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## Nestling provisioning in water pipits (*Anthus spinoletta*): do parents go for specific nutrients or profitable prey?

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**Abstract** In this study, we investigated whether free-living insectivorous water pipits (*Anthus spinoletta*) choose prey according to biochemical quality as measured by protein, lipid, carbohydrate, energy and water contents and/or according to profitability as measured by density, size and catchability. Food preference – expressed in relation to availability – is estimated for 22 arthropod taxa (families and orders). Uni- and multivariate statistics detected no relationships between food preference and nutrient contents, but revealed that more larger prey items are fed to nestlings than smaller ones, both for all prey taken together and within individual taxa. Furthermore, slow-flying arthropods, which are easier to catch, were usually preferred over walking and fast-flying ones. Combined with results from previous studies on the effects of vegetation, prey density and catchability on search times and energy intake, these findings suggest that water pipits select their prey primarily to maximize profitability, i.e. energy intake per unit time. Qualitative traits seem to be important only for specific taxa. For example, toxins or poor digestibility may be responsible for the avoidance of heteropterans, beetles and ants and for feeding the nestlings fewer tipulids than expected at high tipulid densities.

**Key words** Foraging · Nutrients · Energy content · Arthropods · Water pipit

### Introduction

The question as to how animals should choose food in order to maximize their reproductive success was first posed nearly 30 years ago (Emlen 1966; MacArthur and

Pianka 1966) and is the fundamental issue of the large number of studies on optimal diet and foraging theory (reviews by Krebs 1978; Kamil and Sargent 1981; Krebs and McCleery 1984; Stephens and Krebs 1986; Kamil et al. 1987; Hughes 1990, 1993; Endler 1991; Krebs and Kacelnik 1991; Sih 1993). It has been shown that many animals forage in a way that corresponds closely to model predictions based on maximizing energy gain per unit time. More recently, the focus has changed towards understanding additional factors. It has been recognized that the optimal diet and foraging strategy are determined by the simultaneous solution of various cost-benefit functions which ultimately affect the fitness of the foragers. For example, foraging costs may not only include energy and time expenditures for finding, handling and ingesting food (Schoener 1971; Pyke et al. 1977), but also the risk of predation (Lima and Dill 1990), increased thermoregulatory costs, reduced time for territorial activities, or the potential consumption of toxic or inhibitory compounds (Freeland and Janzen 1974; Rowell-Rahier and Pasteels 1992).

For altricial birds it has been shown that the choice of food provided to nestlings by the parents can have a substantial influence on nestling survival and condition at fledging (reviewed in Martin 1987). The amount of energy brought to the nestlings often limits the parents' breeding success. As a consequence, food is often selected to maximize profitability, i.e. net energy gain per unit time. Although the importance of food quality and chemical defences are widely recognized in the literature on herbivorous and frugivorous animals, this aspect has been little studied in insectivorous predators. Krebs and Avery (1984) observed that European bee-eaters (*Merops apiaster* L.) do not feed exclusively on the most profitable prey and they showed experimentally that these birds grow better on a mixed diet of bees and dragonflies than on a pure diet of either. Tinbergen (1981) noted that the breeding success of starlings (*Sturnus vulgaris* L.) is related positively to the amount of caterpillars fed to the chicks even though tipulid larvae are energetically more profitable. Goss-Custard

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(1977a) found that redshanks (*Tringa totanus* L.) prefer amphipods over more profitable nereid worms. Perrins (1976) showed that the tannin content of prey impairs the weight gain of blue tit (*Parus coeruleus* L.) nestlings. Such effects of food quality may require trade-offs between energy gain and maximizing ingestion of specific nutrients (e.g. Ford and Paten 1975; Belovsky 1978, 1990; Mills et al. 1991) or minimizing ingestion of toxic compounds (Freeland and Janzen 1974; Smallwood and Peters 1986). While the relative importance of the various currencies can only be tested under experimental conditions, the set of conditions encountered under natural conditions can only be identified through field studies.

In this paper we provide such a field study for insectivorous water pipits (*Anthus spinoletta* L.). We relate the proportion of different arthropod taxa to contents of protein, lipid, carbohydrate, energy and water, and to size, availability and movement. The results are then used to infer the most likely factors affecting food choice by the parent birds and to estimate the relative importance of food quality and quantity.

## Materials and methods

### Study area and birds

The research was done during May–August 1990–1992 in the central Alps of eastern Switzerland in the valley of Dischma, which is situated near the town of Davos. The study area lies above timberline between 1800 m and 2500 m above mean sea level. The valley floor is dominated by meadows, whereas the slopes are mainly covered by dwarf shrubs and alpine meadows. Most water pipits start breeding between the end of May and the beginning of June. In late June and in July they produce replacement clutches (16.8%,  $n = 303$ ) and second broods (11.9%). The area considered in this study measured 62 ha, with a mean density of 5.72 ( $\pm 0.51$ ) territories/ha. This gives an average distance between adjacent nests of 75 m (assuming regular distribution and circular territories). Further details on the study area and the biology of the birds are given by Frey-Roos et al. (1995), Bollmann et al. (1997), Brodmann et al. (1997a), Rauter and Reyer (1997) and Reyer et al. (1997).

