

Paul. A. Brodmann · Heinz-Ulrich Reyer  
Kurt Bollmann · Alex R. Schläpfer · Claudia Rauter

## The importance of food quantity and quality for reproductive performance in alpine water pipits (*Anthus spinoletta*)

Received: 31 May 1996/Accepted: 12 August 1996

**Abstract** Studies relating reproduction to food availability are usually restricted to food quantity, but ignore food quality and the effects of habitat structure on obtaining the food. This is particularly true for insectivorous birds. In this study we relate measures of reproductive success, time of reproduction and nestling size of water pipits (*Anthus spinoletta*) to biomass, taxonomic composition and nutritional content of available food, and to vegetation structure and distance to feeding sites. Clutch size was positively correlated with the proportion of grass at the feeding sites, which facilitates foraging. This suggests that water pipits adapt their clutch size to environmental conditions. Also, pipits started breeding earlier and produced more fledglings when abundant food and a large proportion of grass were available, probably because these conditions allow the birds to gain more energy in less time. The number of fledglings was positively correlated with the energy content of available food. No significant relationships were found between feeding conditions and nestling size or the time that nestlings took to fledge. This suggests that water pipits do not invest more in individual nestlings when food conditions are favourable but rather start breeding earlier and produce more young. Taxonomic composition and nutritional content of prey were not correlated with any of the reproductive parameters, indicating that profitability rather than quality of food affects reproductive success.

**Key words** Foraging · Habitat structure · Nutrients · Reproductive success · Water pipits

### Introduction

Evolutionary processes act through variability in the reproductive output of individuals which, in turn, depends on ecological variability. Many studies have therefore searched for correlations between environmental factors and reproductive success or have experimentally manipulated environmental conditions to study their effects on breeding success (reviewed for vertebrates by Boutin 1990, for birds by Martin 1987).

Food is one of the most important factors determining the timing and success of reproduction in birds (e.g. Drent and Daan 1980; Martin 1987, 1995). A number of studies have found that birds start breeding earlier and have a higher reproductive success when more food is available. The commonest response to an experimental provisioning of food is an advance in laying date (Boutin 1990; Svensson and Nilsson 1995). This can influence reproductive success in two ways. First, post-fledging survival of the young is inversely related to hatching date in many passerine species (e.g. Perrins 1979; Hochachka 1990; Verhulst and Tinbergen 1991). Second, early breeding may allow the parents to successfully rear more broods in the same season (e.g. Smith et al. 1987). Less common responses to food provisioning are larger clutches, heavier eggs, and more nestlings that fledge (e.g. Arcese and Smith 1988 and literature cited therein; Perrins 1991).

Several studies have investigated how energy or other food components relate to reproduction. In the case of herbivores the available amount of protein, rather than energy, may be limiting (Scriber and Slansky 1981; Owen-Smith and Novellie 1982). Attempts to explain food choice of herbivores as either a function of energy or protein content of plants, however, have had limited success (Neighbors and Horn 1991; Dearing and Schall 1992). This may result from consumers attempting to maximize several nutrients in their diet simultaneously (Pulliam 1975; Belovsky 1978), from eating a mixed diet in order to achieve one that is balanced (Rapport

P. A. Brodmann · H.-U. Reyer (✉) · K. Bollmann ·  
A. R. Schläpfer · C. Rauter  
Zoologisches Institut, Universität Zürich  
Winterthurerstrasse 190, 8057 Zürich, Switzerland  
fax: 0041-1-361 31 85; e-mail: ulireyer@zool.unizh.ch

1980; Greenstone 1979; Dearing and Schall 1992) or to avoid consuming too much of any one defensive compound (Freeland and Janzen 1974). In the case of insectivores, there are only a few studies demonstrating effects of food quality on reproduction (Perrins 1976; Tinbergen 1981; Krebs and Avery 1984).

In our study of the water pipit (*Anthus spinoletta*), an insectivorous passerine, we investigate relations between reproduction and the quantity and quality of food. We relate the timing and success of reproduction, and the size of nestlings, to the quantity and the taxonomic and nutritional composition of the available food. Effects of vegetation structure and distance to foraging sites are also included in our analysis, because these variables influence the time that foraging water pipits need to collect prey (Brodmann et al. 1997).

## Methods

### Study area and birds

The research was done from May to August during 1990–1992 in the alpine valley Dischma near Davos (Kt. Graubünden, Switzerland), which runs from north-west to south-east. The study area lies above timberline at altitudes between 1900 m and 2500 m above sea level. The valley floor is dominated by meadows, whereas the slopes have vegetation typical of acid silicate soil. Between 1800 and 2400 m slopes are mainly covered by dwarf shrubs (*Rhododendron*, *Juniperus*, *Calluna*, *Vaccinium*) and above 2400 m by natural alpine meadows. The highest elevation is 3147 m. From July on, the meadows on the valley floor are used to produce hay or as pastures for cattle. The slopes are grazed lightly by cattle and sheep. Further details on the study area are presented in Frey-Roos et al. (1995).

In our study area, water pipits breed over a period of about two months with a prominent peak of first broods (71.3%) in late May and early June and replacement clutches (16.8%) and second broods (11.9%) from late June to July ( $n = 303$  nests). In order to relate reproductive performance to food conditions, broods hatching up to 25 June (all from first clutches) were assigned to the early prey sampling period, those hatching thereafter (96.6% from replacement and second clutches) to the later period (see below).

