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Diet of Red-footed Falcon *Falco vespertinus* nestlings from hatching to fledging

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The diet of Red-footed Falcon *Falco vespertinus* nestlings was studied continually from their hatching to fledging in four nests during 1991, near the village Melenci in the province of Voivodina, Yugoslavia. In four nests, nestlings were present for 26, 32, 26 and 27 days, respectively. Only 8 of the 13 nestlings lived to fledge, and the death of the remaining 5 coincided with cool, rainy days. Remains of an average of 2.72 prey items per day were found, from which 302 prey items were identified. These included 17 (6%) vertebrate items, while the remaining 285 (94%) were insects. Sixty percent of the insect food were orthopteran species (Orthoptera), 36% were beetles (Coleoptera), and 4% were dragonflies (Odonata). A significant difference was found between the proportion of vertebrate vs. insect prey in the four nests. The food composition of downy, pin feathered and fully feathered nestlings was different. Orthopterans and beatles dominated the diet. The role of dragonflies in the feeding of the nestlings grew as a function of nestling age, while vertebrates played a role in the feeding of nestlings only in the downy and pin feathered stages.

1. Introduction

Adult Red-footed Falcons are considered to be exclusively insectivorous in the western Palearctic, but nestlings are also fed small vertebrates (Glutz et al. 1971, Cramp & Simmons 1980). Several authors have dealt with the diet of nestlings (Balát & Bauer 1955, Horváth 1955, 1956, 1964, Bezzel & Hölzinger 1969, Fülöp & Szlivka 1988, Haraszthy et al. 1994), but, owing to the difference in their methods, comparing their results is problematic. When studies use visual observation (Horváth 1955, 1964, Bezzel & Hölzinger 1969) only large-bodied prey can be recognised more or less reliably. It is impossible to count and taxonomically identify small insects held by the birds in their beak when the nestlings are being fed. It is difficult to tell from collected pellets (Balát & Bauer 1955), how many birds of what age have produced the pellets. Moreover, different taxa are not equally represented in the pellets. Analyses of stomach contents (Fülöp & Szlivka 1988) can only provide information about the food that had been consumed shortly before the birds died. Food remains gathered from the nest usually reflect the larger prey of the diet, since small insects are mostly swallowed in one piece. Moreover, nestlings of older age tend to perch on the edge of the nest while the parents feed them from the branch supporting it, which results in a large proportion of food remains falling to the ground. It is difficult to successfully collect food remains from the undergrowth, which can mix, and thus be mistaken, with remains scattered by other falcon individuals or rooks. Since Red-footed Falcons raise their offspring in nests abandoned by other bird spe-

cies (Hooded Crow *Corvus corone cornix*, Rook *Corvus frugilegus*, Magpie *Pica pica*), there is always a possibility of accidentally collecting old food remains from these birds, too (Haraszthy et al. 1994). Therefore, it is reasonable to remove old remains from the nests before hatching commences.

The food composition of the nestlings from the day of hatching until leaving the nest has not been studied. The primary aim of the present study has been to monitor quantitative and qualitative changes in the food of the nestlings, based on the analysis of the prey remains collected daily from the selected nests.

2. Study area and methods

For these investigations, the most convenient locality was near the village Melenci in the province of Voivodina, Yugoslavia (see: Lukač & Lukač 1990, Purger 1996, 1997, for a further description of this site). Red-footed Falcons nested in abandoned nests of a Rook colony, in a Black Locust *Robinia pseudoacacia* forest. This forest strip was approximately 15–25 m wide and situated between a highway and a village road, running along fields of sunflower, maize, clover and wheat.

Horváth (1964) observed that both the wings and the jumping legs of locusts and grasshoppers were torn off before the animals were offered to the nestlings. Since such parts may remain in the nest, it was necessary to visit the nests studied on a daily basis. On 1 June 1991, 4 Red-footed Falcon nests (A, B, C, D) were selected which were situated on easily climbable trees. The chosen nests were at least 100 meters apart from each other. Starting on the day the first chick hatched and lasting until the last one left the nest (Table 1), the 4 nest contents were checked every afternoon between 16:30 and 18:30. Prey animals were identified from the collected remains with the assistance of experts of the various taxa.