### Nestling food

The nestling food was assessed by collar samples when the young were 6–9 days old. All nestlings in a nest were prevented from swallowing their food by placing a soft plastic-coated wire around their necks. After every two to three feeding visits of the parents, the food was removed from the nestlings' throats with forceps. Sampling lasted for 1 h and the nestlings were then fed with mealworms and with arthropods caught in the study area, such as tipulids, spiders or caterpillars. If one of the nestlings was much smaller than the others it was removed from the nest and fed during the time of sampling to reduce its risk of starvation. A total of 814 prey items were collected from 41 nests, each nest represented on average by 20 items (range 1–82). The arthropods were preserved in ethanol and identified to the order or, in the case of Diptera and Hymenoptera, to the family.

### Available food

In an initial comparison of five potential methods for assessing arthropod availability (sticky traps, pitfall traps, water traps,

suction apparatus and sweep nets), only the sweep net and the suction apparatus succeeded in collecting the five most important prey taxa which account for 77.7% of the food provided to nestlings: Lepidoptera larvae, Tipulidae (Diptera), Araneae, Saltatoria and Rhagionidae (Diptera). Overall, sucking yielded a higher diversity of arthropods than sweep netting but a lower abundance for most taxa, including all five which are most important as nestling food (Brodmann 1995). Sweep netting was particularly successful in catching agile groups (e.g. Saltatoria, Diptera, Lepidoptera imagines) but less so in obtaining ground-living groups (e.g. Coleoptera, Formicidae). With respect to vegetation type, significant differences between the two methods were only found for Opiliones and Lepidoptera larvae (both  $P < 0.001$ ; Fisher exact probability test). For both taxa, availability is underestimated by sweep netting in low vegetation (meadows and short dwarf shrubs) and by the suction apparatus in higher vegetation (medium-sized and tall dwarf shrubs; mainly *Vaccinium* spp., *Caluna vulgaris*, *Rhododendron ferrugineum* and *Juniperus communis*).

Based on this comparison, the suction method – usually considered to be the least biased sampling technique (Southwood 1991) – proved to be relatively inefficient in catching the important Diptera and Saltatoria and was not unaffected by vegetation structure. Therefore, and because use of the suction apparatus is physically exhausting, we chose to assess the available food by sweep netting. Potential biases and consequences for the results will be mentioned in the Discussion.

In all 3 years, the study area was prey sampled between 17 and 24 June, the period when most pipits have their first nestlings, and again between 14 and 21 July, which is representative for replacement and second clutches. All sampling was done between 0900 and 1800 hours, when the vegetation was dry. Sweep net samples were taken according to a 50 × 50 m grid system that was drawn onto maps of the study area. Since about 50% of all water pipit foraging trips lead to areas outside their territories (Frey-Roos et al. 1995), we recorded the food available to a breeding pair in both its territory and its external foraging range. We then averaged samples from all 50 × 50 m squares visited by the same pair (mean  $\pm$  SD: 12.5  $\pm$  5.0 samples/pair). This resulted in 41 values for available food, one for each nest, which could then be compared with the nestling food at the respective nests. More information on the methods is presented in Brodmann (1995) and Brodmann et al. (1997a).

### Nutrient contents and biomass

1178 arthropods from all common orders or families were collected in the field and conserved on the day of capture by drying them in absolute ethanol at 90°C until all ethanol had evaporated (20–30 min). This drying method has routinely been used by insect physiologists for more than 30 years. The animals were measured to the nearest 0.5 mm (length, width), weighed to the nearest 0.5 mg before drying and then reweighed after drying to determine the water content. About half a year later, they were analysed for energy, protein, lipid and carbohydrate contents in the laboratory.

Crude protein was measured by the Kjeldahl procedure (Minari and Zilversmit 1963) and the contents of lipid and carbohydrate by the methods of Van Handel (1984, 1985a, 1985b). While the contents of protein, lipid and carbohydrate were measured for individual arthropods, energy contents were determined by burning ground arthropod samples of 0.1–0.6 g dry weight in an adiabatic bomb calorimeter (IG Instrumenten-Gesellschaft AG, type IKA C400). In three taxa (Ichneumonidae, Syrphidae, Trichoptera) we could not collect enough individuals for the energy measurements and therefore used literature data in our analyses (Cummins and Wuycheck 1971).