### Available food

#### Sampling

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 last two succeeded in collecting the five most important prey taxa which – according to neck collar samples – account for 77% of the nestling food (Brodmann 1995). Since sweep netting was easier and faster than operating the suction apparatus we subsequently used sweep nets as the standard device for arthropod sampling. Details of the methods and potential biases are described in Brodmann (1995).

In all three years, the study area was sampled between 17 and 24 June, the period when most pipits have their first nestlings, and again between 14 to 21 July, which is representative for replacement and second clutches. Samples were taken according to a 50 by 50 m grid system that was drawn onto maps of the study area. In 1990 the samples were distributed regularly over the study area and consisted of 50 sweeps each. About half of all quadrates were

sampled in this year. In 1991 and 1992 all quadrates were sampled, but with only 10 sweeps each. To compare the different sampling regimes in 1990 and 1991–1992 we collected 12 samples of 10 sweeps and 6 samples of 50 sweeps. They were taken in groups of three samples at the same time and place, one sample consisting of 50 and two of 10 sweeps. Each 50-sweep sample yielded on average 4.3 times more arthropod biomass than each 10-sweep sample. Data from 1990 was corrected accordingly by this factor. In addition to this coarse-grained sampling, providing information about the general food situation within territories and beyond, prey was also collected in the exact feeding locations, defined as places where birds searched for food for at least 30 s after arrival (for details see Frey-Roos et al. 1995). Estimates of food available per territory are, on average, based on 2.1 sweep samples in 1990 and on 4.0 samples in the following 2 years. In the feeding places an average of 6.0 samples per nest were collected in 1990 and of 6.5 samples in 1991–1992. All sampling was done between 0900 hours and 1800 hours, when the vegetation was dry.

### Biomass

Arthropods were preserved in ethanol for later identification to taxonomic order or, if important as food for the water pipits, to family. Body length and width were measured for each individual and used to estimate biomass dry weight with the help of regression equations for the different taxa (Brodmann 1995). The sum of the 9 most important prey taxa, identified as such by sampling prey items brought to the young by the collar neck sampling method, was used as an estimate of the total biomass of available food. Each of the nine taxa accounted for at least 1% of the total biomass of invertebrates fed to nestlings, and all nine taxa together amounted to 88.8% of the total biomass. In decreasing order these prey taxa are Lepidoptera larvae, Tipulidae (Diptera), Araneae, Saltatoria, Rhagionidae (Diptera), Trichoptera, Lepidoptera imagines, Tenthredinoidea larvae (Hymenoptera), Plecoptera, and Bibionidae (Diptera). Each of the other taxa accounted for less than 1% of the total biomass.

### Taxonomic composition

In order to study whether the type of prey affects reproduction, the proportions of the different taxa were determined for the available food. As the rarer of the nine most frequent prey taxa occurred in few samples, only the five most common taxa were considered to describe the taxonomic composition (Lepidoptera larvae to Rhagionidae; see section on Biomass).

### Nutritional components

Protein, lipid, carbohydrate, water and energy content were determined for the nine most frequent prey taxa (see section on Biomass). Methods and results of these analyses are described elsewhere (Brodmann 1995). To estimate food quality we multiplied median content per milligram of these prey taxa with the biomass of that taxon and divided the product by the total biomass of available food. This gives an average percentage of protein, lipid, carbohydrate, water and energy of the available food.

### Foraging effort

#### Distance to feeding sites

Water pipits do not forage exclusively in their territories but leave them on about half of the foraging trips (Frey-Roos et al. 1995).

Therefore, all foraging sites in and outside the territory were mapped, their individual distances from the nest measured, median distances between nest and feeding places calculated for each territory and included in our analyses as an additional variable describing food conditions.

### Vegetation structure

Since vegetation affects the foraging success of water pipits (Brodmann et al. 1997), plants were assessed according to the 50 by 50 m grid mentioned before. For every 2500-m<sup>2</sup> square we assessed the coverage of four vegetation types increasing in height from (1) to (4): (1) short dwarf-shrubs, consisting of the species *Loiseleuria procumbens*, *Empetrum hermaphroditum*, *Vaccinium vitis-idaea* and *V. uva-ursi*, various lichens and alpine meadows of high elevation (Nardion); (2) grass and herbs, including meadows and pastures of the valley floor; (3) medium-sized dwarf shrubs of the species *Calluna vulgaris*, *Vaccinium myrtillus* and *V. gaultheroides*; and (4) large dwarf shrubs of the two species *Rhododendron ferrugineum* and *Juniperus communis* (cf. Zumbühl and Burnand 1986). Territory and feeding site specific cover estimates for each of the four vegetation types were made in eight categories: < 1%, 1–5%, 5–10%, 10–20%, 20–40%, 40–60%, 60–80%, and 80–100%, respectively. For the analyses relating feeding conditions to breeding parameters, these categories were replaced by their mean values (e.g. 15% for cover 10–20%).

### Reproduction

In order to study effects of feeding conditions on reproduction, six reproductive parameters were related to available food and vegetation structure: (1) clutch size, (2) number of fledglings, (3) time of reproduction (i.e. the date when the first egg hatched in a nest), (4) nestling period (i.e. the average duration between hatching and fledging), and nestling size, measured by (5) tarsus length and (6) variation in tarsus length within nests. Tarsus length was measured one to three times for each young within a nest between days 3–10 of age and then corrected for age by using the residual values of the measurements, i.e. by subtracting the mean value of the young of all nests at a specific age from the individual value at that age. Means of the residuals and coefficients of variation ( $CV = 100 \times SD/mean$ ) were then calculated for each nest.

