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The Relative Importance of Habitat Structure and of Prey Characteristics for the Foraging Success of Water Pipits (*Anthus spinoletta*)*

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Abstract

While many studies on foraging have related energy gain to the density and the size of prey, only few have investigated whether and how habitat structure modifies the gain through affecting foraging success. In this study, the influences of habitat structure and prey characteristics on the foraging success of water pipits, *Anthus spinoletta*, were investigated experimentally. The birds take longer to find prey in tall than in short vegetation. The effects of vegetation on searching times differ between prey types. These differences are probably caused by variation in prey behaviour and in cryptic colouration, but not by prey size. Searching times increase with decreasing density for mealworms and tipulids, but not for caterpillars. Handling large prey items requires more time than handling smaller prey. Tipulids and caterpillars, which were offered alive, are handled for a longer time than dead mealworms of corresponding size. The success of attacks on flying insects is probably influenced by the prey's flight speed: fast houseflies are missed more often than slow tipulids. Overall, the results show that the time costs of foraging water pipits are influenced to a comparable degree by vegetation structure, by prey density and by other specific prey characteristics such as camouflage, hiding behaviour or agility. The amount of food gathered per unit time is determined primarily by factors that affect searching times, and less by handling and travelling times. Insertion of our data into an optimal diet model leads to the prediction that water pipits should be generalist foragers, which agrees with the observed behaviour.

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Introduction

The amount and quality of food is often a critical resource limiting the fitness of animals. For birds, MARTIN (1987, 1995) reviewed the influence of food on their

* This paper is dedicated to Wolfgang Wickler on the occasion of his 65th birthday.

breeding success and on other life-history traits. Investigations of foraging efficiency in birds have concentrated on the influence of prey characteristics such as density, distribution, size, conspicuousness or behaviour (reviews: BEGON & MORTIMER 1986; BEGON et al. 1986; ENDLER 1991; KREBS & DAVIES 1993; SIH 1993). They have shown that birds forage preferentially in habitats or patches with high food density (WATSON 1970; EVANS & DUGAN 1984) and that searching times are inversely related to food density (SMITH & SWEATMAN 1974; HULSCHER 1976; DAVIES 1977; BARNARD & THOMSON 1985). But predators may also search where prey items are largest (GOSS-CUSTARD 1977; SUTHERLAND 1982) or most readily detectable (GETTY & PULLIAM 1993) rather than where they are most abundant. Visibility of prey can be reduced by morphological and behavioural prey characteristics such as cryptic colouration (ERICHSEN et al. 1980; LAWRENCE 1985), feeding at night or other avoidance behaviour (MAIN 1987; PIERCE 1988).

While foraging theory and field studies on foraging animals mostly consider food characteristics, primarily food density, the effect of habitat structure on foraging success may be equally important. This has long been suggested from observational studies (MOERMOND 1979; ROBINSON & HOLMES 1982, 1984), and some investigations have specifically addressed this topic. Vegetation structure and density affects searching times and capture rates of insects (GREVSTAD & KLEPETKA 1992), aquatic organisms (MAIN 1987; DIEHL 1988; PIERCE 1988; GREFENBERG et al. 1995) and birds (EISERER 1980; BARNARD & THOMPSON 1985); among mammals, ZIV et al. (1995) showed in the field and in laboratory experiments that the substrate influences the foraging success of gerbils digging for seeds. We know, however, of only one experimental bird study investigating the relative importance of habitat structure and food characteristics for foraging strategies. WHELAN (1989) found for two species of paruline warblers (*Dendroica*) that their preference for a certain vegetation structure could be reversed when prey biomass in the initially avoided structure was increased. This suggests that the birds weighed the benefits from different food densities against the costs of foraging in different vegetation structures. However, these results do not allow any conclusions about the relative importance of vegetation structure and prey density under natural conditions, because the author used artificial plants in his experiments.