Regression equations relating dry weight to prey size were calculated and then used to estimate the biomass of arthropods from collar and sweep net samples (Brodmann 1995). As a measure for prey size we used the product of lengths and widths, both measured to the nearest 0.5 mm under a dissecting scope by laying the animals on graph paper. The length × width product yielded a

much better relationship to dry weight than length alone; including body height in the regressions did not improve the correlations. As dry weight is usually measured by drying arthropods in an oven at 150°C for 2 h, we tested the efficiency of the ethanol method by drying 100 *Phormia terre-novae* (Calliphoridae, Diptera) from a laboratory population first in ethanol at 90°C and afterwards in an oven at 150°C. On average, 95% of the water was extracted with ethanol relative to the usual method at 150°C. As both estimates of dry weight are highly correlated ( $r^2 = 0.977$ ), the deviation of our method from the standard procedure is negligible.

Calculations and statistics

For two reasons, food availability and preferences were calculated for the whole study area, rather than on a territory basis: (a) water pipits collect about 50% of their prey outside their own territories (Frey-Ross et al. 1995), which makes measures of territory-specific arthropod density an unrealistic estimate of food availability; (b) with more than 20 prey taxa fed to nestlings but with often only a few items found in the collar samples, the variable/sample size ratio was too high for calculating nest-specific diet estimates and variances over all nests.

In a first step, the food provided to the nestlings was compared with the food available within the territory and foraging range of the nest owners. The resulting 41 matched data pairs (one for each nest) were subjected to Wilcoxon tests. Using a threshold of  $P = 0.10$ , prey types were then classified as preferred (+1), indifferent (0) or avoided (-1) for each of 22 arthropod taxa. These preference values were then related to nutrient contents, prey size, prey density and movement (walkers, poor fliers, good fliers) in an analysis of covariance. For crude protein, lipid, carbohydrate and water we used median rather than mean values for each prey taxon

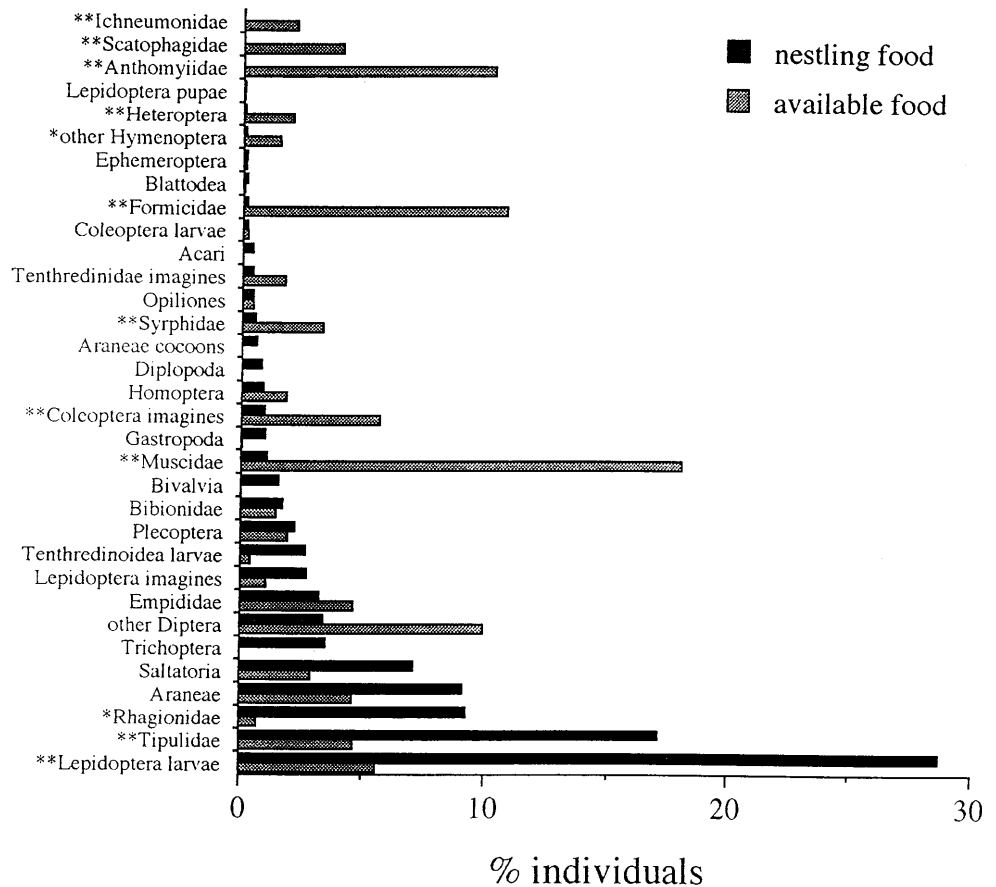
because there are outliers in the data which affect the means substantially. For parametric statistics, absolute values were ln transformed and percentages arcsine-square root transformed.