### Data analysis and statistics

Feeding conditions were measured by the available amount of food biomass, five variables describing taxonomic composition, five nutritional components, four variables on vegetation structure and the distance to the feeding sites. Several of these 16 independent variables are highly correlated among each other. In order to reduce their number, and test for the reliability of the reduction process, we used two different procedures (Appendix 1). First, we chose the variable correlated with the largest number of other variables (proportion of tipulids) and dropped the eight correlated variables; from the remaining variables we again picked the one with most correlations. After two such steps the original number of 16 independent variables had been reduced to 5 uncorrelated variables which are food biomass, distance to feeding sites, proportion of tipulids, energy content, and proportion of grass. Second, we subjected the 16 independent variables to a principal component analysis with subsequent varimax rotation (Aspey and Blankenship 1977). This resulted in five factors with eigenvalues larger than one (Kaiser criterion, Bauer 1986). Two factors described taxonomic food composition, one of them representing Tipulidae, Araneae and Lepidoptera larvae, the other Saltatoria and Rhagionidae. Two factors characterized food quality, one of them protein, lipid and

energy content, the other carbohydrate and water. The fifth factor described vegetation structure with negative loadings of grass and herbs and positive ones of all three dwarf-shrub categories. The five uncorrelated original variables from the first procedure and the scores of the five factors from the second one, respectively, were then related to reproductive parameters by means of analysis of covariance (ANCOVA). Year effects were also included.

The ANCOVA was performed twice, once with conditions within territories and once with those at the feeding sites which include both food samples within and outside the territory boundaries at the time of clutch completion. This distinction between territories and feeding sites was made because a previous study had shown that only about half of all foraging trips are within the territory boundaries (Frey-Roos et al. 1995). Mean feeding conditions in a territory were calculated as unweighted averages of all sample sites located in that territory. Mean feeding site conditions were weighted according to the number of trips to each feeding site (for details see Frey-Roos et al. 1995). As foraging behaviour was only observed for about half of the studied breeding pairs, sample size for number of nests is smaller than for territories.

To reduce variance in reproductive success (number of fledglings) caused by factors other than food, all nests which had been predated or had lost nestlings due to snow fall were excluded from this analysis; but they have been considered in another study (Bollmann 1995). For the analysis relating time of reproduction (hatching date) to food conditions, only first clutches are considered, because initiation of replacement and second clutches mainly depends on when the first brood was lost or fledged.

