Relationships between food resources, foraging patterns, and reproductive success in the water pipit, *Anthus sp. spinoletta*

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A basic but rarely tested assumption in optimal foraging theory is that positive relationships exist between the foraging pattern of an animal, its short-term benefits in feeding, and its long-term fitness. We present evidence for these relationships for a central place foraging situation. We studied the foraging behavior of adult water pipits (*Anthus sp. spinoletta*) feeding nestlings in an Alpine habitat near Davos, Switzerland, with the following results: (1) searching effort decreases with increasing distance from the nest, (2) the amount of prey and the proportion of large items brought to the nest increases with increasing foraging distance, (3) water pipits do not forage according to habitat availability, but prefer vegetation types with the highest food density (mainly grass and herbs) and avoid those with the lowest, and (4) this selectivity is only expressed when the birds forage more than 50 m from the nest, i.e., usually outside the territory. Among the several potential interpretations of these results, the most parsimonious is that foraging decisions are based on profitability, i.e., on the net energy gain per time unit. Additionally, we found that food conditions translate into fitness: the number of fledglings per nest is related positively to the average prey biomass at the foraging place and negatively to the average distance between the foraging place and the nest. Maximum economic distances, which were predicted from this food-fitness relationship, agreed well with the actual foraging distances observed. This suggests a close connection between foraging decisions and fitness. In addition to the theoretical issues, some conservation issues are also briefly discussed. *Key words:* central-place foraging, fitness, habitat use, optimal foraging, reproduction, water pipit. *[Behav Ecol 6:287-295 (1995)]*

Among the most important determinants of an animal's fitness is the amount and quality of food available during reproduction (reviewed by Martin, 1987). Evidence is particularly strong for altricial birds, in which increased food supply has been found to improve both current and future reproductive success. In terms of current success, better food conditions can advance laying date; increase clutch and egg sizes; and improve hatching, growth, and survival rates of the young. In terms of future success, food stress can reduce the residual reproductive value of parents by lowering their survival or by impairing their subsequent production of offspring (reviewed by Nur, 1990; Partridge and Harvey, 1988; Reznik, 1985; Stearns, 1992).

With food having such a strong influence on fitness related traits, we can assume that selection has produced phenotypes which forage in a way that guarantees the best achievable balance between costs and benefits. This idea is at the basis of the large number of theoretical and empirical studies on "optimal foraging" that have been published over the last 30 or so years (for reviews see Kamil and Sargent, 1981; Kamil et al., 1987; Krebs, 1978; Krebs and Kacelnik, 1991; Krebs and McCleery, 1984; Pyke et al., 1977; Stephens and Krebs, 1986). A major problem with tests of optimal foraging is that predictions about the optimal solution and, consequently, agreement with the observed behavior will differ with the currency for the optimum one uses and the constraints and confounding variables one includes in a model. While different combinations of currency, constraints, and confounding variables can usually be identified in simple laboratory experiments,

these are handicapped by the following problem: the observed foraging behaviors only show differences in short-term costs and benefits (e.g., energy intake/time) but are interpreted in terms of optimal solutions selected over evolutionary times. This assumes that foraging differences translate into long-term fitness differences. Fitness differences, however, can be measured only under natural field conditions that are usually far too complex to allow predictions about specific theoretical optima with which the observed foraging patterns can then be compared.

This dilemma has led some authors to doubt the usefulness of optimal foraging notions in field studies (e.g., Zach and Smith, 1981), to criticize the lack of alternative working hypotheses (Ward, 1992, 1993), and even to consider the whole optimal foraging theory a "complete waste of time" (Pierce and Ollason, 1987). Although this skepticism has been countered on several grounds (e.g., Krebs and Kacelnik, 1991; Nonacs and Dill, 1993; Stearns and Schmid-Hempel, 1987; and literature therein), it cannot be denied that few field studies have shown connections between foraging behavior, its short-term costs and benefits in terms of food intake, and its long-term fitness consequences; furthermore, the results are often ambiguous (Blanckenhorn, 1991; Grant and Grant, 1989; Morse, 1988, 1992; Nonacs and Dill, 1990; Ritchie, 1988). Consequently, the need to test the linkage between foraging patterns and fitness has been identified as one of the major requirements for investigating optimal foraging ideas (e.g., Stearns and Schmid-Hempel, 1987; Ward, 1992).

In this study, we present evidence for such a link in the water pipit (*Anthus sp. spinoletta*), a ca. 20-g insect-feeding passerine that breeds in the Alps above the timberline (for details of its biology, see Cramp, 1988; Glutz and Bauer, 1985; Pätzold, 1984). We consider a "central place foraging" situation (Orians and Pearson, 1979; Schoener, 1979) where parent birds move regularly between a nest with chicks and various natural food patches lying within or outside their terri-

tories. Since complex natural field situations do not allow us to specify theoretical optima (see above), we are not pretending to test for optimal foraging hypotheses in the strict sense. Rather, we confine ourselves to providing a logical sequence of three steps. In combination they suggest that there is, indeed, a strong link between short-term time and energy costs and benefits of certain foraging patterns and long-term fitness consequences. First, we investigate several relationships between food resources and the foraging pattern of adults. We then analyze the relationship between food resources and reproductive success. Finally, we use the data on food resources and reproductive success to predict the foraging behavior of parents and compare the predictions with the observed foraging patterns.

Study area

Our study was done in the central Alps of eastern Switzerland in the valley of Dischma, which is oriented NNW-SSE and situated near Davos at 46°46' N, 9°53' E. Compared to the generally temperate climate in Switzerland, the study area is relatively continental with average temperatures of 10.9°C in July and −5.8°C in January, and 1006 mm precipitation per annum in Davos-Dorf. During the study in May-August 1990, temperatures were higher in all 4 months and precipitation was lower in May, July, and August than the longtime averages. The upper part of the Dischma Valley lies above the timberline, which varies between 1800 m and 2000 m above mean sea level. The valley floor is dominated by meadows that are used in summer to produce hay or as pastures for cattle. The slopes have typical vegetation of acid silicate soil dominated by dwarf shrubs between 1800 m and 2400 m and by Alpine meadows above 2400 m. The slopes are grazed by cattle or sheep at relatively low density. The water pipits breed between 1800 m and about 2500 m elevation, where they are the most common bird species. Data for this study were collected on both sides of the valley, close to the settlement of Am Rhin (1845 m elevation). The total study area of 121 ha held 60 breeding pairs, 24 of which were regularly monitored.