In our own field studies we observed water pipits (*Anthus spinoletta* L. 1758) while they were collecting food to provide to their nestlings. We found that foraging birds prefer the vegetation type with the highest food density, and that breeding success is positively related to prey density at the feeding sites (FREY-ROOS et al. 1995). However, the preferred vegetation 'grass' is also short vegetation. Consequently, habitat structure confounds the effects of food characteristics. The aviary experiments presented in this paper were designed to separate the relative importance of vegetation and prey characteristics in foraging success.

Methods

Subjects

Six water pipits (2 males, 4 females) were caught in May 1993 in the Dischma valley (Graubünden, Switzerland) where breeding pipits had been studied during the previous three summers. The six birds were

kept for 10 wk in separate wire-mesh cages. During this time they were fed twice per day with standardized food (dried insects, beef heart, curd, vitamins), at 1000 h after the experimental trials (see below) and at 1600 h. The food was removed at 1800 h to prevent the birds from eating in the morning before experiments started.

Experimental Cages

The cages measured $1.5 \times 1 \times 1.8$ m and were placed in an aviary at the University of Zürich. The front side of each cage had an acrylic window to facilitate observation. The other sides and the roof were covered with gauze to prevent flying insects from escaping. The floors consisted of drawers with vegetation (see below) and could be moved between cages.

Vegetation Treatments

Three of the six cages were equipped with vegetation, one each with juniper (*Juniperus communis*), bilberry (*Vaccinium myrtillus*) and grass (3 treatments), the other three with little rocks and branches (no treatments). The vegetation was planted in a 20-cm-thick layer of soil and maintained fresh for the whole time of the experiment. Bilberry and juniper plants were collected from the field study sites in the Dischma valley, grass from the university grounds. The three types of experimental vegetation corresponded in their height and structure to the main feeding sites in the field (FREY-ROOS et al. 1995) and resembled the natural vegetation.

Prey Types

The birds were offered three types of prey: mealworms (*Tenebrio molitor*, Coleoptera), caterpillars (Lepidoptera) and *Tipula* spp. (Diptera). Mealworms are easily available and standardized prey. They allowed us to test size effects by offering whole and half items (corresponding to size differences between small and large caterpillars; Fig. 1). The mealworms were killed prior to the experiments by crushing their head capsule with forceps. Caterpillars and *Tipula* spp. are the two most important natural prey types (BRODMANN et al. 1996). They were collected at our field study sites and presented alive during the experiment. To make the

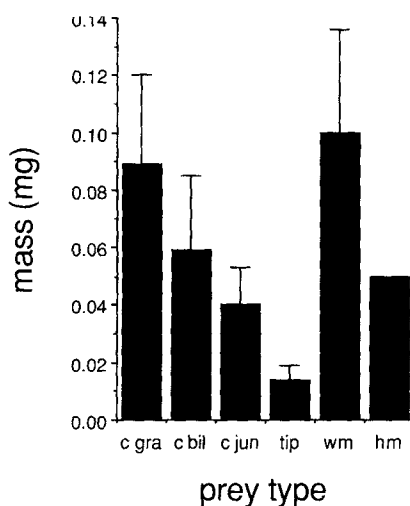


Fig. 1: Mean mass \pm SD (mg dry weight) of the different prey types used in the experiments: c, caterpillars, on gra, grass ($n = 72$ prey individuals), bil, bilberry ($n = 109$), jun, juniper ($n = 108$); tip, tipulids ($n = 90$); wm, whole mealworms ($n = 30$); hm, half mealworms, not weighed but shown as half the mass of whole ones

caterpillars behave as normally as possible, we only used species living naturally on the different plant species. Hence different species of caterpillars were tested on the different vegetation types, namely *Thera cognata* (Geometridae) on juniper, and *Lygris populata* (Geometridae), *Entephria caesiata* (Geometridae) and other Geometridae on bilberry. As we could not find enough caterpillars living on grass, we used sawfly larvae (Tenthredinoidea, Hymenoptera, species unknown) collected on the university grounds. They are very similar to caterpillars in their morphology, behaviour and their protein, lipid and water contents (BRODMANN 1995). Furthermore, the colour of different geometrid caterpillars has been shown to affect the foraging success of birds more than taxonomic differences between caterpillars and sawfly larvae (ALTEGRIM 1990). Therefore they are referred to as 'caterpillars' in the following results.