Dates of hatching and fledging differed between nests (Table 1). Consequently, nestlings of a given age were being raised and fed under different weather conditions. Data on weather conditions during the study period were obtained from the nearest meteorological station at Zrenjanin (Fig. 1).

To analyse the food composition of nestlings of various age, three age groups based on the age of the first nestling in the nest, were established. In the age group of 1–10 days downy chicks, in the age group of 11–20 days pin feathered nestlings, while in the group of ≥ 21 days feathered nestlings were dominant, respectively.

3. Results

Chicks stayed in the four nests for a total of 111 days (Table 1). Food remains were successfully collected 84 times. The ratio of successful vs. unsuccessful collections in the different nests was not different ($\chi^2 = 3.46$, df = 3, p = 0.33), and an average of 2.72 prey items were found in a nest per day.

A total of 302 prey items were identified (Table 2) out of which 17 (6%) were vertebrates, while the remaining 285 (94%) were insect parts. A significant difference was found between the proportions of vertebrate vs. insect prey in the four nests ($\chi^2 = 10.98$, df = 3, p = 0.012). Insect food consisted of 60% orthopterans (Orthoptera), 36% beetles (Coleoptera) and 4% dragonflies (Odonata). Orthopteran, beetle and Spade-foot Toad *Pelobates fuscus* remains were found in all four nests (Table 2). The largest number of prey remains was

Table 1. Breeding parameters of the four nests.

	Nest A	Nest B	Nest C	Nest D
Hatching date of first nestling	27 June	28 June	03 July	07 July
Fledging date of last fledgling	22 July	29 July	28 July	02 August
Nestling days/nest	26	32	26	27
Total number of nestlings	3	3	4	3
Total number of fledglings	2	2	2	2