METHODS

Foraging behavior

We observed foraging water pipits with a telescope (15–45×) or binoculars (8×) from a blind 50–100 m from the nest or without a blind from 150–200 m. Between 15 June and 4 August 1990, parents in 24 territories were observed twice for two hours each when the nestlings were 5–6 and 9–10 days old. Although most birds were color-ringed, identification of feeding birds was not always possible. Therefore, the foraging trips per nests were analyzed for males and females combined rather than separately. To reduce the influence of different weather conditions on the pipits' and the insects' behavior, we collected data when the vegetation was dry rather than at specific hours of the day. The foraging places, defined as places where a bird searched for food for at least 30 s after arrival, were mapped, and their distances from the nest were calculated. In each of the 24 territories, we recorded the available prey and the vegetation in the foraging places, the available vegetation in and outside the territories, and the breeding success of each pair of water pipits. In 11 of the territories, we also identified the nestling food.

Nestling food

We evaluated potential nestling food by direct observation, through collar samples, and from literature data (Cramp, 1988; Glutz and Bauer, 1985; Pätzold, 1984; Wartmann, 1985). Direct observation of the number and size of prey items

Table 1

Relations between body size (mm) and biomass (mg dry mass) used to estimate the amount of food brought to the nestlings (cf. Methods)

Taxon	Log_n(drymass + 1) =
Diptera (incl. *B. pomonae*)[a]	0.827*log_n(length*width) − 0.694
Muscidae (Diptera)	2.136*log_n(length) − 2.530
Glomeridae (Diplopoda)	2.543*log_n(length) − 2.525
Lepidoptera imagines	1.988*log_n(length) − 2.397
Opiliones	1.912*log_n(length) − 0.970
Saltatoria	2.272*log_n(length) − 2.608

[a] Because *Bibio pomonae* could be observed in 1990 only, the overall equation for Diptera including length and width was used.

brought to the nestlings was possible at one nest only. The nest was observed during 3 h in the afternoon of 8 August and for 4 h during the following morning. Out of 108 registered foraging trips, the food items could be identified in 98 cases. The nestling food consisted mostly of grasshoppers (Saltatoria), fever flies (*Bibio pomonae*, Diptera), and other flies (probably Muscidae, Diptera). We estimated the food biomass brought to the brood per foraging trip from regressions between prey size and dryweight (Table 1). These regressions had been calculated in a separate study for all taxonomic groups that are important as food (Brodmann P and Reyer HU, in preparation). Prey length was estimated in the field to the nearest one-fourth cm by using the bill-length of the water pipits as a scale (average 13 mm, Bollmann K and Schläpfer A, unpublished data). In the case of grasshoppers and a few other arthropods, length of individual prey items brought to the nestlings was entered into the equations. In the case of flies, median sizes were used for calculating biomass (*B. pomonae* length 11 mm, width 3 mm, $n = 98$; Muscidae: length 8 mm, $n = 28$). Biomass taken to the nest per foraging trip was then related to the distance to and the time spent in the foraging places. As a measure of time in the foraging place, we used the time between two successive feeding visits to the nest, which includes the travel times between the nest and the foraging area. However, with a measured flying speed of about 10 m/s, this travel time on average amounts to 3% of the total time spent foraging only and, therefore, can be neglected, especially because time was recorded to the nearest minute only.

We took collar samples at 10 nests, totalling 164 prey items. They were dried with a paper towel, measured (length, width, height) to the nearest 0.5 mm, and weighed to the nearest 0.1 mg (wet mass). After pooling data from all taxa, we found a strong correlation between wet biomass and length × width: ln(biomass) = −1.094 + 1.326 ln(length × width) ($r^2 = .885$, $p = .0001$). Including height did not improve the correlation. Three quarters of the prey biomass found in the collar samples consisted of caterpillars (Lepidoptera), crane flies (Tipulidae, Diptera), and sawfly larvae (Tenthredinoidea, Hymenoptera), but prey composition varied between sites. All arthropod orders and Diptera families that were identified through direct observation, found in the collar samples, and registered in the literature were considered suitable prey for water pipits.

Prey availability

We estimated the available prey with a sweep-net in a standardized method by one person. A sample consisted of 50 sweeps; every two steps, the net was swept once in a semi-circle as close to the ground as possible. Zero to 3 days after observing the birds' foraging behavior, food samples were taken
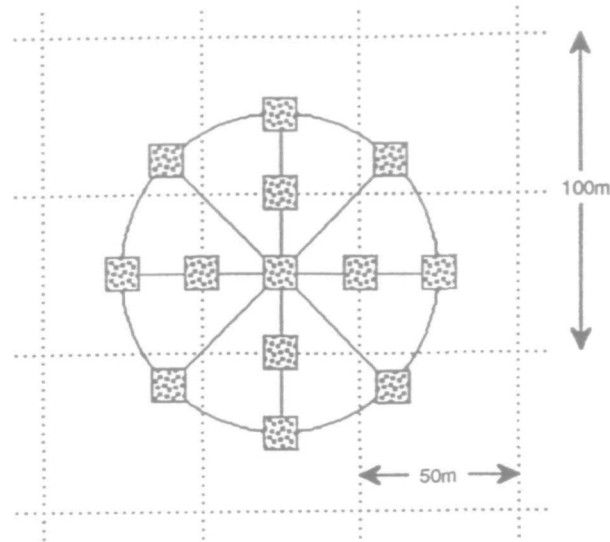
Figure 1
Pattern of plots arranged around the nest to estimate the habitat availability. The thirteen 10 × 10 m plots (stippled) are used for a first comparison between used and available vegetation within the territory, and the larger 50 × 50 m plots are used for preference comparisons within and beyond 50 m.

in the foraging places. All sampling was done between 0900 h and 1800 h, when the vegetation was dry. Measured this way, the arthropod density seems to vary more between wet and dry vegetation than within three days. The sweep-net method was the best of five methods tested, although it is not independent of vegetation structure. In short vegetation, namely Alpine meadows and lichens, caterpillar densities are underestimated relative to those in higher vegetation. For other prey taxa (Diptera, Saltatoria, Araneae), no influence of vegetation structure could be found (Brodmann PA and Reyer HU, in preparation). In this study, only two of the 24 nests were affected by this methodological problem.

Arthropods were killed with ether (aether aceticus) and preserved in 70% ethanol. We examined animals larger than 5 mm² (length × width) and identified them to order or, if important as food for the water pipits, to family. Their lengths and widths were measured and entered into the equation extracted from collar samples (see above) to calculate prey biomass in terms of wet mass.

Vegetation
The vegetation was recorded after the breeding season in 10 × 10 m plots at the foraging places (*n* = 144) and in a regular pattern of 13 plots around each of the 24 nests (*n* = 312; Figure 1). For every 10 × 10 m plot, we registered percentage cover and height of nine plant groups (lichens, grasses and herbs, and seven species of dwarf shrubs) as well as of bare soil and rocks. The proportion of each of these parameters in the foraging places represents the habitat used by water pipits during foraging (=observed values). The proportion in the 13 plots arranged around each nest represents the habitat available within the territories (=expected values), which measure mostly between 1–2 ha. To test whether water pipits select foraging places with certain environmental parameters, rather than foraging randomly (i.e., according to habitat availability), we compared the expected values with the observed ones after weighting each foraging place according to the number of foraging trips it received.