Training Period

Prior to experiments, every pipit was allowed to search for food twice in each vegetation treatment. The birds were offered a fixed number of crickets, mealworms and tipulids but no caterpillars because they were not available in sufficient numbers during this period.

Experimental Design

Every bird was offered each prey type once in each vegetation treatment. A single bird was therefore tested 12 times (3 vegetation treatments, 3 prey types, 2 mealworm sizes), once every other day. During an experimental trial, observations were made from a hide 1.5 m from the cage and lasted for 50 min or until all prey items were eaten. The six cages were arranged in such a way that cages with and cages without vegetation alternated. All drawers (i.e. both with and without vegetation) were rotated daily to the next cage. Every day the birds with vegetation were tested between 0700 and 1000 h.

In each experimental trial, 12 prey items were distributed haphazardly in the vegetation 10 min before the trial was started. In the first set of experimental trials, all birds were presented with tipulids, in the second set caterpillars, and finally whole and half mealworms. As tipulids and caterpillars from the field were only available for short time periods, we could not assign prey types randomly, but had to use the different prey types in the sequence they were available. Consequently, we treat trials with different prey types as separate experiments. In the mealworm experiment we offered three of the birds whole mealworms first and half ones later, the other three birds vice versa. On a few occasions the birds hardly searched for prey during the experimental trials. Therefore, all trials with fewer than three captured prey items were excluded from the statistical analysis. As a consequence, the total degrees of freedom presented in Tables 1 and 3 are smaller than for complete designs and sample sizes vary in Figs 2–5.

Response Variables

During the experiments we made observations on searching times (ST) and handling times (HT). Unlike in early models of optimal foraging where ST mainly reflected travel time between different prey locations (HOLLING 1959), in our study ST to a large extent represents the time needed for detecting a (camouflaged) prey item within a location. Because of the small size of the cage and because the birds rapidly switched between moving around and looking, these two components of searching could not be separated experimentally. We collected the following data: 1. the time when a bird started searching for prey on the ground; 2. the time when it stopped searching, usually to rest on a perch, preen its feathers, or to handle a prey item; 3. the time when it picked up a prey item; and 4. the time when it swallowed the prey item. ST is defined as the duration between the beginning of searching and the time of picking up a prey item, deducting the time intervals when not searching. HT is the time between picking up a prey item and swallowing it. All data were recorded on a computer with the program 'The Observer' (NOLDUS 1990). As tipulids tended to fly around and cling to the walls and the roof of the cages, only tipulids caught in the vegetation were included in the analysis.

Attack Success in Relation to Prey Agility

In a separate experiment, we investigated whether the agility of flying insects affects the catching success of water pipits. We offered captive birds slow tipulids, *Tipula* spp., captured in the field and fast houseflies, *Musca domestica*, from laboratory populations. As the first three experimental trials had suggested that a mutant of the housefly with pale eyes was caught more easily than the wild type, the experiments were