Results

Relative abundance of prey taxa

Food provided to the nestlings of water pipits is diverse, not very specialized and is dominated in decreasing order by caterpillars (Lepidoptera larvae), tipulids (Diptera), spiders (Araneae), grasshoppers (Saltatoria) and rhagionids (Diptera) (Fig. 1). These five taxa account for 71% of the individuals and 77.7% of the biomass provided to the young. Among the 33 invertebrate taxa studied, only Lepidoptera larvae, Tipulidae and Rhagionidae occurred in nestling food more than expected from sampling (henceforth termed “preferred food”), whereas Coleoptera, Heteroptera, and several families of Diptera (Muscidae, Syrphidae, Anthomyiidae, Scatophagidae) and Hymenoptera (Ichneumonidae, Formicidae, other Hymenoptera) occurred less (“avoided food”). A relatively large number of arthropod orders and families, including the spiders and grasshoppers, are fed to the nestlings in proportions which do not differ significantly from expectation based on our estimates of available prey.

**Fig. 1** Taxonomic composition of nestling food (black bars) and the food available in the territories and at the communal feeding places (stipled bars). For both measures, proportions represent means of the respective individual proportions from 41 nests (\*differences between available food and nestling are significant with paired Wilcoxon tests, \*\*significant after Bonferroni correction)



### Changes in food use partly reflect prey availability

Although water pipits were found to prefer certain prey types as food for their nestlings and avoid others (Fig. 1), for some prey types there is also a relationship between the amount available and that provided to the nestlings. The proportions of tipulids and rhagionids fed to the nestlings were significantly correlated with the available proportions for both taxa (Tipulidae:  $r = 0.65$ ,  $P = 0.0011$ ; Rhagionidae:  $r = 0.57$ ,  $P = 0.0057$ ; Pearson;  $n = 41$  nests). For tipulids, however, proportions actually fed to nestlings changed from more than expected at very low tipulid densities to less than expected at high densities; the deviations of observed from expected proportions are correlated inversely to the tipulids available ( $r = -0.69$ ,  $P = 0.0004$ ; Pearson). Furthermore, in a multiple regression analysis, the proportion of tipulids in the nestling food is correlated positively with the proportion ( $P = 0.0001$ ) and negatively with the total amount of tipulids available ( $P = 0.0188$ ). Thus, there may be a trade-off in which parent water pipits avoid feeding their nestlings too many tipulids when they occur in large numbers and compose a large fraction of the available food.

No such correlations between the amount available and that provided to the nestlings were found for caterpillars, spiders or grasshoppers ( $P > 0.10$ ). Yet, even for some of these groups, there are indications that arthropod proportions fed to nestlings are affected by spatial and temporal differences in food availability (Table 1). In terms of space, grasshoppers were more numerous on the south than on the north slope of the valley and were accordingly fed more to nestlings on the south slope. In terms of time, grasshoppers and rhagionids were more common later in the season, while tipulids decreased in numbers. These seasonal changes

were paralleled by the proportions of these arthropods in the nestling food.

### Nutrient contents

Arthropod taxa differ in a number of behavioural, morphological and nutritional aspects which may cause predators to catch a certain type of prey more often than another. To study the importance of nutritional differences, energy, protein, lipid, carbohydrate and water contents were measured for the commonest taxa in the study area (Appendix). The *energy* content varies little within and between arthropod taxa. Taxon-specific energy values are between 22 and less than 26 kJ per gram dry weight, except for the low outlier value of about 17 kJ/g in diplopods. The highest values are reached by rhagionids (25.4 kJ/g) and heteropterans (25.2 kJ/g). Overall, the values are similar to those reported in other studies (review in Cummins and Wuycheck 1971). Protein, lipid and carbohydrate values vary much more than energy content between different groups of arthropods (Appendix). The amount of crude *protein* ranges from 30.5% of the dry weight in grasshoppers to 83.5% in scatophagids. This almost precisely covers the range of 30–88% given for arthropods by Robbins (1993, p. 250). The *lipid* content varies between 2.5% of the dry weight in grasshoppers and 11.1% in plecopterans with most taxa containing 4–7% lipid. *Carbohydrate* varies from 1.0% in spiders to 5.7% in syrphids and probably depends on the feeding habits of the arthropods: animals that eat pollen or nectar generally contain more carbohydrate. The *water* content lies between 41% of the wet weight for trichopterans and 81% for sawfly larvae (Tenthredinoidea, Hymenoptera), with sawfly larvae, caterpillars, grasshoppers and spiders all containing relatively large proportions (69–81%).