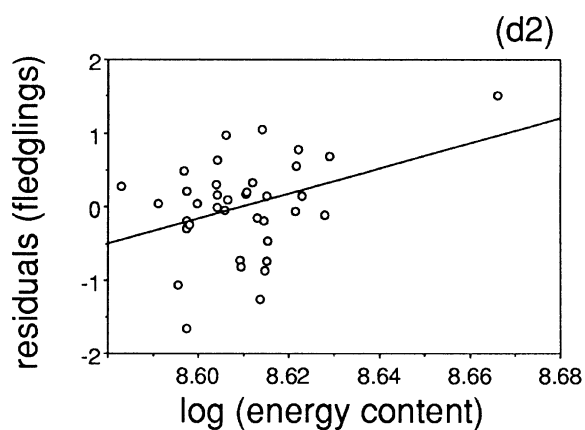
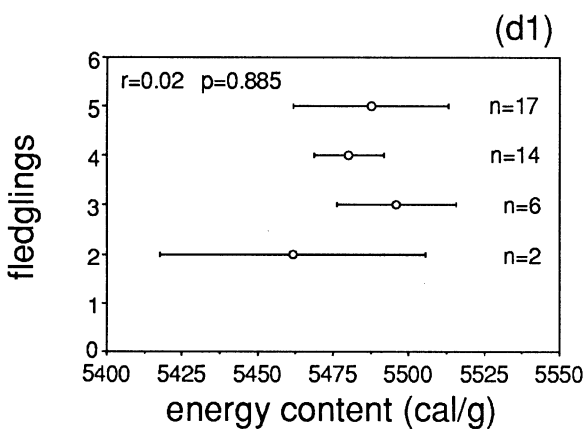
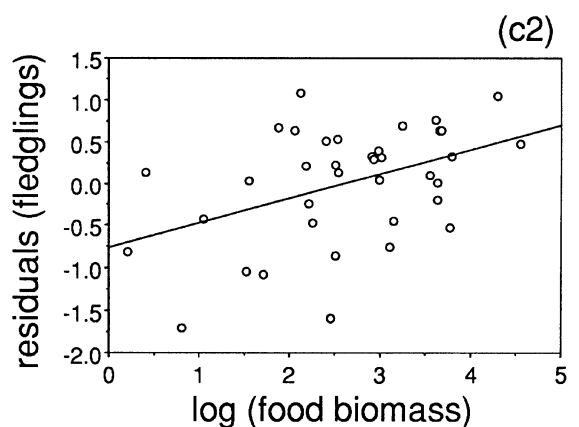
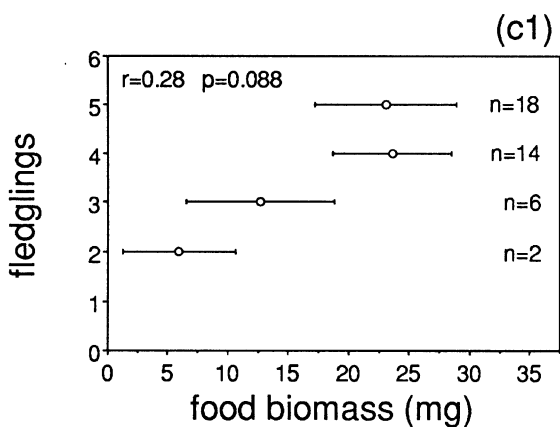
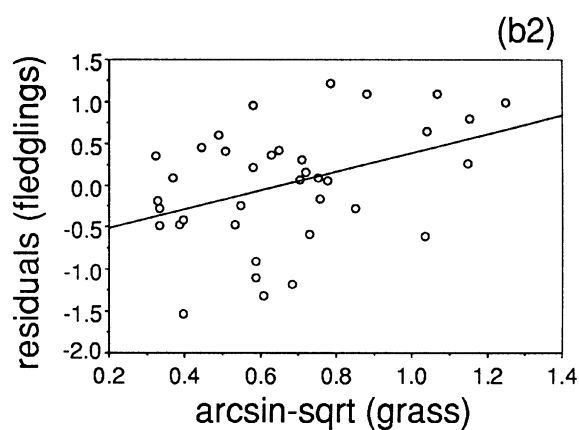
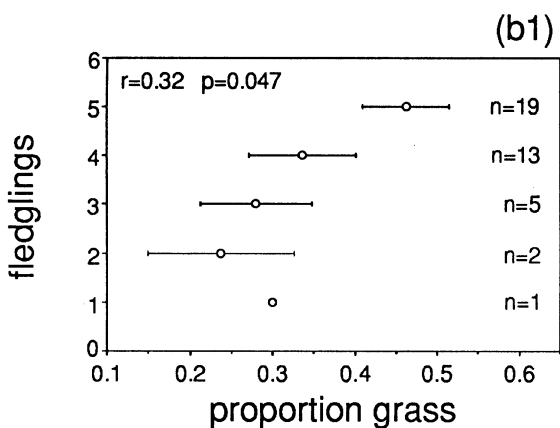
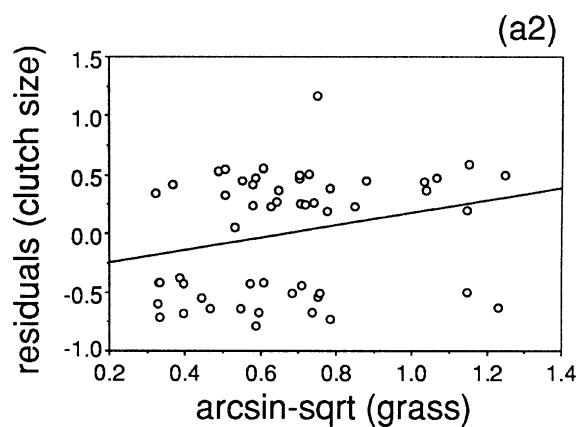
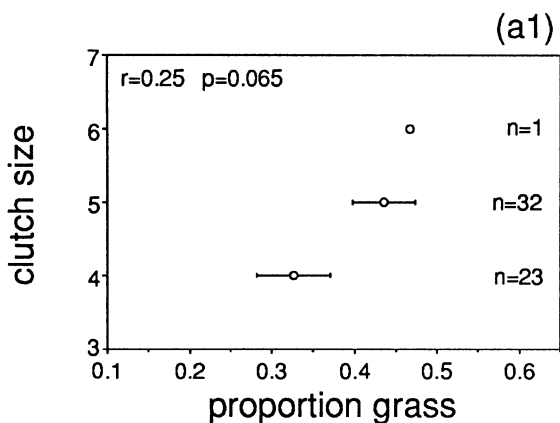
Since slightly different data sets were used to analyse effects on the different dependent variables, the degrees of freedom also vary between the analyses (Table 1). Although we essentially used the same data set to study effects on different reproductive parameters, we did not perform Bonferroni corrections for two reasons: First, the reproductive parameters analysed are not closely related variables; second, valuable information may be lost by using the rather conservative Bonferroni corrections. In this case this would correspond to a critical  $P$  value of 0.0083 for the results presented in Table 1. Statistics were calculated by SAS using the procedures CORR, FACTOR and GLM. All proportions were arcsin-square-root transformed. Food biomass, distances to the feeding site, and the coefficients of variation for tarsus size were log-transformed prior to analysis.