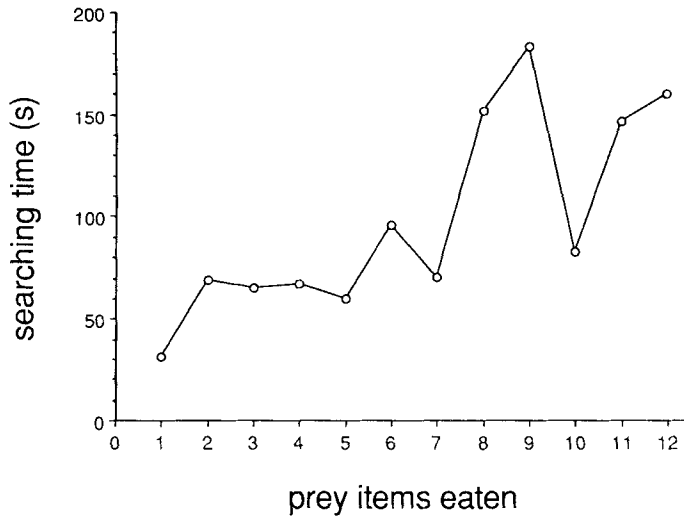


Fig. 2. Mean searching times for the 1st, 2nd, 3rd etc. prey item during experimental trials in which at least three items were caught (see Experimental Design). Means are based on sample size between 64 (items 1–3) and 8 (item 12)

repeated with pure strains of the wild type and the pale-eyed mutant 'yellow' (MILANI 1967). During the experiment each bird was offered 12 tipulids, 15 houseflies of the wild type and 15 mutants. More houseflies than tipulids were offered in a trial because the houseflies were more likely to escape through gaps of the cages. Successful and unsuccessful attacks were counted. A trial was stopped after 40 attacks or after the last prey item had been eaten or had escaped.

Statistics

The experiments were planned according to a within-subject design: the same subject, in our case an individual bird, is tested several times with different vegetation treatments. Therefore data were analysed with an analysis of variance using the interaction of subject by treatments as error term. As dependent variables we used mean ST and HT for the first seven prey items caught. The decision to use the first seven items is based on the marked increase in ST after the 7th item (Fig. 2). To test whether there is a substantial influence of this somewhat arbitrary decision, we repeated our analyses for means of the first six items caught. ST and HT were log-transformed prior to analysis.

To study the influence of prey density, or rather prey depletion, on ST and HT, we calculated mean values from the six birds for the first, the second, etc. prey items eaten, separately for each vegetation type. Mean ST and HT were correlated with the amount of prey items eaten using Spearman rank correlations. The probability values for the three vegetation treatments were then combined according to the method described by SOKAL & ROHLF (1981).

The success of attacks on tipulids and houseflies were compared with Wilcoxon signed-ranks tests. All statistics were calculated on SAS (SAS Inst. 1985) using the procedures CORR, GLM and UNIVARIATE.

Results

Foraging Behaviour

Foraging behaviour of the captive water pipits resembled their natural behaviour. In the field, foraging pipits usually walk along the ground and peck for insects and other

Table 1: Summary statistics of analysis of variance for searching time with the interaction subject by treatments as an error term. Searching times were log-transformed before analysis. p6, probability-value for averages of the first six prey items eaten. All other values correspond to averages of the first seven items eaten (see statistics in Methods section)

Prey type	Source	df	MS	Error term	F	p	p6
Mealworms	Vegetation	2	3.04	Veg × Bird	6.57	0.0151	0.0314
	Prey size	1	0.13	Veg × Size	0.09	0.7782	0.7820
	Bird	5	1.09				
	Veg × Size	2	0.12	Veg × Size × Bird	0.22	0.8072	0.9051
	Veg × Bird	10	0.46				
	Size × Bird	5	1.44				
	Veg × Size × Bird	10	0.56				
Caterpillars	Vegetation	2	7.99	Veg × Bird	29.56	0.0001	0.0004
	Bird	5	0.54				
	Veg × Bird	9	0.27				
Tipulids	Vegetation	2	0.58	Veg × Bird	0.84	0.4952	0.1087
	Bird	5	0.09				
	Veg × Bird	4	0.69				

invertebrates on the soil or on plants. They search dwarf shrubs from the ground, by climbing through the twigs, or by balancing on top of the plants. In the experiments they searched grass by walking on the ground, bilberries both from the ground and by climbing over the twigs, while junipers were mostly searched by climbing around the shrubs. As in the field, the water pipits occasionally caught flying insects by sallying in the manner of flycatchers. When a prey item was caught, the water pipits hit the prey