When the five nutrients are related to the *movement* of the respective prey type, lipids, carbohydrate and energy content do not differ between walking, poorly flying and well-flying arthropods, but water content does (MANOVA:  $F_{2,19} = 4.308$ ,  $P = 0.029$ ) and protein content tends to do so ( $F_{2,19} = 3.068$ ,  $P = 0.070$ ). Water contents are lower in flying than walking arthropod taxa while protein tends to rise with increasing agility (Fig. 2).

### Size differences

Figure 3 presents the size distribution of nestling food and available prey independent of taxonomic membership. The size of food items provided to nestlings is significantly larger than the size of available arthropods (Kolmogorov-Smirnov:  $P = 0.0001$ ). Relatively few large prey items contribute to a large proportion of the nestling food: items larger than 10 mg account for 28.1% of all individuals and 62.6% of the biomass fed to nestlings but for only 1.8% of the individuals and 14.2%

**Table 1** Differences in the spatial and temporal composition of available prey items (percent individuals). Shown are  $P$ -values for spatial comparisons between the north and the south slope during the early breeding season and for temporal comparisons between early and late seasons on the north slope, in both cases for food availability and nestling food.  $P$ -values are given for univariate analyses of variance (ANOVA) on each of the five most important food taxa and for Wilks' lambda from canonical discriminant-function analysis based on all five prey types together. Significant results are *italicized*

	South–north		Early–late	
	Food availability	Nestling food	Food availability	Nestling food
ANOVA				
Lepidoptera larvae	0.162	0.443	0.479	0.431
Tipulidae (Diptera)	0.241	0.409	0.455	0.101
Araneae	0.688	0.377	0.100	0.766
Saltatoria	<i>0.001</i>	<i>0.001</i>	<i>0.048</i>	<i>0.023</i>
Rhagionidae (Diptera)	–	–	<i>0.041</i>	<i>0.004</i>
Discriminant function				
Wilks' lambda	<i>0.001</i>	<i>0.036</i>	<i>0.026</i>	<i>0.018</i>

of the biomass in the arthropods available. The size difference between nestling food and available prey could be due to the parents favouring large taxa. But for individual taxa also, prey size in nestling food is significantly larger than expected from availability (Fig. 4; Wilcoxon's signed-ranks test:  $P = 0.006$ ,  $Z = 2.741$ ,  $n = 17$ ).

Relationships between food preference and prey characteristics

“Food preference” is determined for each taxon as preferred (1), indifferent (0) or avoided (-1) (cf. Materials and methods, Fig. 1 and Appendix). An analysis of covariance related these taxon-specific preference values to eight corresponding prey characteristics: protein,

lipid, carbohydrate, energy and water contents as well as size, density and movement of the prey (Table 2). Only movement showed a significant effect. Using a stepwise backward procedure, all five nutrient variables and prey density were excluded, while size and movement were retained in the final model. Preference tends to increase with prey size, thus supporting the result of the previous analysis which ignored taxonomic membership (Fig. 3). In terms of prey movement (Fig. 2), pairwise comparisons showed that average preference values for the slowly flying arthropods were significantly higher than for the fast-flying and walking ones ( $P = 0.001$  and  $P = 0.009$ , respectively; Scheffe's test), whereas the latter two groups did not differ from each other ( $P = 0.775$ ).

Discussion

Nutrient composition

Our study yielded no evidence for an effect of prey nutrient composition on nestling provisioning. Besides low

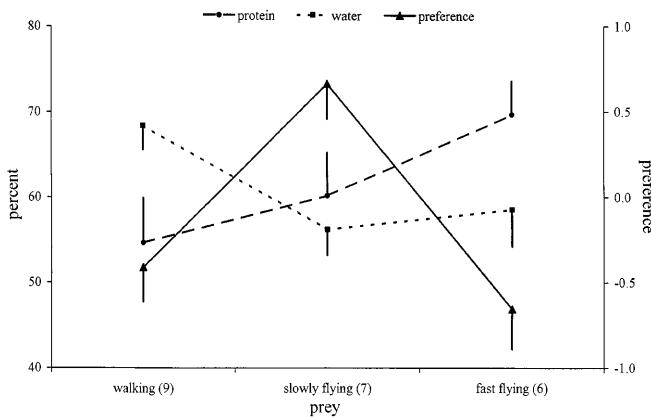


Fig. 2 Percent water (per gram wet mass) and protein (per gram dry mass) as well as food preference in relation to prey movement. Preference and movement categories correspond to the respective classes in the Appendix. Shown are least-square means, i.e.  $\bar{Y}$ -values for which  $\Sigma(Y-\bar{Y}) = 0$  (Sokal and Rohlf 1969, p. 412). Sample sizes are given in parentheses; for clarity, SEs are only drawn on one side

