

EFFECT OF HABITAT AND LATITUDE ON NESTLING DIET OF PIED FLYCATCHERS *FICEDULA HYPOLEUCA*

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Composition and diversity of the nestling diet of Pied Flycatchers *Ficedula hypoleuca* was compared among 17 European study areas that differed in habitat type (deciduous or coniferous forest). The most abundant foods were butterflies and moths (Lepidoptera), with a high proportion of caterpillars. The proportions of beetles (Coleoptera) and Lepidoptera in the nestling diet differed significantly between deciduous and coniferous forests. The contribution of caterpillars to the total number of Lepidoptera was significantly higher in deciduous than in coniferous forests, but did not show any relationship with latitude. Thus, Slagsvold's (1975b) hypothesis that in northern regions passerines breed early in respect to the seasonal development of arthropod food resources (as indicated by relative amount of caterpillars), was not supported. Diversity of nestling diet did not differ between forest types, and neither did it show any relationship with latitude. The probability of two items taken at random being different (another measure of diet diversity, and of the difficulty in obtaining food), did not show relationships with latitude of, or average clutch size in, study areas. The hypothesis, put forward by Von Haartman (1973) and Owen (1979), that geographical variation in prey diversity explains geographical variation in clutch size, was therefore rejected as well.

Key words: *Ficedula hypoleuca* - timing of reproduction - clutch size - diet - nestling - latitude

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INTRODUCTION

Pied Flycatchers *Ficedula hypoleuca* that breed in deciduous and coniferous forests differ in clutch size, laying date and reproductive success (Berndt & Winkel 1967; Källander 1975; Lundberg *et al.* 1981; Alatalo *et al.* 1985; Källander *et al.* 1987; Järvinen 1989; Lundberg & Alatalo 1992; Sanz 1995). The nestling diet composition of Pied Flycatchers is known for a wide range of breeding localities (Lundberg & Alatalo 1992; Cramp & Perrins 1993; Glutz von Blotzheim & Bauer 1993). Insect abundance is usually greater, and the average size of food items larger, in deciduous than in

coniferous forests (Palmgren 1932; Kuusisto 1941; Lundberg *et al.* 1981; Temrin 1984), and this may explain the differences in clutch size, laying date and reproductive success between deciduous and coniferous forests. Nestling diet may be affected by habitat type (Bösenberg 1964; Slagsvold 1975a), but no detailed study has addressed this question.

Clutch size in altricial species usually increases with latitude (Klomp 1970). However, exceptions are not rare (Owen 1979; Orell & Ojanen 1983; Isenmann 1987; Soler & Soler 1992). Lack (1947) suggested that the tendency for clutch size to increase with latitude could be attributed to the

increase in daylight hours available for the parents to collect food for their nestlings. In the Pied Flycatchers clutch size shows a quadratic relationship with latitude (Sanz 1997), increasing from North Africa to central Europe (50°-55°N) and then decreasing to northern Europe. Von Haartman (1973) and Owen (1979) accepted Lack's daylength hypothesis as a partial explanation of latitudinal trend of clutch size, and introduced the diversity of potential food as an additional explanatory factor. Although summer daylengths increase with latitude, a decrease may take place in species diversity of arthropod prey items. Owen (1979) expected a decrease in diversity of food brought to nestlings with latitude. Low diversity of potential food at high latitudes may result in food being easier to obtain. This would lead to a higher food intake, and thus higher clutch sizes (Owen 1979). A prominent effect of latitudinal change is the increase in dominance of a few prey species. From Von Haartman's (1973) and Owen's (1979) hypotheses it follows that the probability of two-items taken at random being different should decrease with latitude and/or clutch size. This probability can be used as a measure of a bird's difficulty in securing food for its nestlings under the additional assumption that diversity is indicative of difficulty (Owen 1979).

