PROVISIONING BEHAVIOUR IN RELATION TO FOOD AVAILABILITY AND NESTLING FOOD DEMAND IN THE WATER PIPIT *ANTHUS SPINOLETTA*

CLAUDIA M. RAUTER [1,2,3], PAUL A. BRODMANN[1] & HEINZ-ULRICH REYER[1]

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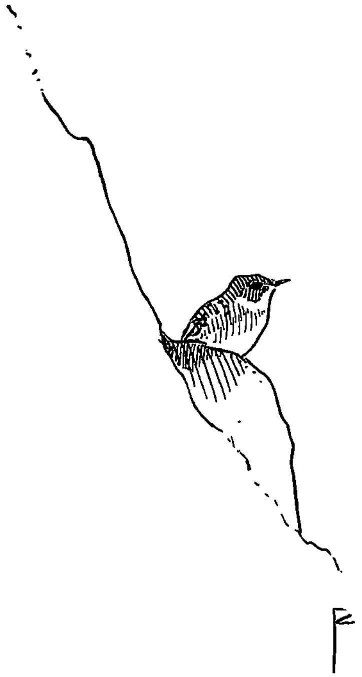

Insufficient food provisioning by parents can reduce growth rate of altricial nestlings, their size and weight at fledging, and also affect survival. Therefore at low food availability, parents should increase their food provisioning effort. In insectivorous Water Pipits *Anthus spinoletta* prey biomass differed up to 50 times among home ranges; nevertheless, number, size and weight of fledglings did not differ between home ranges with low and high prey biomass. Based on predictions from the literature, we investigated whether and how parents adjust their provisioning behaviour to food availability, measured by arthropod biomass, and to nestling demands, measured by brood size, nestling age and ambient temperature. Foraging distances did not vary significantly with any of the four variables. Feeding rates were also not related to food availability, but increased with brood size in both sexes. In addition, females showed a tendency to increase feeding rate with decreasing air temperature. Our results suggest that, at least in some years, arthropod food is so abundant in the birds' environment that it does not limit reproductive success.

Key words: *Anthus spinoletta* – parental care – food provisioning – brooding – food availability – brood size

[1]Zoologisches Institut, Universität Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland; [2]Zoologisches Museum, Universität Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland; [3]*Present address:* S-225 Agricultural Science Center North, Department of Entomology, University of Kentucky, Lexington KY 40546-0091, USA, E-mail: cmraut0@pop.uky.edu

INTRODUCTION

Food supply is critical to growth and survival of young. In birds, low food supply often results in reduced growth rates and lower fledgling size and weight (Ricklefs 1968; 1983; O'Connor 1984; Martin 1987). In altricial species insufficient feeding by parents can cause partial or even complete brood loss, especially when combined with high food demand due to low ambient temperature, large clutch size and increasing nestling age (O'Connor 1975; 1984; Mock *et al.* 1991; Sullivan & Weathers 1992; Dykstra & Karasov 1993). Therefore, when food availability is low, food items are small and/or nestling needs are high, parents should adjust their feeding behaviour to provide still enough food. For meeting this challenge, males and females have several possibilities: they can (1) increase time spent foraging, at the expense of other activities (Best 1977; Wittenberger 1982), (2) raise feeding rate (Wittenberger 1982; Monaghan *et al.* 1989; Darveau *et al.* 1993), (3) extend the foraging distance from the nest (Bryant & Turner 1982; Adams *et al.* 1994), (4) increase the load size brought back to the nest (Wittenberger 1982), and (5) reduce their own food intake in favour of the offspring's intake (Kacelnik & Cuthill 1990; Cucco & Malacarne 1995).

These potential responses are not mutually exclusive and they can interact in complicated ways. Foraging theory predicts, for instance, negative correlations between food availability and time spent foraging at a foraging site, on one hand, and distances flown to foraging sites, on the other, as well as a positive relationship between distance and load size. Whether these correlations affect the total time spent flying to foraging sites, foraging and flying back to the nest, and hence feeding rate, will depend on the precise shapes and relationships of the various gain curves and factors constraining the optimisation such as lack of complete information, predation risk, time limitations, minimum required feeding rates, specific nutrients and toxins as well as the relative values of present and future broods (Andersson 1978; Houston & McNamara 1984; Stephens & Krebs 1986; Beauchamp *et al.* 1991). For example, if the time available for foraging is constrained by the need to guard the offspring, bird parents can respond by reducing the duration of foraging trips (Martindale 1982) which can be achieved by reducing the distance flown to foraging sites and/or reducing the time spent foraging at the foraging site.