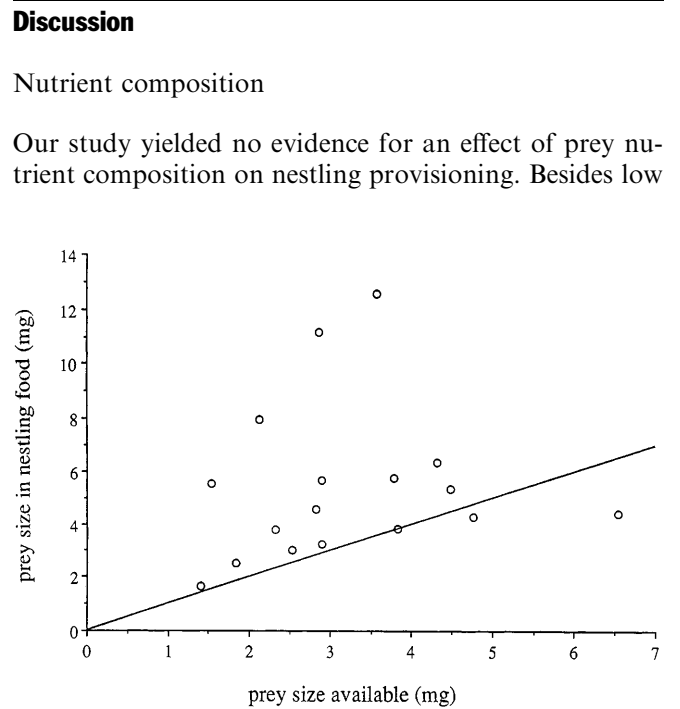


Fig. 4 Relationship between the average size of nestling food and of available food for each of 17 prey taxa. The line indicates equal sizes

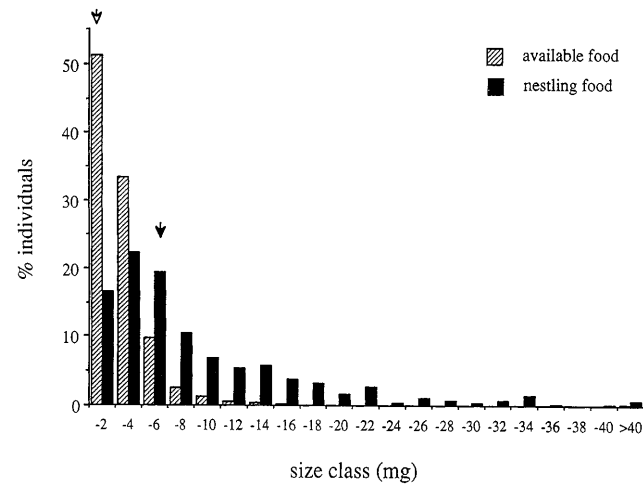


Fig. 3 Differences in the size distribution (mg dry weight) between nestling food and the available food, independent of prey taxa (arrows indicate medians)

Table 2 Summary statistics of the analysis of covariance for prey preference in relation to their movement (walking, slowly flying, fast flying), size, density and nutrient contents ( $n = 22$  taxa).  $R_1^2$  and  $P_1$  refer to the complete model,  $R_2^2$  and  $P_2$  to the model remaining after stepwise variable exclusion (dependent variable: prey preference  $R_1^2 = 0.651$ ,  $R_2^2 = 0.598$ )

Source	df	MS	F	$P_1$	$P_2$
Movement	2	2.405	6.575	0.012	0.001
Size	1	0.572	1.564	0.235	0.070
Density	1	0.293	0.801	0.388	
Protein	1	0.005	0.012	0.913	
Lipid	1	0.096	0.263	0.617	
Carbohydrate	1	0.134	0.365	0.557	
Water	1	0.028	0.076	0.787	
Energy	1	0.095	0.259	0.620	
Error	12	0.366			

statistical power due to high variability and small sample size ( $n = 22$  taxa), three – not mutually exclusive – biological reasons may be responsible for this result.

First, in arthropods, contents of protein, lipid, carbohydrate, energy and water may exceed the minimal avian requirements and, therefore, may not have a limiting effect (Studier et al. 1991; Robbins 1993). Second, food choice could be based on other quality factors such as essential amino acids (e.g. Greenstone 1979), minerals and trace elements (e.g. Chambers et al. 1966; Anderson and Stewart 1969, 1973; Seastedt and MacLean 1977; Ohlendorf et al. 1986; St. Louis and Breebaart 1991), food digestibility (e.g. Smith and Follmer 1972) or toxins (e.g. Smallwood and Peters 1986). The smaller than expected proportion of coleopterans, heteropterans and ants suggests that toxins and/or poor digestibility of high chitin proportions might influence the water pipits' food choice in specific cases.