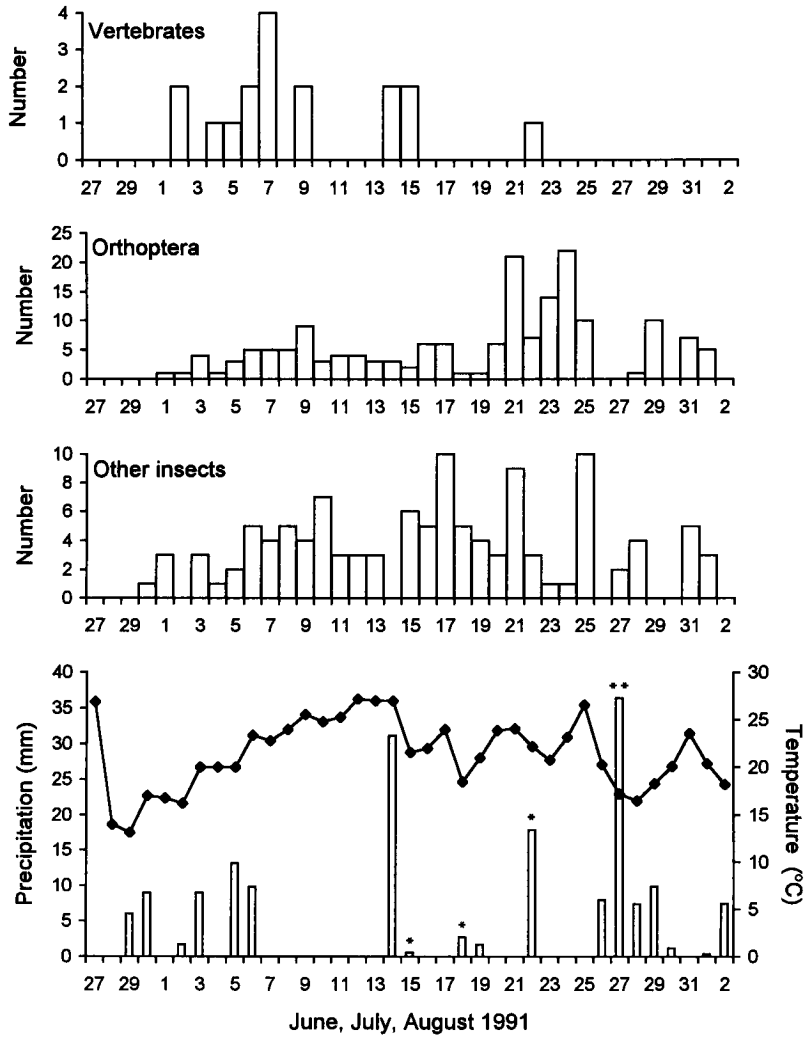

Fig. 1. Number of different prey categories collected daily from the four nests, precipitation (bars: bottom chart), and mean air temperature (curve) during the study period. * = chicks deaths.

found in nest B in which nestlings spent 32 days (Table 1). Dragonflies were found exclusively in this nest as well as mammal and reptile remains (Table 2). Nests A, C and D were left by the nestlings at the age of 26–27 days (Table 1), and these nests yielded smaller numbers of food remains (Table 2).

The hatching of the first nestlings (nest A and B) coincided with relatively low air temperatures and a rainy period lasting one week (Fig. 1). More than 10 days passed until temperatures reached the previous level again. Rain was common later on, too, and was accompanied by temperature fluctuations (Fig. 1). All nestling deaths (on 15, 18, 22 and 27 July; two chicks on the latter day) occurred on cool and rainy days (Fig. 1). Because of the small number of prey remains recovered, it was not possible to determine precisely the relationship between diet and weather conditions. Accordingly, no significant correlation was found between the daily amount of precipitation and the number of Spade-foot Toad remains found in the nests ($r_S = 0.24$, $n = 37$, $p = 0.15$).

The food composition of downy chicks could be assessed based on 71 (23.5%) prey items, of older pin feathered nestlings on 90 items (29.8%), and of fully feathered nestlings on 141 items (46.7%). The differences among the three age groups and the four main categories of prey found (Odonata, Orthoptera, Coleoptera and Vertebrata), were very highly significant ($\chi^2 = 58.18$, $df = 6$, $p = 0.00001$). Orthopterans and beetles dominated

the food composition of nestlings of each age group. The proportion of dragonflies grew as the season progressed, while vertebrate prey played a role mainly in the early season (Fig. 2).

4. Discussion

During the present study on the diet of Red-footed Falcon nestlings, remains of 75.5 prey items per nest were found. When ringing three-week old nestlings, Haraszthy et al. (1994) collected remains of 887 prey items from a total of 47 nests, i.e. 18.9 prey items per nest. The dissimilarity between the two studies emphasises the importance of the daily collection of prey remains from hatching to fledging. During a 4-day observation, Horváth (1964) recorded 222 feedings, while Haraszthy et al. (1994) observed 648 feedings in a period of 84 hours. In view of these figures, even the 302 prey item remains collected from the 4 nests in my study certainly represented only a small minority of all prey brought in.

An important question is whether any taxa were underrepresented among the prey because of the method used. Published results which are based on direct observations, suggest that vertebrates usually play a more important role in the feeding of nestlings than found in my study (Horváth 1955, 1964, Bezzel & Hölzinger 1969). Analysis of stomach contents of dead nestlings showed that 36% of the prey were vertebrates (Fülöp &

Table 2. Numbers of different prey remains collected from the four nests.

