1982). The diet of kestrels in relation to vole abundance. — *Bird Study* 29: 129-138.
- Village, A. (1990). *The kestrel*. — T. & A. D. Poyser, London.
- Yalden, D. (1980). Notes on the diet of urban kestrels. — *Bird Study* 27: 235-238.
- Yalden, D. & Yalden, D.W. (1985). An experimental investigation of examining kestrel diet by pellet analysis. — *Bird Study* 32: 50-55.
-