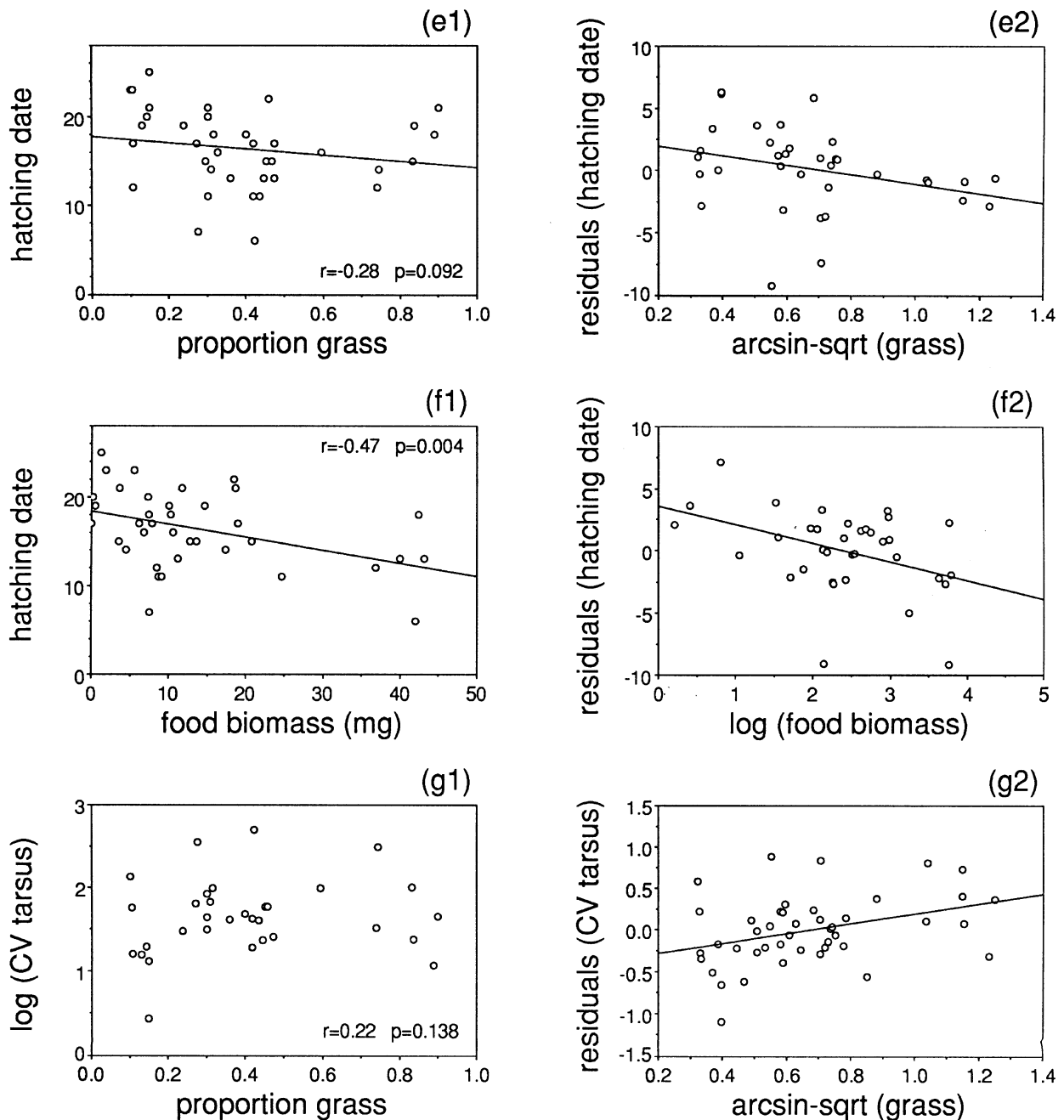
## Results

Reproductive performance was related to available food and foraging conditions in several ways. Both procedures of variable reduction (see Methods) yielded the same results. Since results based on mathematically constructed factor scores are more difficult to interpret, the following sections focus on results based on the five original variables selected according to Appendix 1; we only mention results from the principal component analysis at the end.

### Effects of food conditions in the territories

There were only two significant effects of feeding conditions in territories on the breeding parameters tested ( $P < 0.05$ , Table 1). The number of fledglings was inversely related to the energy content of the prey, opposite to the pattern found for feeding sites, and hatching date was negatively correlated with the proportion of grass, both in territories and feeding sites.





**Fig. 1** Relations **a** between clutch size and the proportion of grass, **b–d** between the number of fledglings and **b** the proportion of grass, **c** the available food biomass, and **d** the energy content of the available food, **e–f** between the hatching date (1 = 1 June) and **e** the proportion of grass and **f** the available food biomass, and **g** between the variation in tarsus length and the proportion of grass. All variables describing available food and vegetation are for conditions at the feeding sites (see Methods). **a1–g1** show univariate relations with original data; means and standard errors are given in **a1–d1**;  $n$  = sample size for each class: samples are not identical and therefore sample sizes differ slightly among **b1–d1**;  $r$  Pearson correlation coefficient,  $P$  probability, for univariate relations with transformed data. **a2–g2** show residuals of the models as presented in Table 1, but calculated without the independent variable on the  $x$ -axis

**Table 1** Summary statistics of analyses of covariance for 6 reproductive parameters in relation to food conditions. Separate analyses were calculated for food conditions at the feeding sites and in the territories. The detailed statistics are for the feeding sites. For the territories only significant relations are shown (*rel ter*). Proportions of tipulids and grass were arcsin-square-root-transformed, food biomass, distance and energy were log-transformed prior to analysis. Relations for feeding sites (*rel fs*) and for territories (*rel ter*): +/−/×  $P < 0.05$ ; (+)/(−)  $P < 0.10$