Prey	Nest A	Nest B	Nest C	Nest D	Total
INSECTA					
Odonata					
Aeschna spp.	–	1	–	–	1
Gomphus flavipes	–	2	–	–	2
Gomphus spp.	–	2	–	–	2
Orthetrum cancellatum	–	4	–	–	4
Orthetrum spp.	–	3	–	–	3
Orthoptera					
Tettigonia viridissima	29	55	31	14	129
Decticus verrucivorus	2	3	2	2	9
Platicleis spp.	2	17	–	13	32
Coleoptera					
Calosoma auropunctatum	1	4	–	2	7
Carabus cancellatus	–	2	–	1	3
Carabus ullrichi	–	–	–	3	3
Carabus spp.	–	1	–	1	2
Pterostichus spp.	–	7	–	–	7
Silpha carinata	–	1	–	–	1
Silpha spp.	–	13	5	13	31
Pentodon idiota	2	18	–	7	27
Anisoplia austriaca	–	14	2	1	17
Coccinella septempunctata	–	1	–	–	1
Dermestes spp.	–	3	–	1	4
AMPHIBIA					
Pelobates fuscus	7	5	1	2	15
REPTILIA					
Lacerta agilis	–	1	–	–	1
MAMMALIA					
Microtus arvalis	–	1	–	–	1
Total	43	158	41	60	302
Prey/day	1.65	4.94	1.58	2.22	2.72

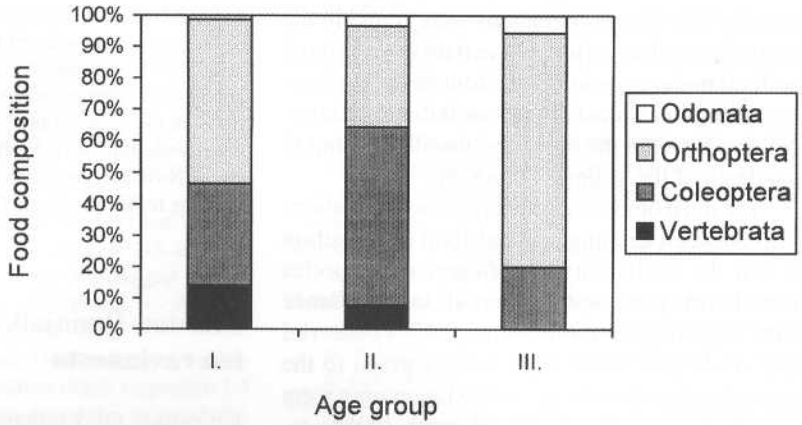

Fig. 2. Food composition (based on the number of collected prey remains) of Red-footed Falcon nestlings of different age. I. age group = downy chicks; II. age group = pin feathered nestlings; III. age group = fully feathered nestlings.

Szlivka 1988). Both pellet analyses (Balát & Bauer 1955) and investigations of collected prey remains (Haraszthy et al. 1994, present study) have indicated a much lower ratio of vertebrates. It seems likely, then, that vertebrates leave fewer traces, possibly because they are eaten whole and are usually completely digested by the falcons. Horváth (1964) found that the major vertebrate prey delivered to the nestlings was Spade-foot Toad, as 97.6% of vertebrate prey in that study was made up by this amphibian. He also calculated the total mass of food carried by the parents to the nest, and found that 73.7% of the food mass was Spade-foot Toads. If Spade-foot Toads are not available when the young are being raised, Red-footed Falcons may prey upon other vertebrates, such as Common Voles *Microtus arvalis* (Haraszthy et al. 1994). During their observations in 1964, Bezzel and Hölzinger (1969) found a high percentage of Common Voles in the food of the Red-footed Falcons, which was related to a population explosion of *Microtus arvalis* and *M. agrestis* that year.

According to Horváth (1964), vertebrate prey is used exclusively for feeding the nestlings. This is in accordance with theories on optimal foraging, because large prey are more profitable to transport to the nest than are small prey (e.g. Sonerud 1992). Based on the Spade-foot Toads in nestlings found dead, Horváth (1964) concluded that beetles had got into the stomach of the nestlings through ingestion by toads. This was suggested by the fact that only orthopterans were found in the stomach of the old birds. However, in addition to orthopterans, Csiki (1910), Budnitshenko (1950), Keve and Szijj (1957) also found beetles and vertebrates in the stomach of the adult birds. Thus, the distinction between the feeding of nestlings and adult birds may be less clear than suggested by Horváth (1964).