In Water Pipits *Anthus spinoletta*, prey biomass can vary up to 50 times among home ranges (Bollmann *et al.* 1997; Rauter & Reyer 1997). Nevertheless this difference does not necessarily affect the number of fledglings per brood or per season (Frey-Roos *et al.* 1995; Bollman *et al.* 1997; Brodmann *et al.* 1997b), or their size at fledging and duration of nestling period (Brodmann *et al.* 1997b). In this study we test predictions (2), (3) and indirectly also prediction (1) of the above list, i.e. we investigate whether Water Pipits adjust feeding rate and foraging distances in response to differences in brood size, ambient temperature and food availability. Due to the birds' shyness and often hidden foraging, relevant data for testing predictions (4) and (5) could not be collected in the field.

METHODS

Study area and birds

The study was conducted during the breeding seasons of 1991 and 1992 in the Dischmatal near Davos, Switzerland. The study area of about 200 ha covers a cross section through the valley and lies above the timberline between 1820 and 2400 m elevation. The valley floor is characterised by meadows, which are used to graze cattle or to grow hay. Dwarf shrubs mainly cover the slopes.

Water Pipits are common in the Alps above the timberline (Glutz von Blotzheim & Bauer 1985; Cramp 1988). In our study area these small, insectivorous passerines return to their breeding sites in late April where males defend territories and attract females by singing. Territories of breeding pairs have an average size of 1.51 ± 0.28 ha (Bollmann *et al.* 1997). Nesting begins in late May or early June (Bollmann *et al.* 1997). Only the females build the nests and incubate the eggs (usually four or five), but the males often provision the attending females with food (Böhm 1988; Rauter & Reyer 1997). On average, the eggs hatch after 15 days of incubation. Both parents feed the nestlings, but only the females brood the chicks. Fledging takes place at about the 15th nestling day (Böhm 1988; Bollmann 1996; Rauter 1996).

Water Pipits feeding young carry several prey items in their beak (multi-prey loader) back to the nest. There is evidence that with increasing distance of the foraging site to the nest Water Pipits select heavier prey and increase load size (Frey-Roos *et al.* 1995). Parents do not forage exclusively in their territory. They search for food up to 300 m from the nest. With increasing distance from the nest Water Pipits show an increasing preference for vegetation with higher arthropod biomass (Frey-Roos *et al.* 1995). Collar samples indicate that nestling food varies in space and time; but these differences reflect mainly differences in prey availability (Bauer 1992; Bollmann *et al.* 1997; Rauter & Reyer 1997; Brodmann & Reyer 1999): food availability is generally lower in meadows than in areas with dwarf shrubs, and it increases with progressing breeding season in all vegetation types.

Behavioural observations of feeding rate and foraging distances

We collected data on male and female foraging behaviour at 17 nests in 1991 and 23 nests in 1992. At least one bird at each nest was colour-ringed. Six males and six females bred in both years. Because the behaviour of these birds might not be independent between years, we used only one randomly chosen observation per bird in the analyses. Further, for two nests the data set was incomplete. Therefore, we used in the subsequent analyses only ten nests from 1991 and 16 nests from 1992. In 1991 five of the 10 nests were initiated in the first half of the breeding season (i.e. when all first breeding attempts and most replacement broods occurred) and five nests in the second half of the breeding season (i.e. when second broods occurred). In 1992 all 16 nests were initiated in the first half of the breeding season.

Each nest was observed once when the nestlings were six to eight days old. At this stage of the nestling period we expected food demand of the nestlings to be highest, because the daily increase of nestling body mass is highest at this nestling age (Biber 1982; Verbeek 1988). At each nest we observed the behaviour of the male and female simultaneously for two to five hours. The observations were carried out either in the morning between 6:00 and 12:00 CET or in the afternoon between 13:45 and 19:30 CET. As we also studied several other aspects of the birds' biology, we were not able to watch each nest from dawn until dusk. Hence, we do not know whether birds extend their time spent foraging into dusk or dawn or skip periods of relative rest at noon to cope with increased nestling demands and unfavourable environmental conditions.