Third, nestling water pipits may require a balanced diet, rather than maximum concentrations of certain compounds. Protein has a positive influence on nestling growth (Parks 1982); high energy and lipid values increase profitability directly and indirectly; carbohydrate provides a type of energy that is easily metabolized, and a high water content may be required to prevent dehydration which, in some periods and places, seems to threaten the survival of nestlings (Bollmann 1995; Rauter 1995). The results on tipulids also suggest that a one-sided diet may have negative effects on the nestlings: at high densities, water pipits feed their nestlings fewer tipulids than expected, a result in line with Tinbergen's (1981) finding that large quantities of tipulids may be detrimental to the health of the nestlings. Finally, the dominating role of prey with intermediate agility (Fig. 2) could also be interpreted in terms of diet balancing: a shift from walking to fast-flying prey will increase protein and decrease water intake.

### Profitability

A further potential explanation for the dominance of prey with intermediate agility comes from complex interactions between nutrients and size, crypsis, behaviour or catchability of prey. The low preference value for walking arthropods, for example (Fig. 2), results from the fact that coleopterans, heteropterans and ants are avoided, probably for the reasons mentioned above. When these three groups are eliminated from the analysis, preference values for walking and slow-flying arthropods no longer differ ( $P = 0.154$ ), but both exceed those of fast-flying insects ( $P = 0.070$  and  $P < 0.001$ , respectively). Together with the finding that preference is positively related to prey size, both for all prey taken together (Fig. 3) and within taxa (Fig. 4), and that catching success of water pipits increases with decreasing agility and crypsis of prey types (Brodmann et al. 1997b), these results suggest that foraging water pipits primarily go for large and easily caught prey, i.e.

for profitability. The fact that this is not reflected in a preference for prey of high energy is probably due to the low variation in energy values between taxa (Appendix 1).

A further measure of profitability is prey density. This positively affects overall feeding rates in several bird species (e.g. Goss-Custard 1980; Begon and Mortimer 1986), including water pipits (Brodmann et al. 1997b). Our tests for density effects on taxonomic preference, however, yielded mixed results. Although the proportion of certain taxa in nestling food increased with their availability (Table 2), the preference decreased, as demonstrated for tipulids. Overall there was no effect of prey availability on preference for the five most important taxa. Avoidance of toxic compounds or the need for a balanced diet (see above) may have prevented the birds from concentrating on the most abundant prey (cf. Krebs and Avery 1984). Furthermore, profitability often depends more on prey size than on density; therefore, large prey occurring at low density may be preferred (e.g. Goss-Custard 1977b; Sutherland 1982).

### The role of the sampling method

Statements about preferences crucially depend on reliable estimates of food availability. These are difficult to obtain in the field, because measured densities vary with sampling techniques, vegetation structure, prey characteristics and other factors (Southwood 1991). Our evaluation of such confounding factors revealed the superiority of sweep netting in terms of measuring overall arthropod abundance and a significant effect of vegetation for only one taxon important as nestling food: caterpillars were better caught by sweep nets in high and by the suction apparatus in low vegetation. Since these two vegetation types occurred in similar proportions in our study area, the overall success of the two techniques would probably have been comparable. We, therefore, believe that our estimates come as close to actual prey availability and preferences as one can get in a study under natural conditions. Moreover, our comparisons within taxa are unlikely to be confounded by prey- and vegetation-specific effects of the sampling technique. They show larger average prey size in nestling than in available food (Fig. 4) and positive relationships between the proportions of available and fed prey (Table 2).

Overall, our results suggest that water pipits maximize energy intake of their nestlings by feeding them large, conspicuous or easily accessible prey such as caterpillars, tipulids or spiders. While toxins and digestibility may influence food choice in specific cases, there is no evidence that the birds prefer or avoid taxa according to their protein, lipid, carbohydrate or water contents. Further evidence that food quantity is more important than quality comes from our finding that the number of fledglings is correlated with the amount of available food (Frey-Roos et al. 1995), but not with qualitative traits of prey (Brodmann et al. 1997a).

**Appendix 1** Protein, lipid, carbohydrate, energy and water contents of arthropods. The difference between 100% and the sum of protein, lipid and carbohydrate percentages is due to chitin, faeces and other indigestible roughage. Shown are medians, interquartile ranges (25%–75%) and sample sizes (*n*) [*DW* dry weight, *WW* wet weight, \*data from the literature (see Methods); Preference: -1 = avoided ( $P < 0.10$ ), 0 = indifferent, 1 = preferred ( $P < 0.10$ ); Agility: 1 = walker, 2 = slow flier, 3 = fast flier]