To test whether habitat selectivity was greater for more dis-

tant foraging places than for near ones, we compared the differences between expected and observed values for areas within 50 m of the nest (=roughly the territory limits) with those for areas beyond 50 m (up to 300 m). As we had no information about habitat availability for areas further than 50 m from the nest in terms of 10 × 10 m plots, we calculated expected values for this comparison from a slightly rougher scale, namely a 50 × 50 m grid covering the whole study area. This grid yielded nine squares for calculating availability within 50 m of each nest (Figure 1) and 36 to 101 squares for areas beyond 50 m. The same habitat parameters were registered as before, and the foraging places were again weighted by the number of visits. For this second analysis (based on 50 × 50 m squares), we pooled the vegetation taxa that were preferred, treated indifferently, or avoided, respectively, according to the first preference analysis (based on 10 × 10 m squares).

Relationship between habitat and food
Our method to estimate arthropod density allowed us to relate food abundance only to whole study plots and not to single plant species. To test whether the preferred habitats had a higher food abundance, we, therefore, had to classify the 10 × 10 m plots. With the help of a non-hierarchical cluster analysis (k-means-method, Bortz, 1989), we created 10 habitat types based on the coverage of the different plant taxa within the plots. As before, we then compared conditions at the foraging places with the available habitat to decide which habitat types were preferred. Finally, we compared food abundance between the preferred, indifferent, and avoided habitat types. As we only took food samples in the foraging places, the different habitats are represented unequally.

Reproductive success
We measured the reproductive success by the number of nestlings that were alive during the last observation before fledging, i.e., when the brood was at least 11 days old. We subtracted dead nestlings found right beside the nest after fledging and excluded from this analysis nests that had obviously been preyed upon. Theoretically, this could introduce a bias if hungry nestlings call louder and attract predators. In this case, predation is not random with respect to food availability. In our study, however, this does not apply because total losses of nests were almost exclusively caused by common vipers (*Vipera bera*), which are not attracted to nestling calls. After omitting cases of predation, 17 nests remained for which breeding success was related to the average distance to and the average prey biomass in the foraging places of the respective territories.

Statistical analysis
All comparisons between observed and expected values of habitat use were made with the Wilcoxon matched-pairs signed-rank test. Where several comparisons were made within the same analysis, we divided the conventional significance level (*p* = .05) by the number of comparisons to obtain the new critical value (Bonferroni adjustment). We used multiple and simple linear regression analyses to test for significant relationships between (a) prey biomass and prey size, (b) prey biomass brought to the nest and distance to and time in a foraging place, (c) reproductive success and distance to and food abundance in the foraging place, and (d) expected and observed foraging distances. In analysis (d), we used untransferred data. In cases (a), (b) and (c), data was ln-transformed.
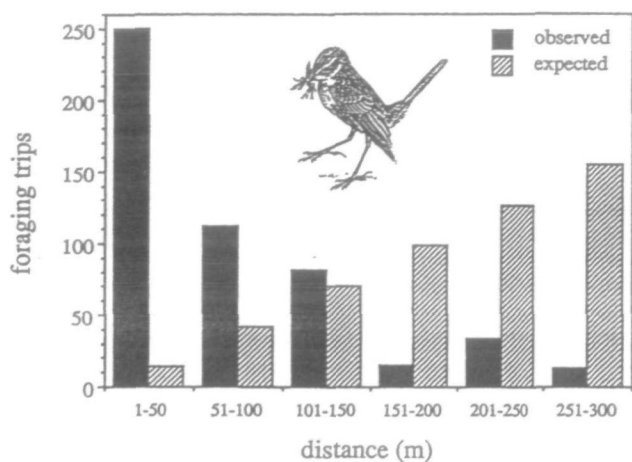
Figure 2
Frequency distributions of expected and observed foraging trips in relation to the distance from the nest. Expected values were calculated by assuming concentric rings in distances of 50, 100, 150, 200, 250, and 300 m around the nest and multiplying the number of total foraging trips ($n = 506$) by the proportion of the total area ($\pi\ r^2 = 282,743\ m^2$) lying in the respective ring. Since the number of foraging places used was similar for all nests, data from all nests have been pooled. Water pipit drawing by F. Weick from Glutz and Bauer (1985).

RESULTS

General feeding behavior

Foraging water pipits usually walk along the ground and peck for insects and other invertebrates on the soil or on plants. They search dwarf shrubs mainly for caterpillars and spiders either from the ground, by climbing through the twigs, or by balancing on top of the plants. Rarely, the water pipits catch flying insects by sallying from a perch in the manner of fly-catchers. When the snow melts in spring, the birds often follow the edges of snow patches, but also forage on snow for drifted insects and on flooded meadows.

Foraging in relation to distance from the nest

The water pipits did not search for food exclusively in their territories but flew up to 300 m in search of food (Figure 2). Of the foraging places observed, 43.7% were situated farther than 50 m from the nest ($n = 144$). They included 50.6% of all foraging trips ($n = 506$) and roughly represented the foraging places outside the territories. The number of foraging trips declined with distance, and only 7.7% of all places and 12.2% of all trips were farther away than 150 m (Figure 2). This observed distribution of foraging trips differs significantly from the one expected under the null hypothesis that search effort per unit area is equal over the entire foraging range ($p < .001$; Kolmogorov-Smirnov test). Under the assumption that areas in different distances from the nest do not differ systematically in their patch quality, the distance-decay function in Figure 2 suggests that the intensity of space use is inversely related to the effort needed to reach the place (Anderson, 1981; Getty, 1981).

Load size in relation to distance of the food patches and time the parent spent searching for food

When returning to the nest to feed their young, parent birds carry several prey items at a time (multi-prey loader), but both the type and amount of prey varies with distance to the food
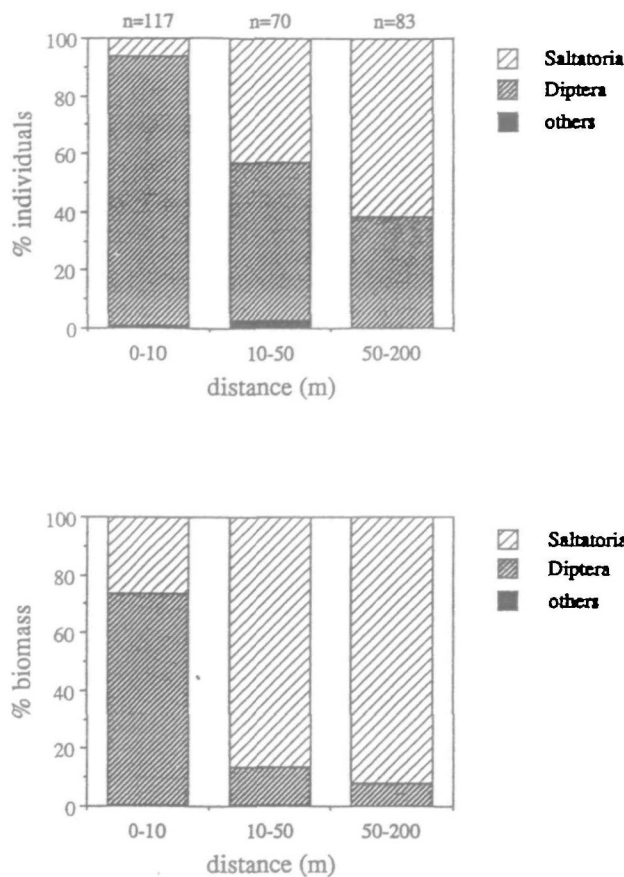