My results have proved not to be supportive enough to directly confirm the study of Horváth (1963), who observed that on cold, damp days the adult birds carried mostly Spade-foot Toads to the nest, while in clear, mild weather, the general prey was orthopterans. On days with calm weather and sunshine, generally more food was taken to the nest than in rainy and windy weather (Horváth 1964). These observations are similar to those by Haraszthy et al. (1994), who found that Spade-foot Toads were caught mostly during the dawn hours which is in accordance with the nocturnal activity of the toads. On cloudy days with gentle rain in the morning, the toads retire later in the morning, and thus remain available for a longer period. As air temperature rises and humidity decreases, locusts and grasshoppers will gradually become more and more active, and become substitutes for inactive Spade-foot Toads.

The hatching of the chicks lasted for several days in all four nests. Only 8 of the 13 hatched chicks lived to fledge, and the younger nestlings always died. In addition to the effect of the age gap existing between the chicks, both unfavourable weather and shortage of food may have influenced their survival. It is difficult, however, to tell, based on the available data, to what extent weather and the lack of food, respectively, were responsible for the outcome. Since hatching coincided with a cool, rainy period, it is not surpris-

ing that only few prey remains were found in the nests during that period. On certain days I found no food remains in any of the four nests. A shortage of food is almost always an initiator of competition between the nestlings, usually leading to the death of the youngest chick(s).

The most obvious explanation for the relationship between nestling age and food composition is that the availability of different prey species varied during the nestling period. In accordance with my study, Osmolovskaya (1939) observed that small prey items were usually given to the more developed nestlings, while larger prey were provided to smaller chicks. Horváth (1964) recorded that during the first two weeks of their lives, nestlings were fed on toads, lizards, bird hatchlings and Great Green Bush-crickets *Tettigonia viridissima* (i.e. soft-bodied prey). After the first two weeks have passed, more and more orthopterans were brought, mostly larger ones. He also found that younger chicks received more food than the older ones. Similarly, Fülöp and Szlivka (1988) recorded that younger nestlings were fed more frequently and more regularly.

It is almost certain that the nestlings in my study were continuously supplied by the adults with orthopterans and other insects from the moment they hatched through fledging. Vertebrate prey (mostly Spade-foot Toad) was offered the chicks only during the first three weeks. It is possible that, prior to fledging, the adults hunted exclusively on insects, though it seems more likely that sources of Spade-foot Toad had run short.

To conclude, the qualitative findings about the food composition of Red-footed Falcon nestlings show a great deal of variance, since authors have used different methods during their studies at various places and at different times. It is apparent that results obtained by applying various methods are not only almost incomparable, but also, each of the methods eventually produce partial results. Consequently, to better understand the feeding biology of the Red-footed Falcons, the combination of different methods should be preferred in order to achieve progress.

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Selostus: **Punajalkahaukan pesäpoikasten ravinnosta**

Kirjoittaja tutki punajalkahaukan pesäpoikasten ravinnon koostumusta Jugoslaviassa neljältä haukan pesältä kerätystä materiaalista. Pesäpoikasaika kesti keskimäärin 27 vuorokautta. Yhteensä 13 kuoriutuneesta poikasesta 8 selvisi lentopoikasvaiheeseen (Taulukko 1). Poikasten kuolemat ajoittuivat kylmille, sateisille päiville (Kuva 1). Pesille kertyi jälkiä kaikkiaan 2.72 saaliseläimestä vuorokaudessa. Kirjoittaja määritti yhteensä 302 saalisyksilöä. Pääosa saalisyksilöistä (94%) oli selkärangattomia, ja pikkunisäkkäitä löytyi saalisvalokoimasta vain yksi yksilö. Suurin saaliseläinryhmä oli suorasiipiset (Orthoptera, 60% selkärangattomista) ja niistä erityisesti hepokatit (Tettigoniidae). Kovakuoriaiset muodostavat 36% ja sudenkorennot 4% selkärangatonravinnosta. Eri pesien välillä oli kuitenkin huomattavia eroja ravinnon koostumuksessa (Taulukko 2). Samoin ravinnon koostumus vaihteli poikasten iän mukaan (Kuva 2).

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