Another hypothesis (Slagsvold 1975b), suggested that in northern regions birds breed early with respect to the seasonal development of the food for the young. The young may therefore be reared at a more favourable time in respect to the amount of available food, and this may ultimately have affected clutch size (Slagsvold 1975b). The seasonal variation of caterpillars (an important component of nestling diet) is related to the development of the vegetation (Blondel *et al.* 1993). If the timing of reproduction gives a closer fit with the seasonal development of vegetation and invertebrates with increasing latitude (Slagsvold 1975b), it is predicted that the proportion of caterpillars (out of all Lepidoptera) would be higher towards the north.

The aim of this paper is to compare, on the ba-

sis of a literature review, the composition and diversity of the diet of nestling Pied Flycatchers from populations that differ in breeding habitat type (coniferous and deciduous forests) and latitude, and thus to test the predictions of the hypotheses by Von Haartman (1973), Owen (1979) and Slagsvold (1975b).

METHODS

Data on the composition of nestling diet were available for 17 study areas (see Appendix). The most common methods involve the use of neck collars on nestlings (preventing them from swallowing the food) and nestbox cameras. For each study area, latitude and habitat type (deciduous and coniferous) are known. Invertebrate orders were used as the food groups for comparison of the qualitative composition of the food obtained. For each study area, the proportion of prey items given to nestlings of each food group was calculated. The diversity of the diet was estimated by the diversity index (λ) of Simpson (1949):

$$\lambda = \frac{\sum_{j=1}^k n_j(n_j - 1)}{N(N - 1)}$$

N is the total sample size of prey items and n_j is the number of prey items of food group j . The absolute numbers of each food group was calculated from the total sample size and the frequencies of each food group in the diet. The probability of two food items taken at random being different (β) was calculated as $\beta = 1 - \lambda$ (Owen 1979), where λ is Simpson's diversity index (Simpson 1949). The estimate of β has a minimum of zero (when only one food group is taken) and a maximum of one (when every item is different). No direct clutch size data were available from the populations studied by Mansfeld (1942), Berndt & Rapsch (1958), Bösenberg (1964) and Dornbuch (1981): for their study areas I used data presented

by Curio (1959), Berndt & Winkel (1967), Von Haartman (1967) and Creutz (1955), respectively. No clutch size data were available for the study area of Bureš (1995); it was excluded from the relevant analyses. Proportions were arcsine transformed before parametric statistical analysis. Statistics are presented as means \pm SD.

RESULTS AND DISCUSSION

There were five main food groups: beetles (Coleoptera), butterflies and moths (Lepidoptera), true flies (Diptera), bees, ants, sawflies and wasps (Hymenoptera) and spiders (Arachnida). These constituted 85.7% of the food brought to the nestlings (Table 1). Using the data available in the 17 studies of nestling diet, the main food group given to the nestlings was Lepidoptera (28.7% of prey

items given to nestlings; Table 1) with a high proportion of caterpillars. That the contribution of flying insects is high may be due to the high tail/wing ratio of Pied Flycatchers that gives them a high manoeuvrability in flight (Bureš 1995). Nevertheless, the main prey fed to nestlings were caterpillars. Caterpillars may be taken directly from the foliage, from the ground or in mid-air when descending on silk to pupate. Previous studies have shown that in 15% (Von Haartman 1954) or 43% (Alatalo & Alatalo 1979) of the cases Pied Flycatchers were found foraging in the foliage of trees.

In a comparison between study areas, the proportion of Lepidoptera was negatively correlated with the proportion of Diptera ($r_{16} = -0.52$, $P = 0.033$). Table 2 shows the proportions of food groups representing at least a 10% of the nestling diet in coniferous and deciduous forests. The proportion of Coleoptera in the diet was significantly higher in coniferous than in deciduous forests, while the proportion Lepidoptera was significantly lower in coniferous than in deciduous forests (Table 2). Differences in nestling diet composition between coniferous and deciduous forests may affect nestling growth, but differences in the amount of food are likely to be more important (Lundberg *et al.* 1981).