Figure 3
Prey composition in terms of individuals (top) and biomass (bottom) in relation to the distance of the foraging places. All data are from a single nest and were collected on two consecutive days with the same weather conditions.

patch. This is shown by data collected at only one nest with a single female water pipit feeding. Of 286 prey items brought to the brood, 43.7% were *Bibio pomonae* (Diptera), 21.0% other Diptera (probably Muscidae), 33.9% grasshoppers (Saltatoria), and only 1.4% other arthropods. In the vicinity of the nest, the female collected mostly Diptera with an estimated median dryweight of 8.6 mg for *B. pomonae* and 6.1 mg for Muscidae. Farther from the nest, she caught more of the heavier Saltatoria, weighing 57.1 mg on average (Figure 3). The amount of food brought to the nest increased significantly with the distance to the foraging place ($r^2 = .556$, $p = .0001$) and with the time away from the nest ($r^2 = .393$, $p = .0001$). Since distance and time of absence were correlated as well ($r^2 = .602$, $p = .0001$), a multiple regression analysis yielded only one significant predictor for biomass, which turned out to be distance (multiple $r^2 = .570$, $p = .0001$). The increase in food brought to the nest with distance was most pronounced for the first 20–30 m and then leveled off (Figure 4). The finding that food brought to nestlings is better predicted by distance than by foraging time probably results from the fact that time data are less precise than distance data, partly because birds often disappear in high grass or behind shrubs and partly because time in a food patch is not determined by food gathering for the nestlings only but by other activities as well (e.g., self-feeding, vigilance).
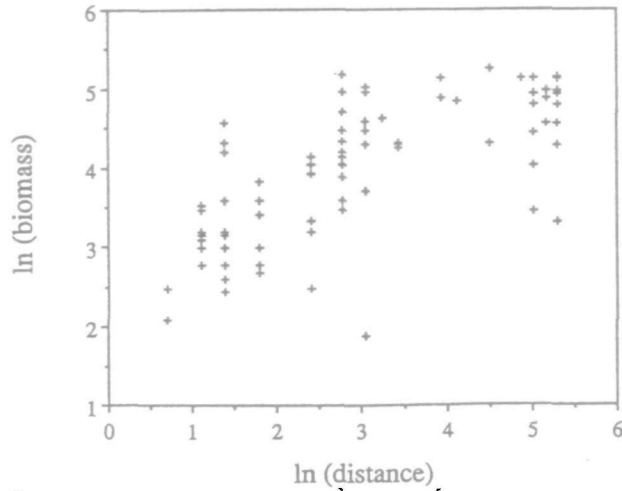
Figure 4
Relationship between the amount of food brought to the nestlings and the distance to the foraging places: ln(biomass) = 2.656 + 0.432 ln(distance); $r^2 = .556$, $p = .0001$.

Figure 5
Differences in selectivity (=observed-expected values) for near and distant foraging places of 24 territories in relation to vegetation groups. Vegetation was classified as avoided, indifferent, or preferred according to the results [+, 0, (−)] in the right half of Table 2. Wilcoxon matched-pairs signed-rank tests were calculated for differences within and between groups: ns not significant, *$p <$ .05, **$p <$ .005.

Foraging in relation to vegetation

Foraging places are distinguished from the available habitat in the territories by a higher percentage of grass and herbs, fewer dwarf shrubs, fewer rocks, and lower vegetation (Table 2, left). Thus, foraging birds do not visit vegetation types according to their availability, but prefer relatively unstructured types. In terms of blueberries (*Vaccinium myrtillus*) and bare soil, observed and expected habitat use do not differ. This overall conclusion is independent of whether critical significance levels are Bonferroni adjusted.
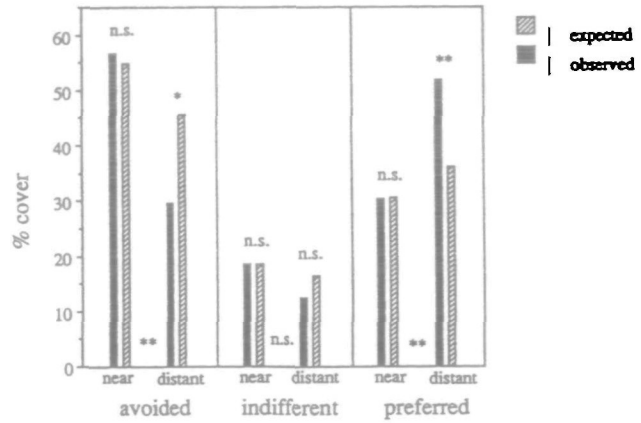
Selectivity in relation to distance between nest and foraging places

We tested selectivity—defined as the difference between observed and expected values—in relation to distance for three groups of plants: the preferred ones (grass and herbs), the one treated indifferently (*V. myrtillus*), and the avoided group that contained the pooled data for all plant species which are avoided according to the left half of Table 2. For this test we divided the foraging places into near ones (up to 50 m from the nest) and more distant ones. For the near foraging places,

Table 2

A comparison of the areas used by foraging water pipits with the available habitat for 10 vegetational and 4 structural variables (left) and 10 habitat types (right) that were identified by means of a cluster analysis.