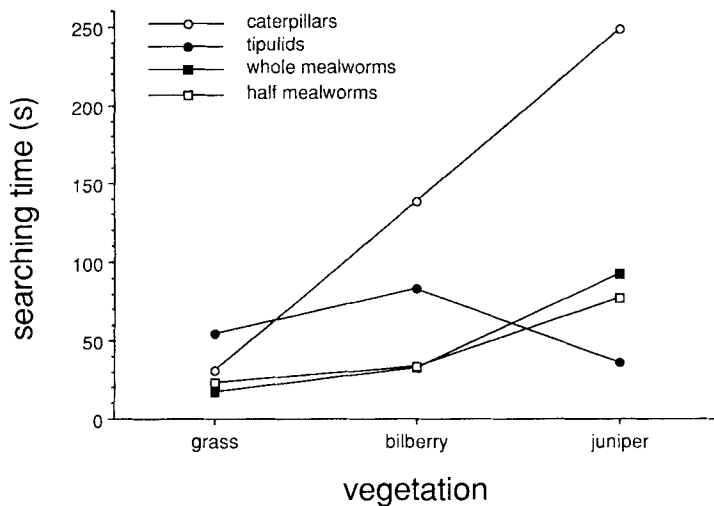


Fig. 3: Average searching times for four types of prey in three different vegetations, which increase in height from grass to juniper. Each value represents a mean of 4–6 birds

Table 2: Spearman rank correlation coefficients (rs) between the number of prey items eaten and searching times, and between items eaten and handling times. p comb, combined probability value for each prey type over all three vegetation types (SOKAL & ROHLF 1981)

Prey type	Vegetation	Searching time			Handling time		
		rs	p	p comb	rs	p	p comb
Whole mealworms	Grass	0.95	0.000	<0.01	0.50	0.095	ns
	Bilberry	0.79	0.002		0.20	0.542	
	Juniper	0.58	0.060		0.35	0.285	
Half mealworms	Grass	0.77	0.003	<0.01	0.65	0.022	ns
	Bilberry	0.81	0.003		0.46	0.151	
	Juniper	0.82	0.001		0.06	0.863	
Caterpillars	Grass	0.51	0.090	ns	-0.13	0.697	ns
	Bilberry	0.45	0.224		0.00	1.000	
	Juniper	0.14	0.787		-0.49	0.329	
Tipulids	Grass	0.23	0.471	<0.05	-0.60	0.041	ns
	Bilberry	0.94	0.005		0.09	0.872	
	Juniper	0.41	0.212		0.06	0.853	

back and forth against a branch or on the ground, probably to kill or stun the arthropod, and kneaded and rotated it in the bill before swallowing it. While the birds usually took more time to handle live than dead insects in this manner, the actual act of swallowing a prey item was always very quick (<1 s), independent of size or prey type.

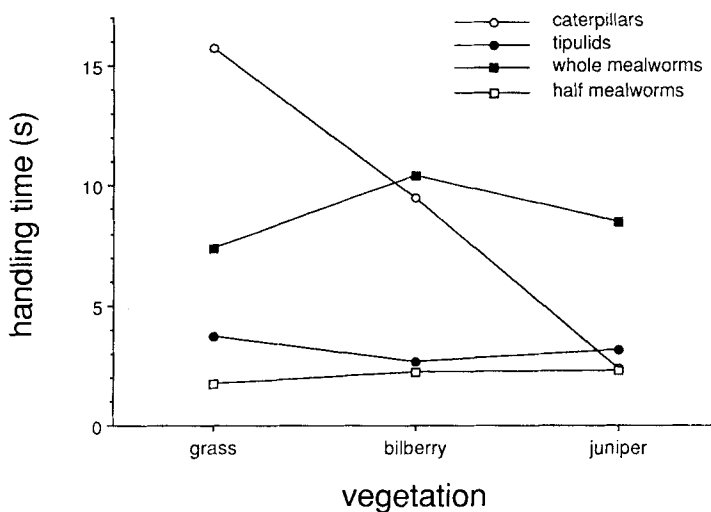


Fig. 4: Average handling times for four types of prey in three different vegetations. Each value represents a mean of 4–6 birds