Source	<i>df</i>	MS	<i>F</i>	<i>P</i>	Rel fs	Rel ter
Dependent variable: clutch size						
Model	7	0.4017	1.52	0.1840		
Error	45	0.2637				
Food biomass	1	0.5788	2.19	0.1454		
Distance feeding sites	1	0.0216	0.08	0.7761		
Proportion tipulids	1	0.8875	3.37	0.0732	(−)	
Energy content	1	0.0127	0.05	0.8270		
Proportion grass	1	1.4094	5.34	0.0254	+	
Year	2	0.2150	0.82	0.4489		
Dependent variable: number of fledglings						
Model	7	2.2237	5.08	0.0008		
Error	29	0.4381				
Food biomass	1	4.3468	9.92	0.0038	+	
Distance feeding sites	1	0.1662	0.38	0.5427		
Proportion tipulids	1	1.0751	2.45	0.1281		
Energy content	1	2.4956	5.70	0.0237	+	−
Proportion grass	1	4.8264	11.02	0.0024	+	
Year	2	3.8006	8.68	0.0011	×	×
Dependent variable: hatching date						
Model	7	51.2513	4.61	0.0017		
Error	27	11.1084				
Food biomass	1	72.1053	6.49	0.0168	−	
Distance feeding sites	1	2.5892	0.23	0.6331		
Proportion tipulids	1	36.5282	3.29	0.0809	(+)	
Energy content	1	2.9007	0.26	0.6135		
Proportion grass	1	73.8107	6.64	0.0157	−	−
Year	2	65.3967	5.89	0.0076	×	×
Dependent variable: nestling period						
Model	8	5.1137	1.74	0.1253		
Error	34	2.9433				
Food biomass	1	0.5935	0.20	0.6562		
Distance feeding sites	1	10.9792	3.73	0.0618	(−)	
Proportion tipulids	1	1.5439	0.52	0.4739		
Energy content	1	11.1549	3.79	0.0599	(+)	
Proportion grass	1	4.1398	1.41	0.2439		
No. of nestlings	1	6.9092	2.35	0.1347		
Year	2	1.8507	0.63	0.5393		
Dependent variable: tarsus length						
Model	8	0.4144	0.57	0.7956		
Error	35	0.7278				
Food biomass	1	0.0880	0.12	0.7301		
Distance feeding sites	1	0.0641	0.09	0.7684		
Proportion tipulids	1	0.6713	0.92	0.3435		
Energy content	1	0.1164	0.16	0.6917		
Proportion grass	1	0.4316	0.59	0.4464		(−)
No. of nestlings	1	0.4020	0.55	0.4623		
Year	2	0.9822	1.35	0.2725		
Dependent variable: variation (CV) in tarsus length within broods						
Model	8	0.4623	3.49	0.0047		
Error	35	0.1327				
Food biomass	1	0.0963	0.73	0.4001		
Distance feeding sites	1	0.0382	0.29	0.5952		
Proportion tipulids	1	0.2712	2.04	0.1616		
Energy content	1	0.0057	0.04	0.8364		
Proportion grass	1	0.6318	4.76	0.0359	+	
No. of nestlings	1	1.0849	8.18	0.0071	+	+
Year	2	0.0355	0.27	0.7670		

## Effects of food conditions at the feeding sites

We found several effects of food conditions at the feeding sites, even though sample sizes were smaller (range 35–53 nests) than for the territories (range 66–102; see Methods). The following description is based on the significant results from the multivariate statistics presented in Table 1. These results may differ from the results based on univariate relations, some of which are not significant. In Fig. 1 we present both univariate relations and residuals from the multivariate models. *Clutch size* was larger for nests with a large proportion of grass at their feeding sites (Fig. 1a). The *number of fledglings* per nest was positively related to the proportion of grass (Fig. 1b), to the total amount of food biomass available (Fig. 1c), and to the energy content of the available food (Fig. 1d). Differences between the years were also significant, probably due to other environmental factors not considered. With respect to *time of reproduction*, birds foraging in places with abundant food and a high proportion of grass started breeding earlier than those with little food or low grass proportions (Fig. 1e, f). The *nestling period*, from hatching until fledging, was not related significantly to any of the independent variables studied. Nestling size, as measured by tarsus length, was not significantly affected by food conditions. But the variation in tarsus length was related positively to the amount of grass at the feeding sites (Fig. 1g) and to the number of nestlings in a nest. The effect of nestling number on tarsus variation is not plotted in Fig. 1 because this relation will be analysed in more detail for a larger data set (K. Bollmann and A. Schläpfer, unpublished work).

The analysis of covariance based on factor scores yielded the following significant relations ( $P < 0.05$ ) supporting the above results in terms of clutch size, reproductive success and time of reproduction. Clutch size was related to the vegetation factor, and increased with increasing grass cover, respectively decreasing proportions of dwarf shrubs. Number of fledglings was related to vegetation in the same way and, in addition, increased with available food biomass and with protein, lipid and energy content represented by the first food quality factor. Finally, hatching date for first clutches was negatively related to food biomass, i.e. birds with poor feeding sites laid later than those with good sites. In addition to these consistent results emerging from both analyses, the analysis based on factor scores yielded a few more significant effects suggesting that taxonomic or nutritional composition may be more important than in the analyses performed on the original variables. However, the meaning of these factors is difficult to assess, since some independent variables correlated only weakly with them (loadings between 0.4 and 0.5). For this reason we restrict our discussion to results based on the original variables, which are easier to interpret, yield fewer significant relations and therefore seem to be

more conservative than the analyses based on the factor scores.

---

## Discussion

More significant correlations were found between reproductive parameters and feeding conditions at feeding sites than on territories. Combined with the observation that half of the feeding sites lie outside of the territory boundaries (Frey-Roos et al. 1995), this suggests that territories do not function primarily as food sources for raising nestlings. Rather, they may serve as multi-purpose territories which also provide food for fledged young, protection from predators or suitable nest sites.

### Food quantity

Among the ecological variables considered in this study, the major effects on reproduction were exerted by (1) the amount of food at the feeding sites, (2) the energy content of prey items, and (3) the proportion of grass at the feeding sites.

#### *Amount of food*

The number of fledglings is related positively and the time of reproduction negatively to the amount of food at the feeding sites. Several studies have shown that energy intake of foraging animals is positively correlated with the density and the size of food items (e.g. Goss-Custard 1977, 1980; Sutherland 1982; Begon and Mortimer 1986). In our studies on water pipits we also showed that increasing prey density decreases searching times (Brodmann et al. 1997).