Variable	Abbreviation	Relation	p	p	Relation	Habitat type	Composition
Grasses and herbs	Gh	+	.001	.001	+	Grass, high percentage	Gh > 67%
				.420	0	Grass, low percentage	Gh 33–67%
Rhododendron ferrugineum	Rf	−	.001	.007	(−)	Rhodod., high percentage	Rf > 50%
				.010	(−)	Rhodod., low percentage	Rf 20–50%
Calluna vulgaris	Cv	(−)	.011	.135	0	Calluna, high percentage	Cv > 50%
				.260	0	Calluna, low percentage	Cv 25–50%, Gh 27%
Juniperus communis	Jc	−		.004	.026	(−)	Juniperus	Jc > 29%, Gh 14%, Rf 13%
Vaccinium gaultheroides	Vg	(−)	.013	.180	0	Gaulterhoides	Vg > 50%
Vaccinium myrtillus	Vm	0	.195	.011	(−)	Myrtillus	Vm > 28%, Rf 16%, Vg 14%
Lichenes	Li	−		.001	.334	0	Lichenes	Vg 10–50%, Li 15%, Vm 13%
Empetrum hermaphroditum	Eh	−	.003				
Loiseleuria procumbens	Lp	(−)	.019				
Rocks and boulders		−	.001				
Bare soil		0	.105				
Vegetation height		−	.003				
Rock height		0	.118				

The composition of the habitat types in terms of the cover of the dominant plant taxa is given as well. For each of the 24 nests, expected and observed values were compared (separately for each of the 13 variables and the 10 habitat types), and the 24 data pairs were then subjected to a Wilcoxon matched-pairs signed-rank test. Results are given for both the conventional significance level ($p = .05$) and the Bonferroni adjusted ones ($p = .004$ and $p = .005$ in the left and right part of the table, respectively): + preferred, 0 indifferent (i.e., observed use does not differ from expectation), − avoided; (−) refers to cases that are only significant without Bonferroni correction. For further details see Methods.

cover in the foraging areas (=observed) does not differ from cover in the available habitat (=expected) for any of the three vegetation groups (Figure 5). At more distant foraging areas, however, observed values are significantly lower than expected ones for the avoided vegetation and significantly higher for the preferred one. For the indifferent group, there is again no difference in cover between the used and the available habitat (Figure 5). Thus, selectivity increases with distance, both in terms of preference and avoidance.

Preference and avoidance in relation to food abundance

To test whether the preferred and avoided feeding areas differed in food availability, we assigned all 10 × 10 m plots to different habitat types by means of a cluster analysis. We then compared the use of the different types to their availability as before. In accordance with the results above on single plant taxa, the birds preferred plots consisting mostly of grass and herbs (>67%) and avoided *Rhododendron* and *Juniperus* plots, at least when no Bonferroni adjustment is applied (Table 2, right). In the other vegetation categories, results seem to differ slightly between the two analyses. Habitat types dominated by *Calluna vulgaris*, *Vaccinium gaultheroides*, or lichens are used according to their availability while the single plant taxa are avoided in these three cases. Conversely, pipits avoided *V. myrtillus* in the analysis based on plots but not in the one based on single plant species. One possible explanation for such differences is that other plant species in the plot obscure the effect of the dominant one (see, e.g., shift in *V. myrtillus* from "indifferent" to "avoided" through a high percentage of avoided *Rhododendron* and *V. gaultheroides* in "Myrtillus" habitats). Another explanation is that the assignment of plots to habitat types is much cruder than the measurement of cover in single plant taxa. In the first case, a plot is either assigned to a given type or not; in the second case, a continuous range from 0 to 100% is measured. Moreover, almost all the categories that shift from avoided to indifferent and vice versa between the two analyses also change their assignment after Bonferroni correction within each of the two analyses. This indicates that differences between used and available habitat may be less pronounced with respect to avoidance than with respect to the more consistent preference pattern. However, in no case are the above—not mutually exclusive—reasons strong enough to reverse the preference pattern, i.e., to categorize a habitat type as preferred while its dominant plant species is avoided and vice versa.

The preferred, indifferent, and avoided habitat types differ in their average amount of arthropods (Kruskal-Wallis test: $p = .004$) with highest prey abundance occurring in the preferred pastures (Figure 6). In univariate comparisons, the preferred pastures ($n = 33$) have significantly more prey than the avoided ($n = 17$) or the indifferent habitats ($n = 51$) (Mann-Whitney U test: $p = .039$ and $p = .001$, respectively). No differences could be found between the indifferent and the avoided habitats ($p = .533$). This supports the previous notion that differences in indifferent and avoided habitats seem to be smaller than those between preferred habitats and the other two categories.

Food conditions, foraging patterns, and reproductive success

The number of fledglings (f) increased significantly with the average biomass of prey (b) at the foraging places ($p < .001$) and decreased with the average distances (d) to these places ($p = .006$) according to the following equation:

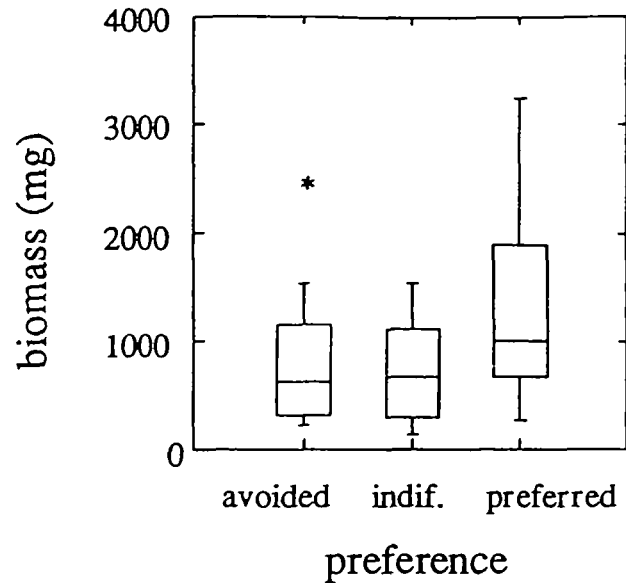$$f = 0.286 \ln(b) - 0.219 \ln(d) + 0.295. \qquad (1)$$

Figure 6
Average prey biomass in avoided, indifferent, and preferred habitat types. Shown are medians with interquartile ranges (=hinges) and total range of data (=whiskers).

The closer food patches are to the nest and the more food they contain, the more young fledge (multiple $r^2 = .660$, $p < .001$; Figure 7).

We then used the above regression model to predict maximum distances that birds should fly from their territories to forage in the profitable grass habitats. The boundary condition for our prediction was that the number of young raised should be equal for birds foraging within their territories (f_i) and those foraging outside (f_o). In mathematical terms, this condition ($f_i = f_o$) together with Equation 1 can be written as

$$0.286 \ln(b_i) - 0.219 \ln(d_i) + 0.295$$

$$= 0.286 \ln(b_o) - 0.219 \ln(d_o) + 0.295 \qquad (2)$$

where b_i and d_i stand for average biomass and average foraging distances, respectively, inside the territory while b_o and d_o refer to the same parameters for places outside the territory. After setting d_i to 30 m, which is the median foraging distance within the territory, Equation 2 can be modified to