Effect of Vegetation on Searching Times for the Three Prey Types

On average, the water pipits searched longest to find a caterpillar, an intermediate amount of time for a tipulid and shortest for mealworms. The type of vegetation has a significant effect on the searching times (ST) for mealworms and for caterpillars, but not for tipulids (Table 1). Average ST are shortest in grass, intermediate in bilberry and longest in juniper (Fig. 3). Within this sequence there is an eightfold increase in ST for caterpillars, a fourfold increase for mealworms and no difference for tipulids. No significant difference in ST could be detected between whole and half mealworms. Therefore prey size does not influence ST within the size range of small and large caterpillars. Analysing mean ST of the first six instead of the first seven prey items eaten, did not alter the results (Table 1). For mealworms and tipulids, ST increased with the number of prey items eaten (Table 2). This may be due either to reduced density or to satiation (see Discussion). We found no correlation between ST and the number of caterpillars eaten.

Effect of Vegetation on Handling Times for the Three Prey Types

The handling times (HT) are shortest for half mealworms, followed by tipulids, whole mealworms and caterpillars (Fig. 4). There is a significant effect of prey size on the HT of mealworms. Vegetation has an effect on the HT of caterpillars (Table 3) with a marked decrease from grass through bilberry to juniper (Fig. 4). However, different species of caterpillars were used in the different vegetations, and effects of vegetation are confounded with effects of caterpillar species. Because these species differ in size, and because size but not vegetation affects HT in mealworms, it seems more likely that HT for caterpillars are actually influenced by size rather than by vegetation (see Discussion). No correlation exists between HT and the number of prey items eaten.

Table 3: Summary statistics of analysis of variance for handling time, as in Table 1

Prey type	Source	df	MS	Error term	F	p	p6
Mealworms	Vegetation	2	0.12	Veg × Bird	1.16	0.3534	0.4426
	Prey size	1	9.98	Veg × Size	38.73	0.0016	0.0018
	Bird	5	0.92	Veg × Size × Bird	0.04	0.9579	0.9448
	Veg × Size	2	0.01				
	Veg × Bird	10	0.10				
	Size × Bird	5	0.26				
	Veg × Size × Bird	10	0.11				
Caterpillars	Vegetation	2	4.41	Veg × Bird	12.36	0.0026	0.0048
	Bird	5	0.41				
	Veg × Bird	9	0.36				
Tipulids	Vegetation	2	0.03	Veg × Bird	0.10	0.9076	0.4672
	Bird	5	1.08				
	Veg × Bird	4	0.27				

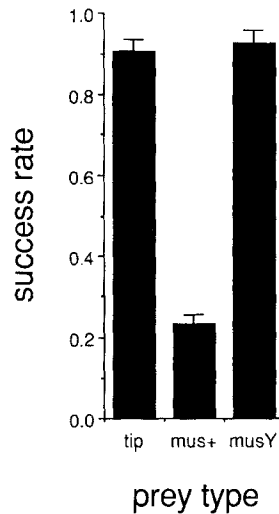


Fig. 5: Mean proportions of successful attacks on tipulids (tip), wild-type *Musca domestica* (mus +), and yellow-eyed *Musca domestica* (musY). Error bars are standard errors, $n = 6$ birds for each prey type, 12–40 attacks per experimental trial with each bird

Therefore prey depletion or satiation does not affect HT within the tested range (Table 2).

Effect of Agility on Attack Success

All six water pipits were more successful at catching the slow tipulids than the fast houseflies of the wild type (Wilcoxon $p = 0.028$). On average, nine out of 10 attacks on *Tipula* spp. were successful as opposed to slightly over two out of 10 on *Musca domestica* of the wild-type strain (Fig. 5). Mutated *Musca* with yellow eyes are caught as easily as the tipulids (Wilcoxon $p = 0.686$) and more often than the wild type ($p = 0.028$). The mutation changes the eye pigmentation, which most likely affects the ability to see by reducing the contrast sensitivity (HENGSTENBERG & GOETZ 1967; GRIBAKIN 1988), and perhaps other phenotypical traits expressed by linked genes.