#### *Energy content of prey*

The observed positive correlation between the energy content of available food and the number of fledglings is caused by a single data point (Fig. 1, d2). Other evidence also suggests that the correlation is spurious. First, the univariate comparison does not indicate any relation (Fig. 1, d1); secondly, the analysis for the foraging conditions in the territories results in an inverse relation between number of fledglings and energy content of available food; and thirdly, the differences in energy content between arthropod taxa are small, i.e. usually less than 10% (Brodmann 1995).

#### *Proportion of grass*

The proportion of grass at the feeding sites is correlated positively with clutch size, number of fledglings, variation in nestling size and negatively with the time

of reproduction. Grass is representative for vegetation structure as a whole since the proportion of grass is related inversely to the proportions of the other three vegetation categories (short, intermediate and large dwarf shrubs) (Appendix 1). In other studies (Frey-Roos et al. 1995; Brodmann et al. 1997) we have shown that (1) "grass" is the one out of ten vegetation types which is preferred in the field by foraging water pipits, (2) the total amount of available food based on sweep netting is highest in this vegetation type, (3) searching times for prey increase from grass through medium sized dwarf shrubs (bilberry) to tall dwarf shrubs (juniper), and (4) food density and searching times are negatively correlated. Therefore, a high proportion of grass increases the amount of energy gained per unit time, through both high biomass and shorter searching times. The effects of grass, food biomass and the energy content of available food all indicate that the energy gain crucially influences reproduction.

### Food quality

We found no relationships between reproduction and the proportion of tipulids in the available food, which is related to all other measurements of food quality (Appendix 1). According to the results based on factor scores, it is possible that we underestimated the importance of food quality in the analysis based on the selected variables. But results on the food use of water pipits also suggest that food quality is much less important than profitability (Brodmann 1995). This is similar in other insectivorous bird species. Only a few studies have shown either a negative effect of unbalanced nutrition (Krebs and Avery 1984), or secondary compounds in the insect food (Perrins 1976), or detrimental effects of specific food taxa on reproduction (Tinbergen 1981). This study indicated no such effects for the main prey types fed to the water pipit nestlings. However, tipulids are actually eaten less than expected at high tipulid densities, and other prey types, such as heteropterans, are avoided completely (Brodmann 1995). Both findings suggest a potential for food quality effects under certain circumstances. Finally, there are significant year effects on the number of fledglings produced and on the time of reproduction. This suggests that influences other than feeding conditions also have an important effect on reproduction.

Overall, our results fit the general picture that reproduction in insectivores is usually limited by the amount of food or energy and less by specific nutritional compounds (Robbins 1993). In several bird species breeding success is positively, and breeding time negatively, related to available food (reviewed by Martin 1987); and birds provisioned experimentally with extra food often start to breed earlier (Boutin 1990; Nilsson 1994; Svensson and Nilsson 1995) and sometimes have a higher reproductive success (e.g. Arcese and Smith 1988). Water pipits, too, adjust their clutch size to food

conditions, which – through the energy gain of foraging birds – affect both reproductive success and timing of breeding. No relationships could be detected between the amount of available food or vegetation structure and the size of nestlings or the time until fledging. This indicates that water pipits do not invest more food per nestling under favourable feeding conditions, but rather try to breed earlier and produce more offspring. The increase in clutch size and number of fledglings, however, may not reliably reflect reproductive success, because nestling number is positively related to variation in nestling size (Table 1) and size differences can affect the chances of surviving and becoming established as a breeder (e.g. Perrins and Birkhead 1983).

**Acknowledgements** We are grateful to the Swiss National Foundation (SNF) for supporting the project through a grant to H.-U. Reyer (No. 31-26308.89). The paper greatly benefited from the constructive criticism of B. Anholt, P. Hendricks and two anonymous reviewers. D. Bauer and F. Frey-Roos collected and identified a significant proportion of the arthropods.

### References

- Arcese P, Smith JNM (1988) Effects of population density and supplemental food on reproduction in song sparrows. *J Anim Ecol* 57: 119–136
- Aspey WP, Blankenship JE (1977) Spiders and snails and statistical tales: Application of multivariate analysis to diverse ecological data. In: Hazlett BA (ed) *Quantitative methods in the study of animal behavior*. Academic Press, London, pp 75–120
- Bauer F (1986) *Datenanalyse mit SPSS*. Springer-Verlag, Heidelberg
- Begon M, Mortimer M (1986) *Population ecology – a unified study of animals and plants*, 2nd edn. Blackwell, Oxford, pp 103–152
- Belovsky GE (1978) Diet optimization in a generalist herbivore: the moose. *Theor Popul Biol* 32: 262–288
- Boutin S (1990) Food supplementation experiments with terrestrial vertebrates: patterns, problems and the future. *Can J Zool* 68: 142–153
- Bollmann K (1995) The mating system of the alpine water pipit in a variable environment: ecological, demographic and fitness aspects. PhD thesis, University of Zürich, Switzerland
- Brodmann PA (1995) Relations between food conditions, foraging behaviour and reproductive performance in the water pipit (*Anthus spinoletta*). PhD thesis, University of Zürich, Switzerland
- Brodmann PA, Reyer H-U, Baer B (1997) The relative importance of habitat structure and of prey characteristics for the foraging success of water pipits (*Anthus spinoletta*). *Ethology* (in press)
- Dearing MD, Schall JJ (1992) Testing models of optimal diet assembly by the generalist herbivorous lizard *Cnemidophorus murinus*. *Ecology* 73: 845–858
- Drent RH, Daan S (1980) The prudent parent: energetic adjustments in avian breeding. *Ardea* 68: 225–252
- Freeland WJ, Janzen DH (1974) Strategies in herbivory by mammals: the role of plant secondary compounds. *Am Nat* 108: 269–289
- Frey-Roos F, Brodmann PA, Reyer H-U (1995) Relationships between food resources, foraging patterns and reproductive success in the water pipit, *Anthus sp. spinoletta*. *Behav Ecol* 6: 287–295
- Goss-Custard JD (1977) Optimal foraging, and the size selection of worms by redshank, *Tringa totanus*, in the field. *Anim Behav* 25: 10–29