$$\ln(d_o) = 1.306[\ln(b_i) - \ln(b_o)] + 3.401. \qquad (3)$$

By entering the average biomass values of foraging places inside the territory (b_i) and those for the nearest grass areas outside the territory (b_o), we predicted the maximum economic travel distances for each of the 17 territories and compared them with the ones actually observed. The result is shown in Figure 8. For the area below the solid line, actual distances from the nest to grass plots are smaller than the predicted maximum; for the area above the line, they are larger. With a perfect match between prediction and observation, all cases in which birds did fly to grass (dots) should lie below the line, and all cases in which they did not (circles) should lie above. Among the 17 territories, only three cases do not uphold expectation. In all three of them, birds did not fly to grass plots although they occurred within the predicted range. One of these three cases lies only slightly beyond the boundary. This close match between predicted and observed frequencies differs significantly from a random distribution ($p = .015$; Fisher's Exact test, one-tailed, applied to inserted table in Figure 8). Moreover, in the 10 cases where birds did fly to
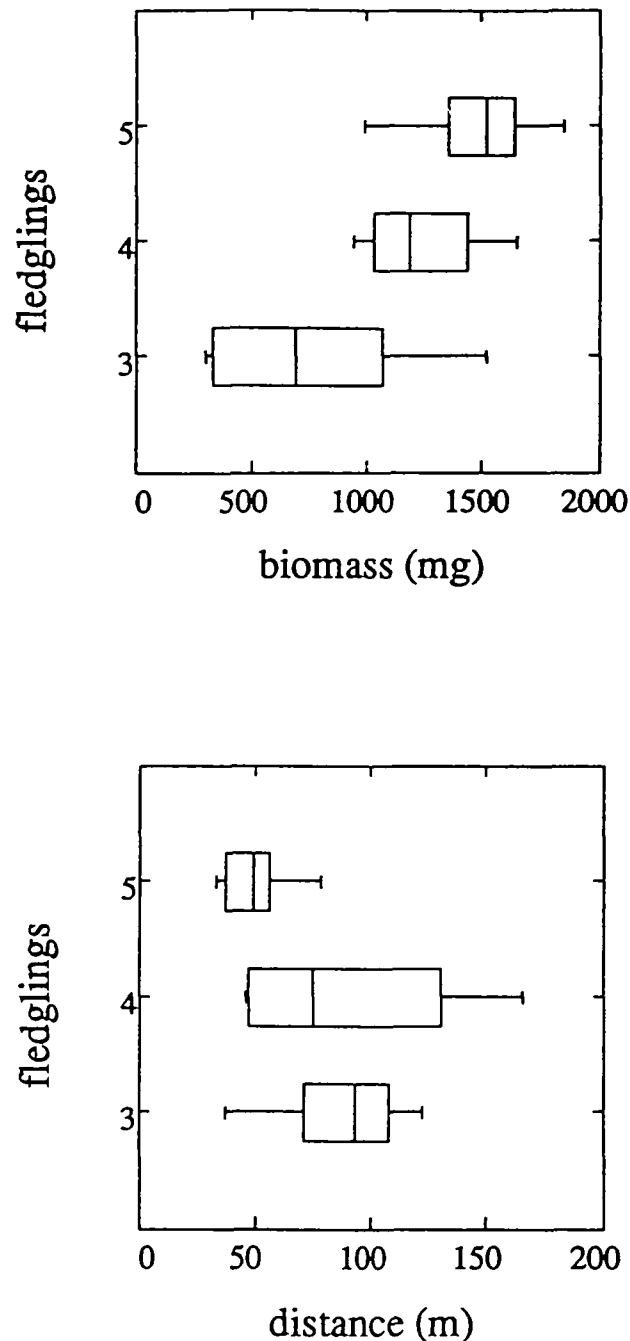
(Figure 7). The high proportion of variance explained by these two variables (66%) indicates that food provisioning ranks extremely high among the factors determining the reproductive success of water pipits. This should create a strong selection pressure on efficient foraging. The prediction is supported by the direct link between reproductive success and foraging that we found: maximum distances that birds flew from their territories to forage in the profitable grass habitats could be reliably predicted from the relationship between food conditions and reproductive success (Figure 8).

Further evidence for efficient foraging comes from our various analyses of the water pipits' behavior. Birds minimized traveling costs by concentrating foraging on areas close to the nest (Figure 2), they maximized the amount of prey brought to the nest (Figures 3 and 4), and they preferred patches with high insect biomass (Figure 6, Table 2), especially when foraging far from the nest (Figure 5). The most parsimonious interpretation is that foraging decisions of adult water pipits are made on the basis of profitability, i.e., the net energy gain per unit time (Anderson, 1981; Getty, 1981; Schoener, 1979; Stephens and Krebs, 1986).

This interpretation implicitly makes the following assumptions with respect to net energy gain (a) and alternative explanations (b): (a) energy intake/time increases linearly with biomass in a food patch, and energy expenditure is directly proportional to foraging time; (b) other currencies for efficiency as well as constraints and confounding variables are relatively unimportant. How valid are these assumptions?

Net energy gain per time

The assumed linear relationship between energy intake and biomass is very likely to be fulfilled. Water pipits are food generalists and feed on a wide range of arthropods (Glutz and Bauer, 1985; Pätzold, 1984; Wartmann, 1985) with similar energy content per g body mass (Brodmann PA and Reyer HU, in preparation). Although the maximum energy intake is constrained and will not continuously increase with biomass, it is unlikely that a plateau will be reached under natural food conditions. Recognition of suitable patches is probably easy because the mosaic of different vegetation types with their different arthropod biomass (Figure 6; see also Bauer, 1992) plus the information collected during previous foraging trips will provide birds with an expectation about average food patch quality. Actual patch quality can be judged only after sampling for some time because of diurnal, seasonal, spatial, or stochastic variation in food availability (Stephens and Krebs, 1986; Yoccoz et al., 1993), but it is unlikely that such variation will systematically differ among patches. Thus, recognition times for patch quality probably are not only small, but also similar for all available patches.

The assumed linear relationship between energy expenditure and time investment, for various reasons, is more difficult to justify:

(1) Although there is a linear relationship between distance to a patch and travelling time, short flights are energetically more expensive than long ones because of the high costs associated with maneuvering during take off and landing (Carlson and Moreno, 1992; Norberg, 1989; Tatner and Bryant, 1986).

(2) Foraging on shrubs is accompanied by a lot of balancing movements and wing flapping, which probably requires more energy than foraging in grass or on bare ground.

(3) Search and handling times vary with the type of the vegetation and the prey. Experiments on captive water pipits have shown that search time for craneflies is independent of the vegetation type while that for caterpillars increases by a factor of about 8 (30–250 s) from grass through blueberry to

Figure 7
Relationship between number of fledglings and weighted averages of biomass in the food patches (top) and distance between nest and food patches (bottom). Shown are medians with interquartile ranges (=hinges) and total range of data (=whiskers).

grass, there is a significant positive relationship between expected and observed distances (p = .012; broken line in Figure 8).