Discussion

In the course of our field studies we posed the question whether foraging success of water pipits is primarily influenced by prey density or whether other specific prey characteristics (e.g. size, crypsis or agility) and vegetation structure had an effect comparable in magnitude.

How is the Foraging Success Affected by Prey Density?

Possible effects of prey density were only studied through the prey depletion during an experimental trial. We found a positive correlation between the number of prey items eaten and the ST for mealworms and tipulids. During the experiments, ST

increases by approximately one order of magnitude from high to low density. This increase can be explained as an effect of either prey density or predator satiation. For two reasons, depletion of prey density is the more likely interpretation. Firstly, there is no correlation between depletion and ST for caterpillars, although they yielded more biomass than the tipulids or the half mealworms and therefore should have satiated the birds more. For caterpillars other factors, such as camouflage (see below), seem to affect searching times more than density, within the range of densities tested. Secondly, we found no correlation between the number of prey items eaten and the handling times of any of the prey types tested. This again suggests that there was no satiation of the birds during the experiments. An inverse relation between food density and searching times corresponds to observations from several other studies (SMITH & SWEATMAN 1974; HULSCHER 1976; DAVIES 1977; BARNARD & THOMPSON 1985).

How is Foraging Success Affected by Vegetation Structure and by Specific Prey Characteristics?

Effects on searching times. We found no effect of vegetation on ST for tipulids. For whole and half mealworms, there is about a fourfold increase in ST from grass through bilberry to juniper and an eightfold increase for caterpillars. Results for caterpillars are confounded by the fact that different species were used for the experiments in the different vegetation types. Consequently, these caterpillars differ in size and in their behaviour. Those living on juniper are both the smallest and, to our eyes, the most cryptic ones, often hiding under branches. The caterpillars presented on bilberry are intermediate in size and camouflage and imitate little branches, whereas the sawfly larvae on grass are the largest and most obvious prey, because they climb to the tips of grasses. The effects of vegetation structure on foraging are in agreement with two field studies on birds. BARNARD & THOMPSON (1985) observed that ST of plovers were shorter in sparse than dense grass and EISERER (1980) found that American robins preferred short grass for foraging to long grass.

If we use the differences in ST for mealworms as an estimate for the effect of vegetation per se, we see that vegetation explains only part of the variation in ST for caterpillars (Fig. 3). As no differences were found between half and whole mealworms, which correspond roughly in size to the smallest and largest caterpillars (Fig. 1), it seems likely that most of the remaining variation is explained through the effects of behaviour and camouflage of the different caterpillars rather than by their size differences. Both cryptic colouration and behaviour have been shown to affect foraging success substantially (ERICHSEN et al. 1980; LAWRENCE 1985; ALTEGRIM 1990). We found no influence of the vegetation on ST for tipulids, possibly because the tipulids tend to fly when disturbed and are therefore rather obvious and easy to catch in all three vegetations.

The different prey types were tested in sequence and the birds were not experienced with caterpillars in captivity prior to the experiments (see Methods). Therefore, we treated the trials with each type of prey as a separate experiment. However, it is unlikely that sequential or time effects during the experiment change the general effects of vegetation. The differences between the three prey types (i.e. no effect of vegetation on ST for tipulids, intermediate effect for mealworms and strongest effect

for caterpillars) therefore suggest that specific differences between prey types substantially influence foraging success. If all prey types are included in a single analysis of variance, prey type has a significant effect on both ST ($p = 0.0014$) and HT ($p = 0.0498$).