- Goss-Custard JD (1980) Competition for food and interference among waders. *Ardea* 68: 31–52
- Greenstone MH (1979) Spider feeding behaviour optimises dietary essential amino acid composition. *Nature* 282: 501–503
- Hochachka W (1990) Seasonal decline in reproductive performance of song sparrows. *Ecology* 71: 1279–1288
- Krebs JR, Avery MI (1984) Chick growth and prey quality in the European bee-eater (*Merops apiaster*). *Oecologia* 64: 283–299
- Martin TE (1987) Food as a limit on breeding birds: a life-history perspective. *Annu Rev Ecol Syst* 18: 453–487
- Martin TE (1995) Avian life history evolution in relation to nest sites, nest predation, and food. *Ecol Monogr* 65: 101–127
- Neighbors MA, Horn MH (1991) Nutritional quality of macrophytes eaten and not eaten by two temperate zone herbivorous fishes: a multivariate comparison. *Marine Biol* 108: 471–476
- Nilsson J (1994) Energetic bottle-necks during breeding and the reproductive cost of being too early. *J Anim Ecol* 63: 200–208
- Owen-Smith N, Novellie P (1982) What should a clever ungulate eat? *Am Nat* 119: 151–178
- Perrins CM (1976) Possible effects of qualitative changes in the insect diet of avian predators. *Ibis* 118: 580–584
- Perrins CM (1979) British tits. Collins, London
- Perrins CM (1991) Tits and their caterpillar food supply. *Ibis* 133 suppl 1: 49–54
- Perrins CM, Birkhead TR (1983) Avian ecology. Blackie, Glasgow
- Pulliam HR (1975) Diet optimization with nutrient constraints. *Am Nat* 109: 765–768
- Rappot DJ (1980) An optimization model of food selection. *Am Nat* 105: 575–587
- Robbins CT (1993) Wildlife feeding and nutrition, 2nd edn. Academic Press, San Diego
- Scriber JM, Slansky F Jr (1981) The nutritional ecology of immature insects. *Annu Rev Entomol* 26: 183–211
- Smith HG, Källander H, Nilsson J-A (1987) Effect of experimentally altered brood size on frequency and timing of second clutches in the great tit. *Auk* 104: 700–706
- Sutherland WJ (1982) Spatial variation in the predation of cockles by oystercatchers at Traeth Melynog, Anglesey. II. The pattern of mortality. *J Anim Ecol* 51: 491–500
- Svensson E, Nilsson J-A (1995) Food supply, territory quality, and reproductive timing in the blue tit (*Parus caeruleus*). *Ecology* 76: 1804–1812
- Tinbergen JM (1981) Foraging decisions in starlings. *Ardea* 69: 1–66
- Verhulst S, Tinbergen JM (1991) Experimental evidence for a causal relationship between timing and success of reproduction in the great tit *Parus m. major*. *J Anim Ecol* 60: 269–282
- Zumbühl G, Burnand J (1986) Vegetationskarte Davos-Parsenn-Dischma, 1:25,000 In: Wildi O, Ewald K (eds) Ergebnisse des MAB-Projektes Davos, Beilage. Eidgenössische. Anstalt für forstliches Versuchswesen, Birmensdorf

**Appendix 1** Partial correlations (Pearson) between 16 variables describing foraging conditions at the feeding sites. (+)/(-)  $P < 0.10$ ; +/-  $P < 0.05$ ; +/+/-  $P < 0.01$ ; +/+/-  $P < 0.001$ ; n = 53 nests. For further analyses, first tipulids with the highest number of correlations with  $P < 0.05$  are considered to represent the 8 correlated variables, then grass and the remaining variables. Abbreviations of the variables are given in parentheses

Variable	Bio	Cat	Tip	Spi	Grh	Rha	Pro	Lip	Car	Wat	Ene	Sds	Mds	Lds	Gra	Dis	No. $P < 0.05$	Considered
Food biomass (Bio)	XXXX										(+)						0	yes
Proportion caterpillars (Cat)	XXXX			(+)					+++								3	1.no
Proportion tipulids (Tip)	---	XXXX		+++		+			+++								8	1.yes
Proportion spiders (Spi)	(+)		+++	XXXX			+++			+++							5	1.no
Proportion grasshoppers (Grh)					XXXX	+				(+)	+++						5	1.no
Proportion rhagionids (Rha)			+			XXXX	+++										5	1.no
Protein content (Pro)			---	+++		+++	XXXX										5	1.no
Lipid content (Lip)			---	---				XXXX									4	1.no
Carbohydrate content (Car)	+++		+++	---				XXXX	XXXX	+++							4	1.no
Water content (Wat)			---	+++		(+)			+++	XXXX							6	1.no
Energy content (Ene)	(+)					+++				XXXX							1	yes
Small dwarf shrubs (Sds)												XXXX					2	2.no
Medium dwarf shrubs (Mds)						(+)						XXXX					2	2.no
Large dwarf shrubs (Lds)												XXXX					3	2.no
Grass (Gra)													XXXX				3	2.yes
Distance feeding sites (Dis)								(-)								XXXX	0	yes