Proportions of the numerically important food groups (Table 2) were not correlated with latitude if the effect of habitat types was controlled (ANCOVA, all $P > 0.12$). In deciduous forests, caterpillars contributed on average 94.2% (range 90%-99%, $n = 5$ study areas) to all lepidopteran prey. In coniferous forests, the average value was 69.3% (range 60%-81%, $n = 5$ study areas). In an ANCOVA, with types of forest as factor and latitude as covariate, the proportion of caterpillars within Lepidoptera differed significantly between coniferous and deciduous forests but did not show any relationship with latitude (Factor $F_{1,7} = 26.43$, $P = 0.001$; Covariate $F_{1,7} = 0.29$, n.s.). Contrary to the Slagsvold (1975b) hypothesis, the caterpillar-contribution to the lepidopteran part of nestling diet did not correlate with latitude. Although the geographical variation in breeding times of birds

Table 1. Summary of the mean proportion (%) of prey items of different food groups in the nestling diet of Pied Flycatchers ($n = 17$ study areas).

| Food group | | % |
|---------------|--------------------------------|--------|
| Lepidoptera | butterflies and moths | 28.7 |
| Diptera | true flies | 18.8 |
| Coleoptera | beetles | 13.7 |
| Arachnida | spiders | 13.6 |
| Hymenoptera | bees, ants, sawflies and wasps | 10.9 |
| Hemiptera | bugs | 6.2 |
| Orthoptera | crickets and grasshoppers | 1.2 |
| Myriapoda | millipedes and centipedes | 1.1 |
| Isopoda | pillbugs | 1.0 |
| Neuroptera | lacewings | 0.9 |
| Trichoptera | caddisflies | 0.7 |
| Mollusca | molluscs | 0.7 |
| Plecoptera | stoneflies | 0.5 |
| Psocoptera | booklice and psocids | 0.2 |
| Dictyoptera | cockroaches | 0.1 |
| Crustacea | crustaceans | 0.1 |
| Annelida | annelids | 0.1 |
| Odonata | dragonflies | 0.1 |
| Ephemeroptera | mayflies | < 0.05 |
| Dermaptera | earwigs | < 0.05 |
| Others | | 1.2 |

Table 2. Mean proportions of prey items of food groups that represented at least a 10% of the nestling diet of Pied Flycatchers breeding in coniferous and deciduous forests. Student *t*-tests were used to test significant deviations between forest habitats for a given group.

| | Coniferous forests (<i>n</i> = 8 study areas) | Deciduous forests (<i>n</i> = 9 study areas) | <i>t</i> | <i>P</i> |
|-------------|---|--|----------|----------|
| Coleoptera | 17.60 | 10.21 | 2.93 | 0.01 |
| Lepidoptera | 20.62 | 35.96 | 2.39 | 0.03 |
| Diptera | 22.72 | 17.02 | 0.45 | 0.66 |
| Hymenoptera | 10.71 | 11.14 | 0.23 | 0.82 |
| Arachnida | 16.17 | 11.32 | 1.62 | 0.12 |

does not correlate perfectly with phenological development of the environment (Slagsvold 1975b), the present results suggest that over a large range of latitudes young flycatchers are reared during favourable time windows with respect to (caterpillar) food abundance (Perrins & McCleery 1989).

The hypothesis that daylength and food diversity together can explain latitudinal variation in clutch size, as proposed by Von Haartman (1973) and Owen (1979), could be investigated on the basis of all 17 studies (Appendix). Using an ANCOVA with habitat type as factor and latitude as covariate, diversity of nestling diet (λ) appeared not to differ between habitat type; neither did it show any relationship with latitude (deciduous forest 0.25 ± 0.10 , $n = 9$ study areas; coniferous forest 0.20 ± 0.05 , $n = 8$ study areas; ANCOVA, Factor $F_{1,14} = 1.61$, n.s.; Covariate $F_{1,14} = 0.28$, n.s.). Also, the probability of two-items taken at random being different (β) did not differ between habitat type and did not correlate with latitude (ANCOVA, Factor $F_{1,14} = 1.61$, n.s.; Covariate $F_{1,14} = 0.28$, n.s.). Also contrary to the hypothesis, the probability of two-items taken at random being different (β) did not show any relationship with mean clutch size ($r_{15} = -0.03$, n.s.). I reject the presented hypotheses and conclude that the diversity of food does not affect latitudinal variation in clutch size in the Pied Flycatcher.