Observations were made from blinds, which were erected at locations, from where the nest entrances as well as the foraging sites were visible. At each nest we recorded feeding rate (number of feedings per hour by a parent) and foraging distances from nest (m) of both, male and female Water Pipit. Foraging distances were taken as a straight line between the nest and the centre of the foraging site. We defined foraging sites as places where a bird foraged for at least 30 s after arrival. We marked the foraging site of each foraging trip by a bird on a map (scale 1:2500) of the study area and calculated the distances afterwards. We used the information on the position of the foraging sites to estimate food availability at the foraging sites. For further details see below. Brooding was taken as the time per hour, which the female spent in the nest.

Food availability

As a measure for food availability we used arthropod biomass, assessed by sweep netting. Samples were taken according to a 50 by 50 m grid system that was drawn onto the map of the study area. For two reasons, we sampled food availability in a 50 by 50 m grid system, rather than at the actual foraging sites. First, the often hidden foraging behaviour of Water Pipits did not allow us to locate and estimate the size of the foraging sites precisely. Second, while foraging Water Pipits can travel considerable distances (pers. observ.); the 50 by 50 m squares were assumed to provide a representative picture of areas they visit for foraging.

All 313 squares were sampled once between 17 and 24 June, the period when most of the first broods were in the nestling stage, and once between 14 and 21 July, the period when most replacement and second broods had nestlings. All sampling was done between 8:00 and 17:00 CET, when the vegetation was dry. Arthropods were conserved in ethanol for later identification to the level of orders or - if important as nestling food- to the level of families. Length and width were measured for each individual and used to calculate dry weight with the help of taxon-specific regression analyses. Total biomass of available food was expressed by the weight sum of the nine most important prey taxa, which were identified through collar neck samples. Further details of methods for sampling and analysing available food of the study area are given by Brodmann (1995), Brodmann *et al.* (1997b) and Brodmann & Reyer (1999).

We estimated food availability at a specific foraging site by first marking the site on a map (scale 1:2500) of the study area during the behavioural observations and later assigning it to the appropriate cell of the 50 x 50 m grid system used to assess food availability. For each bird we averaged arthropod biomass from all the foraging sites it visited during the behavioural observations, weighted by the frequency the bird visited each foraging site. These average arthropod biomass values were used as a measure of food availability in the analyses. We used food availability at foraging site instead of food availability within territories, because Water Pipits do not exclusively forage in their territory and shift their preferences for vegetation types with increasing distance from the nest (Frey-Roos *et al.* 1995).

Air temperature

Air temperature was measured by a thermistor (Type AT1, Delta-T Devices Ltd, Cambridge, U.K.), located 2 m above ground in the centre of the study area, which is the standard setup by Delta-T Devices Ltd for meteorological measurements. Every 10 minutes air temperature was recorded and hourly means were stored by a logger (Type DL2, Delta-T Devices Ltd). The hourly means were used to calculate mean air temperature for each session during which feeding behaviour was observed. Since air temperatures measured in the centre of our study area, the vegetation and the nest were strongly correlated (Rauter 1996), this method yields an adequate measure of the thermal environment that adult and nestlings experience.

Statistical analyses

Statistical analyses were performed using SYSTAT 7.0 (SPSS Inc. 1997). To test the predictions (2) and (3) we performed separate multiple regression analyses for feeding rate and foraging distance with brood size, nestling age, air temperature and food availability as independent variables. We tested prediction (1) indirectly by analysing the influence of brood size, nestling age, air temperature or food availability on the ratio of time spent brooding to time spent foraging of female Water Pipits by using a multiple regression analysis. To estimate time spent foraging per hour, we first multiplied the number of feedings observed per hour by twice the mean distance to the foraging sites to get the mean total distance flown per hour. Secondly assuming a flying speed of 10 m s^{-1} (Frey-Roos *et al.* 1995), we multiplied the mean total distance flown per hour by $(10 \text{ m s}^{-1})^{-1}$ to estimate time spent foraging per hour.