Effects on catching success. In field studies, we found that water pipits rarely feed their nestlings on fast-flying insects (BRODMANN et al. 1996). As some of these taxa, e.g. muscid flies, occur in high densities and are very obvious in the field, we expect searching times to be short. But if prey have a good chance of escaping, the predator's energy intake per unit time is affected by the rate of successful attacks. In our experiments, only two out of 10 attacks on *Musca domestica*, but nine out of 10 attacks on *Tipula* spp., were successful. These results therefore suggest that fast insects are avoided because too few attacks are successful, lowering profitability relative to slow insects.

Effects on handling times. HT are affected by prey size, as measured by the difference between whole and half mealworms. These results agree with observations on wading birds, which also showed an increase in HT with increasing prey size (GOSS-CUSTARD 1977; SUTHERLAND 1982). The apparent decrease in HT of caterpillars from grass to juniper is also likely to result from corresponding prey size differences rather than from vegetation effects per se, because these were not found for any of the other three prey types. Caterpillars and tipulids, which were always presented alive, took longer to handle than dead mealworms of corresponding size.

How Important are the Different Time Costs and the Variables Affecting these Time Costs?

The relative importance of different time costs depend on their ratios. The ratio of handling time to searching time is on average 1:21. It varies between 1:2 for caterpillars and whole mealworms in grass and 1:103 for caterpillars in juniper. In our field study area, water pipits fed their nestlings primarily tipulids caught in meadows, and caterpillars and spiders from dwarf shrub habitats, and handled them in a manner similar to that observed in the aviary. Therefore, handling times are probably also one to two orders of magnitude shorter than searching times in the natural situation. Also, with a measured flying speed of about 10 m/s, travel times on average amount to only 3% of total foraging time. Consequently, travel time and handling time contribute much less to the time costs of foraging water pipits than searching time.

The implications of these ST/HT ratios for prey choice can be illustrated by a simple equation (KREBS & DAVIES 1993, p. 61): when encountering two prey types, big prey₁ with an energy value E_1 , a handling time h_1 and a search time S_1 , and small prey₂ with the corresponding values E_2 , h_2 and S_2 , a predator should take both types when $S_1 > (E_1 * h_2 / E_2) - h_1$ (generalist), but take only the bigger type when the reverse is true (specialist). If we take the masses from Fig. 1 to reflect prey-specific energy content (E) (BRODMANN 1995; BRODMANN et al. 1996) and use the values for searching (S) and handling times (h) from Figs 3 and 4, the above equation for generalizing is fulfilled under all possible conditions. In other words, searching times are long enough to lower encounter rates to such an extent that no prey choice is to be expected.

Although this agrees with the fact that water pipits are generalist insectivores (BRODMANN 1995), our estimates of handling single prey may not accurately reflect the

handling times of parents gathering food for their nestlings, because the birds are multiple-prey loaders. Because overall time costs depend greatly on specific prey characteristics and on environmental conditions such as habitat structure, ST/HT ratios will vary accordingly within and between species. Foraging oystercatchers, for instance, take about 30% of the total foraging time to handle their prey (ZAWARTS & WANINK 1984), while in winter, black-headed gulls spend up to 25% of the daytime travelling between their roost and feeding places (BRODMANN et al. 1991). If, under more natural conditions, handling times of water pipits for, say, the small caterpillars in juniper were 10% rather than measured 1% of the searching time, specializing on the big caterpillars in grass would pay according to the above equation. Similarly, low success rates in catching fast-flying insects (Fig. 5), an equivalent of high handling times, could make such prey items unprofitable. This may explain why water pipits – despite being rather generalist foragers – avoid, e.g. agile muscid flies.

Overall, however, our results suggest that the time costs of foraging water pipits are determined mostly by search time, which itself is substantially affected not only by prey density, but also by vegetation structure and by species-specific prey characteristics such as prey behaviour and camouflage. Optimal foraging models and field studies on foraging most often consider effects of prey density, prey size and one or more nutritional constraints. Our results show that the foraging situation in the field can be more complex. Specific prey and habitat characteristics should also be considered, because they may substantially influence foraging success and decisions.

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