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SAMENVATTING

Dit is een literatuur-onderzoek op grond van 17 gepubliceerde studies naar de samenstelling en de diversiteit van het aan jonge Bonte Vliegenvangers in Europa aangeboden voedsel. Er worden vergelijkingen gemaakt tussen het dieet in loof- en naaldbossen en er wordt gezocht naar verbanden tussen dieet, breedtegraad en legselgrootte. Vlinderachtigen (Lepidoptera), waarvan rupsen een groot deel uitmaken, vormen het belangrijkste type prooien dat door Bonte Vliegenvangers bij het nest wordt aangebracht. Kevers (Coleoptera) zijn relatief belangrijk voor Bonte Vliegenvangers in naaldbossen. Het percentage rupsen binnen de vlinder-prooien is hoger in loof- dan in naaldbossen. Er bestaat geen ver-

band tussen het percentage rupsen (ten opzichte van adulte vlinders) en breedtegraad en daarmee kan de hypothese van Slagsvold, dat in het noorden zangvogels zoals vliegenvangers slechter in staat zijn om de broedtijd zo uit te kienen dat de jongentijd samenvalt met de rupsentijd, verworpen worden. Er worden ook geen correlaties gevonden tussen de variatie binnen het kuiken-dieet en breedtegraad of legselgrootte. Daarmee wordt ook een tweede hypothese uit de literatuur verworpen dat een eenzijdiger dieet leidt tot een kleinere legselgrootte en dat dit juist in het hoge noorden voor zou komen. (TP)

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Appendix. Diet (% of prey items given to nestlings) of the Pied Flycatcher in different study areas.

| | Mansfeld (1942) | Mansfeld (1942) | Mansfeld (1942) | Creutz (1953) | V Haartman (1954) | V Haartman (1954) | V Haartman (1954) | Berndt & Rapsch (1958) | Meidell (1961) |
|--------------------|--------------------|--------------------|--------------------|------------------|----------------------|----------------------|----------------------|---------------------------|-------------------|
| Latitude | 52°00'N | 52°00'N | 52°00'N | 51°03'N | 60°30'N | 60°30'N | 51°03'N | 52°30'N | 59°30'N |
| Forest type | Deciduous | Coniferous | Coniferous | Coniferous | Deciduous | Coniferous | Coniferous | Coniferous | Deciduous |
| Mollusca | 0 | 4.3 | 0 | 0 | 0.7 | 0 | 0 | 1 | 0.9 |
| Annelida | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Myriapoda | 0 | 0 | 1.4 | 2.3 | 0 | 0 | 2.3 | 8.4 | 0 |
| Ephemeroptera | 0 | 0 | 0.4 | 0 | 0 | 0 | 0 | 0 | 0 |
| Odonata | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 | 0 |
| Dyctioptera | 0 | 0 | 0 | 0 | 0 | 1.0 | 0 | 0 | 0 |
| Isopoda | 3.3 | 2 | 2.1 | 0.9 | 1.4 | 0 | 0.9 | 3.5 | 0 |
| Plecoptera | 0 | 0 | 0 | 0 | 0 | 3.85 | 0 | 0 | 0 |
| Orthoptera | 4.6 | 2.7 | 3.2 | 0 | 0.7 | 0 | 0 | 5.4 | 0 |
| Dermaptera | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Psocoptera | 0 | 0 | 0 | 0 | 1.4 | 1.0 | 0 | 0 | 0 |
| Hemiptera | 0 | 0 | 0 | 3.6 | 5.6 | 1.9 | 3.7 | 2.8 | 0.9 |
| Neuroptera | 0 | 0 | 0 | 0.5 | 0 | 1.9 | 0.5 | 0.6 | 0 |
| Coleoptera | 2.0 | 12.7 | 15.3 | 20.4 | 8.5 | 12.5 | 20.4 | 23 | 16.3 |
| Trichoptera | 0 | 0 | 0 | 0.9 | 0.7 | 4.8 | 0.9 | 0.3 | 0 |
| Lepidoptera adults | 66.2 | 29.4 | 19.3 | 6.5 | 25.4 | 16.4 | 9.3 | 16.4 | 21.1 |
| Lipidoptera larvae | 0.7 | 15.1 | 13.1 | 2.8 | 2.8 | 3.9 | | 3.8 | 2.1 |
| Diptera | 5.0 | 3.0 | 5.1 | 42.6 | 22.5 | 22.1 | 42.6 | 23 | 9.9 |
| Hymenoptera | 0.3 | 5.7 | 23.1 | 9.2 | 12.0 | 9.6 | 9.3 | 4 | 38.6 |
| Crustacea | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Spiders | 17.9 | 25.1 | 17.0 | 10.2 | 18.3 | 21.2 | 10.2 | 7.3 | 8.3 |
| Others | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1.9 |
| No. of items | 302 | 299 | 908 | 908 | 142 | 104 | 216 | 1563 | 586 |