DISCUSSION

Foraging and reproductive success

Reproductive success increased significantly with biomass in food patches and decreased with distance from nest to patches

Figure 8
Observed distances between nests and grass areas that were visited (black dots) and not visited (open circles), respectively, in relation to predicted distances. In the area below the solid line, observed distances are lower; in the area above, they are higher than predicted distances. The inserted 2 × 2 table compares observed and predicted frequencies (p = .015, Fisher's Exact test, one-tailed). The broken line illustrates a significant positive relationship between observed and predicted distances for the 10 territories from which parents did fly to grass areas: observed = 0.869 + 0.542 predicted (r^2 = .563, p = .012).
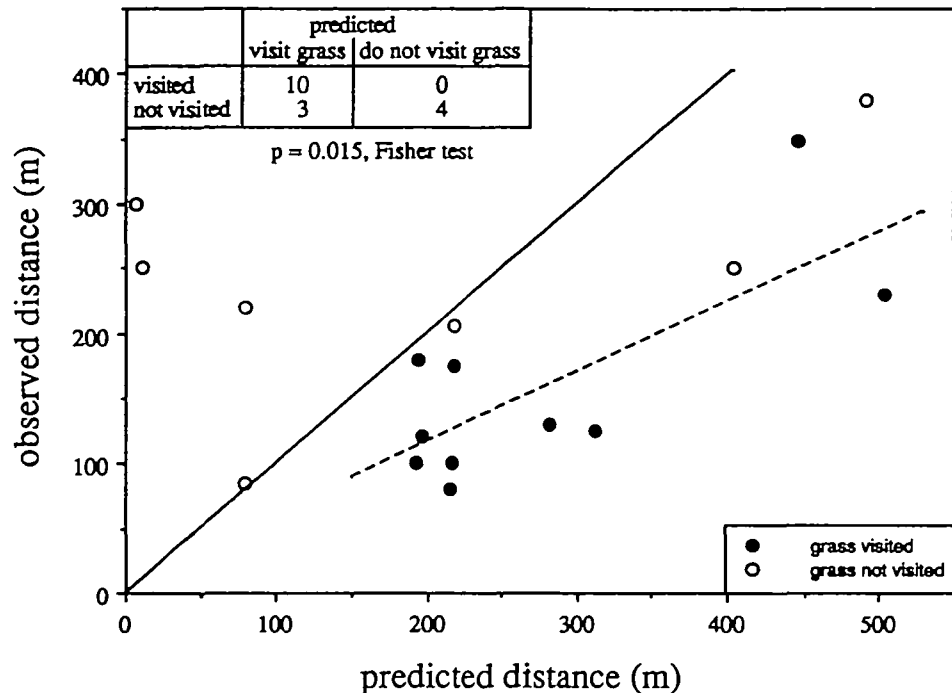
juniper. Similarly, handling time for different prey items varies by a factor of about 5 (3–16 s) (Brodmann PA et al., in preparation).

These reasons potentially challenge our assumption that distance and time are reliable measures of net energy gain. Yet, we do not think that under natural foraging conditions the assumption is seriously violated. Water pipits usually visit more than one vegetation type and also take a mixture of different arthropod groups, some of which are equally accessible in all habitats (Brodmann PA et al., in preparation). This is likely to make overall differences in energy expenditure and searching and handling times less extreme than those for particular groups in particular vegetation. Moreover, potential differences in handling time due to size differences of the prey are compensated for by corresponding differences in energy return. Finally, water pipits seem to avoid the relatively high energetic costs of short flight by usually covering short distances (ca. < 20 m) between the nest and the foraging patch on foot. In this way, they may still achieve a fairly linear relationship between distance and energy budget (cf. Figure 4).

Other currencies, constraints, and confounding variables

In addition to the above mentioned more or less realistic simplifications, a whole range of additional factors can affect the correct interpretation of the foraging pattern. They include constraints such as a maximum load that birds can carry in their beak without losing prey (Cuthill and Kacelnik, 1990), confounding variables such as age and past experience that can influence foraging skills (e.g., Cuthill et al., 1990; Marchetti and Price, 1989; Nishimura, 1991; Valone, 1992), and optimality currencies other than net energy gain per time. Predicted optima depend, for example, on the relative importance of self-feeding and provisioning young (Houston 1987) and on whether foraging constraints result from time or energy limits (Ydenberg et al., 1994). Moreover, foraging has to be compromised with thermoregulation, vigilance, nest protection, territorial defense, and other activities (Grubb

and Greenwald, 1982; Lima and Dill, 1990; McNamara et al., 1991; Milinski and Parker, 1991; Real and Caraco, 1986). Under complex natural conditions, like those of our study, no rigorous test of these and other—not mutually exclusive—alternatives is possible. Nonetheless, the good agreement between flying distances predicted from reproductive success and those actually observed (Figure 8) strongly suggests that profitability, as expressed by biomass, distance, and time, affects foraging decisions of Alpine water pipits much more than the above-mentioned variables.

Do water pipits forage optimally?

In spite of this evidence, it would be premature to interpret the observed foraging patterns in Alpine water pipits as the optimal outcome of natural selection as assumed by optimal foraging theory. We have shown neither a connection between foraging and lifetime reproductive success nor that heritable differences in foraging behavior exist which correlate with differences in fitness. Our study does suggest, however, a potential for selection because it reveals a positive phenotypic correlation between short-term benefits in foraging and fledgling production. This is a basic, but rarely tested assumption in optimal foraging theory (for exceptions, see Blanckenhorn, 1991; Morse 1988, 1992) and a key issue for distinguishing between optimal (i.e., fitness maximizing) behavior and satisficing, i.e., satisfying of a certain aspiration level (Nonacs and Dill, 1993; Ward 1992, 1993).

Conservation issues

Our study also allows some conclusions that are relevant for conservation issues. Undisturbed grass habitats with their high insect biomass were regularly used for foraging by almost 60% of all pairs (10 out of 17; Figure 8). After mowing or grazing, insect biomass was almost 80% lower than before and even ca. 25% lower than within territories that are usually dominated by dwarf shrubs. As reproductive success is directly related to biomass (Figure 7), a more intensive use of the mead-

ows on the valley floor may have marked negative effects on populations of water pipits. On the other hand, giving up grazing of the slopes would increasingly shift vegetation cover from grass and herbs to the less profitable dwarf shrubs and similarly impair reproductive success. Thus, for maintaining present populations of water pipits and other organisms with a similar biology and for preserving the diversity of plants and animals in Alpine valleys like the Dischma, it is important to continue the diverse traditional farming systems.

REFERENCES

Anderson M, 1981. Central place foraging in the whinchat, *Saxicola rubetra*. Ecology 62:538–544.

Bauer D, 1992. Arthropodenbestand in Abhängigkeit von Vegetation und abiotischen Faktoren im Dischmatal (MSc thesis). Zürich: University of Zürich.

Blanckenhorn WV, 1991. Fitness consequences of foraging success in water striders (*Gerris remigis*, Heteroptera: Gerridae). Behav Ecol 2:46–55.

Bortz J, 1989. Statistik für Sozialwissenschaftler. Berlin: Springer-Verlag.