Taxon	Preference	Agility	Protein (%DW)				Lipid (%DW)				Carbohydrate (%DW)				Energy (kJ/g DW)				Water (% WW)			
			Median	25%	75%	<i>n</i>	Median	25%	75%	<i>n</i>	Median	25%	75%	<i>n</i>	Mean	SD	<i>n</i>	Median	25%	75%	<i>n</i>	
Araneae	0	1	63.79	54.63	84.23	30	6.56	5.09	8.42	28	1.04	0.57	1.99	30	22.91	0.33	7	69.18	64.48	73.76	88	
Coleoptera	-1	1	61.41	54.85	69.10	14	6.22	4.55	6.95	15	1.92	1.35	3.18	14	23.40	0.38	5	63.33	56.17	69.34	44	
Diptopoda	0	1	38.20	33.27	39.21	9	5.58	4.46	7.10	10	3.83	3.21	4.25	10	17.15	0.29	2	65.09	63.17	67.22	30	
Anthomyiidae	-1	3	64.40	58.68	70.68	10	9.38	6.87	9.51	10	5.08	4.27	6.22	10	23.04	-	1	43.33	32.00	51.38	23	
Bibionidae	0	2	51.36	44.13	60.98	11	4.25	3.87	5.01	10	3.59	1.69	8.50	10	22.41	0.31	4	60.71	54.26	66.18	31	
Empididae	0	2	69.07	63.67	73.54	20	5.41	4.79	7.76	15	2.79	1.46	3.80	14	22.46	0.13	3	60.00	54.49	66.10	30	
Muscidae	-1	3	77.57	72.64	83.66	10	5.98	4.56	8.23	10	3.30	1.28	6.20	10	23.46	0.11	4	60.39	55.65	66.35	29	
Rhagionidae	1	2	66.96	49.90	76.42	16	7.22	5.99	10.61	20	1.30	0.98	1.70	16	25.41	0.68	4	56.30	49.54	61.43	45	
Scatophagidae	-1	3	83.49	78.96	91.85	8	6.81	6.39	8.88	10	1.11	0.95	1.56	11	22.93	0.13	2	72.04	68.32	74.31	30	
Syrphidae	-1	3	56.35	48.81	68.86	11	5.41	4.22	6.49	9	5.67	4.02	10.37	10	24.19	-	*	64.58	55.29	73.68	30	
Tipulidae	1	2	36.95	31.50	57.11	11	5.33	3.25	6.54	19	4.56	2.92	7.26	17	22.87	0.79	12	65.25	61.43	66.92	32	
Heteroptera	-1	1	49.95	45.06	62.80	11	10.24	6.04	14.73	11	1.70	1.06	2.14	11	25.24	0.41	3	51.81	44.72	56.26	30	
Ichneumonidae	-1	3	66.27	60.78	73.65	10	8.95	6.22	18.36	10	1.54	1.19	2.12	10	22.13	-	*	48.85	40.00	59.06	22	
Tenthredinidae	0	3	69.83	66.04	70.70	10	5.02	4.04	5.28	10	1.89	1.19	2.74	10	23.04	0.29	4	62.05	56.82	64.65	30	
Tenthredinoidea larvae	0	1	49.18	38.75	59.50	11	4.45	3.78	5.51	10	5.69	4.88	7.47	10	23.11	0.06	2	80.74	78.95	82.84	31	
Formicidae	-1	1	80.82	72.11	86.33	24	4.64	4.24	5.37	24	2.35	2.16	2.73	24	21.94	-	*	74.07	70.22	78.12	72	
Lepidoptera	1	2	66.99	61.03	71.16	30	5.03	4.06	9.82	17	1.91	1.64	2.40	10	22.42	-	1	50.45	38.46	56.00	42	
Lepidoptera larvae	1	1	47.62	39.88	52.85	13	4.87	4.34	6.63	13	4.94	3.32	6.19	10	22.95	0.26	10	75.15	70.63	78.06	36	
Opiliones	0	1	70.27	67.91	75.48	11	6.56	4.90	7.87	10	2.77	1.86	3.36	10	22.68	0.20	3	64.44	55.00	68.32	29	
Plecoptera	0	2	54.19	41.84	64.09	33	11.14	8.78	18.92	31	1.68	1.05	2.54	19	23.22	0.33	2	59.44	45.00	63.89	73	
Saltatoria	0	1	30.53	26.12	37.59	42	2.52	1.47	3.48	22	1.58	1.21	2.12	19	22.44	0.34	13	70.83	65.62	72.54	65	
Trichoptera	1	2	75.84	67.71	77.13	11	11.18	7.96	12.69	10	4.08	2.44	5.80	10	22.95	-	*	41.43	33.00	54.34	27	
Averages			60.50	53.56	68.50	16	6.49	4.99	8.83	15	2.92	2.03	4.30	13	22.83	0.32	5	61.79	55.15	66.85	40	

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