| | Bösenberg (1964) | Bösenberg (1964) | Bösenberg (1964) | Dornbusch (1981) | Alatalo <i>et al</i> (1988) | Lifjeld & Slagsvold (1988) | Bureš (1995) | Moreno <i>et al</i> (1995) |
|--------------------|---------------------|---------------------|---------------------|---------------------|--------------------------------|-------------------------------|-----------------|-------------------------------|
| Latitude | 51°00'N | 51°00'N | 51°00'N | 52°30'N | 59°50'N | 63°20'N | 49°40'N | 40°48'N |
| Forest type | Deciduous | Deciduous | Coniferous | Coniferous | Deciduous | Deciduous | Deciduous | Deciduous |
| Mollusca | 1.1 | 0.4 | 0.5 | 0.6 | 0 | 1.3 | 0.3 | 0.5 |
| Annelida | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1.3 |
| Myriapoda | 0.7 | 0.8 | 1 | 1.1 | 0 | 0 | 1.1 | 0.1 |
| Ephemeroptera | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Odonata | 0 | 0 | 0.3 | 0 | 0 | 0 | 0 | 0 |
| Dyctioptera | 0 | 0 | 0 | 0 | 0 | 0 | 1.5 | 0 |
| Isopoda | 0 | 0 | 0 | 0 | 0 | 0 | 1.9 | 0.9 |
| Plecoptera | 0 | 0 | 0 | 0 | 4 | 0 | 1.3 | 0 |
| Orthoptera | 0.3 | 0.3 | 1.4 | 0 | 0 | 0 | 0.3 | 2.1 |
| Dermaptera | 0 | 0 | 0 | 0 | 0 | 0 | 0.3 | 0 |
| Psocoptera | 0 | 0 | 0 | 0 | 0 | 0 | 0.3 | 0 |
| Hemiptera | 13.9 | 8.4 | 2.1 | 19.4 | 11.8 | 4.1 | 9.1 | 18.5 |
| Neuroptera | 1.3 | 0.3 | 4.2 | 4.4 | 0 | 0 | 2.0 | 0 |
| Coleoptera | 9.2 | 11.5 | 16.8 | 19.7 | 4.4 | 8.9 | 8.8 | 22.4 |
| Trichoptera | 0 | 0.1 | 4 | 0 | 0 | 0 | 0 | 0 |
| Lepidoptera adults | 37.4 | 20.7 | 19.7 | 9.4 | 32.2 | 49.1 | 21.3 | 42.0 |
| Lepidoptera larvae | | | | | | 1.1 | 1.6 | |
| Diptera | 17.4 | 36.3 | 10.3 | 17.1 | 22.8 | 12.1 | 23.3 | 3.9 |
| Hymenoptera | 4.8 | 7.9 | 15.2 | 9.6 | 6.7 | 11.2 | 15.6 | 3.3 |
| Crustacea | 0.5 | 1.7 | 0.1 | 0 | 0 | 0 | 0 | 0 |
| Spiders | 13.4 | 11.6 | 24.2 | 14.3 | 13.1 | 4.7 | 11.51 | 3 |
| Others | 0 | 0 | 0.2 | 4.4 | 5 | 7.5 | 0 | 2.1 |
| No. of items | 12672 | 9811 | 6436 | 20499 | 298 | 992 | 747 | 1330 |