Carlson A, Moreno J, 1992. Cost of short flights in the willow tit measured with doubly-labelled water. Auk 109:389–393.

Cramp S, 1988. Handbook of the birds of Europe, the middle east and north Africa: the birds of the western palearctic, vol. 5. Oxford: Oxford University Press.

Cuthill IC, Kacelnik J, 1990. Central place foraging: a reappraisal of the 'loading effect'. Anim Behav 40:1087–1101.

Cuthill IC, Kacelnik J, Krebs JR, Haccou P, Iwasa Y, 1990. Patch use by starlings: the effect of recent experience on foraging decisions. Anim Behav 40:625–640.

Getty T, 1981. Analysis of central-place space-use patterns: the elastic disc revisited. Ecology 62:907–914.

Glutz von Blotzheim UN, Bauer KM, 1985. Handbuch der Vögel Mitteleuropas, Vol. 10/II. Wiesbaden: Aula-Verlag.

Grant PR, Grant BR, 1989. Natural selection in a population of Darwin's finches. Am Nat 133:377–393.

Grubb TC, Greenwald L, 1982. Sparrows and bushpile: foraging responses to different combinations of predation risk and energy cost. Anim Behav 30:637–640.

Houston AI, 1987. Optimal foraging by parent birds feeding dependent young. J Theor Biol 124:251–274.

Kamil AC, Krebs JR, Pulliam HR, 1987. Foraging behavior. New York: Plenum Press.

Kamil AC, Sargent TD, 1981. Foraging behavior: ecological, ethological and psychological approaches. New York: Garland STM Press.

Krebs JR, 1978. Optimal foraging: decision rules for predators. In: Behavioural ecology: an evolutionary approach, 1st ed (Krebs JR, Davies NB, eds). Oxford: Blackwell; 23–62.

Krebs JR, Kacelnik A, 1991. Decision-making. In: Behavioural ecology: an evolutionary approach, 3rd ed (Krebs JR, Davies NB, eds). Oxford: Blackwell; 105–136.

Krebs JR, McCleery RH, 1984. Optimization in behavioural ecology. In: Behavioural ecology: an evolutionary approach, 2nd ed (Krebs JR, Davies NB, eds). Oxford: Blackwell; 91–121.

Lima SL, Dill LM, 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640.

Marchetti K, Price T, 1989. Differences in foraging of juvenile and adult birds: the importance of developmental constraints. Biol Rev 64:51–70.

Martin TE, 1987. Food as a limit on breeding birds: a life-history perspective. Annu Rev Ecol Syst 18:453–487.

McNamara JM, Merad S, Houston AI, 1991. A model of risk-sensitive foraging for a reproducing animal. Anim Behav 41:787–792.

Morse DH, 1988. Relationship between crab spider *Misumena vatia* nesting success and earlier patch choice decisions. Ecology 69:1970–1973.

Morse DH, 1992. Predation on dispersing *Misumena vatia* spiderlings and its relation to maternal foraging decisions. Ecology 73:1814–1819.

Milinski M, Parker GA, 1991. Competition for resources. In: Behavioural ecology: an evolutionary approach, 3rd ed (Krebs JR, Davies NB, eds). Oxford: Blackwell; 137–168.

Nishimura K, 1991. Utilization of different prey type patches in the Ural owl (*Strix uralensis*): a sit-and-wait predator. Behav Ecol 2:99–105.

Nonacs P, Dill LM, 1990. Mortality risk vs. food quality trade-offs in a common currency: ant patch preferences. Ecology 71:1886–1892.

Nonacs P, Dill LM, 1993. Is satisficing an alternative to optimal foraging theory? Oikos 67:371–375.

Norberg UM, 1989. Vertebrate flight. Berlin: Springer-Verlag.

Nur N, 1990. The costs of reproduction in birds: evaluating the evidence from manipulative and non-manipulative studies. In: Population biology of passerine birds: an integrated approach (Blondel J, Gosler A, Lebreton J-D, McCleery RH, eds). Berlin: Springer-Verlag; 281–296.

Orians GH, Pearson NE, 1979. On the theory of central place foraging. In: Analyses of ecological systems (Horn DJ, Mitchell RD, Stairs GR, eds). Columbus: Ohio State University Press; 154–177.

Partridge L, Harvey PH, 1988. The ecological context of life history evolution. Science 241:1449–1455.

Pätzold R, 1984. Der Wasserpieper. Wittenberg Lutherstadt A. Ziemsen Verlag.

Pierce GJ, Ollason JG, 1987. Eight reasons why optimal foraging theory is a complete waste of time. Oikos 49:111–118.

Pyke GH, Pulliam HR, Charnov EL, 1977. Optimal foraging: a selective review of theory and tests. Q Rev Biol 52:137–154.

Real L, Caraco T, 1986. Risk and foraging in stochastic environments: theory and evidence. Annu Rev Ecol Syst 17:371–390.

Reznick D, 1985. Costs of reproduction: an evaluation of the empirical evidence. Oikos 44:257–267.

Ritchie ME, 1988. Individual variation in the ability of Columbian ground squirrels to select optimal diet. Evol Ecol 2:232–252.

Schoener TW, 1979. Generality of the size-distance models of optimal feeding. Am Nat 114:902–914.

Stearns SC, 1992. The evolution of life histories. Oxford: Oxford University Press.

Stearns SC, Schmid-Hempel P, 1987. Evolutionary insights should not be wasted. Oikos 49:118–125.

Stephens DW, Krebs JR, 1986. Foraging theory. Princeton, New Jersey: Princeton University Press.

Tamer P, Bryant DM, 1986. Flight cost of a small passerine measured using doubly-labelled water: implications for energetics studies. Auk 103:169–180.

Valone TJ, 1992. Information for patch assessment: a field investigation with black-chinned hummingbirds. Behav Ecol 3:211–222.

Ward D, 1992. The role of satisficing in foraging theory. Oikos 63:312–317.

Ward D, 1993. Foraging theory, like all other fields of science, needs multiple working hypotheses. Oikos 67:376–378.

Wartmann BA, 1985. Vergleichende Untersuchungen zur Populations-, Brut- und Nahrungsökologie von Wasserpieper und Steinschmätzer im Dischmatal GR (PhD dissertation). Zürich: University of Zürich.

Ydenberg RC, Welham CVJ, Schmid-Hempel R, Schmid-Hempel P, Beauchamp G, 1994. Time and energy constraints and the relationships between currencies in foraging theory. Behav Ecol 5:28–34.

Yoccoz NG, Engen S, Stenseth NC, 1993. Optimal foraging: the importance of environmental stochasticity and accuracy in parameter estimation. Am Nat 141:139–157.

Zach R, Smith JNM, 1981. Optimal foraging in wild birds? In: Foraging behavior: ecological, ethological, and psychological approaches. (Kamil AC, Sargent TD, eds). New York: Garland STPM Press; 95–113.