Foraging distances of males and females, ratio of brooding to foraging in females and food availability were not normally distributed (Lilliefors test: all $P < 0.1$; Sachs 1984). Thus, we log-transformed these variables. All other continuous variables (i.e. feeding rate of males and females, air temperature) were normally distributed (Lilliefors test: all $P > 0.1$). We tested for effects of year, season and time of day (i.e. observation made in the morning or in the afternoon) on all response variables using separate *t*-tests (Sachs 1984). Neither feeding rate, foraging distance nor ratio of brooding to foraging was effected by year, season or time of day (all $P > 0.08$). Thus, we pooled all data in the regression analyses. To test for differences between males and females, we used *t*-tests for paired groups in the case of behavioural variables and Wilcoxon matched pairs signed rank test in the case of food availability at foraging sites (Sachs 1984).

RESULTS

Both parents together provisioned 6-8 day old nestlings 10.8 ± 3.3 (mean ± SD) times per hour with arthropods collected at a mean distance of 62 ± 25 m. When broken down by sex, females fed nestlings 6.0 ± 2.4 times per hour. Males made 4.9 ± 1.4 feeding visits per hour which is significantly lower than the female value ($t = 2.719$, $df = 25$, $P = 0.012$). Average foraging distances for females (59 ± 26 m) and males (66 ± 28 m) did not differ significantly ($t = 1.646$, $df = 25$, $P = 0.112$). Brood size did not differ between or within years. Age of nestlings, however, differed both between and

Table 1. Brood size, nestling age (days), and air temperature (°C) during behavioural observations and food availability (mg dry weight per sample) at foraging sites. Mean and SE are presented. t-Tests were used to test for difference between and within years. The degrees of freedom were 24 for all tests. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s. $P > 0.05$. Sample sizes are given in brackets.

	1991 (10)		1992 (16)	Early broods (21)		Late broods (5)
Brood size	4.8 ± 0.1	n.s.	4.6 ± 0.1	4.6 ± 0.1	n.s.	4.8 ± 0.2
Nestling age	7.2 ± 0.2	**	6.4 ± 0.1	6.5 ± 0.1	***	7.6 ± 0.2
Air temperature	12.4 ± 1.8	n.s.	9.8 ± 0.7	9.5 ± 0.8	***	16.2 ± 0.8
Food availability						
Female foraging sites	18.6 ± 5.2	n.s.	13.6 ± 3.2	12.3 ± 2.6	*	28.9 ± 7.7
Male foraging sites	11.9 ± 3.8	n.s.	12.2 ± 2.9	11.3 ± 2.3	n.s.	15.2 ± 6.8

Table 2. Results from regression analyses relating feeding rates and foraging distances of both parents as well as the ratio of brooding time to foraging time, respectively, to three correlates of nestling food demand (brood size, nestling age [days], air temperature [ºC]) and one measure of food availability (arthropod biomass at foraging sites [mg dry mass per sample]). Significant tests of significance of coefficients are shown in bold. b: regression coefficient. * $P < 0.05$, ** $P < 0.01$.

		Brood size		Nestling age		Air temperature		Prey biomass	
	df	b	*t*	b	*t*	b	*t*	b	*t*
Female feeding rate	1, 21	**2.090** *	2.547	0.622	0.948	**-0.236** *	2.403	-0.381	0.888
Male feeding rate	1, 21	**1.165** *	2.213	-0.100	0.254	-0.113	1.844	-0.141	0.602
Female brooding / foraging ratio	1, 21	**-1.026** **	2.827	**-1.008** **	3.475	-0.034	0.793	0.308	1.619
Female foraging distance	1, 21	-0.017	0.110	-0.059	0.491	0.028	1.559	-0.076	0.956
Male foraging distance	1, 21	-0.020	0.130	-0.162	1.402	0.016	0.898	-0.038	0.550

within years (Table 1). This was due to three nests, which were observed late in the year 1991. The nestlings were eight days old in these nests, whereas in all other nests the nestlings were six or seven days old. During the nest observations air temperature ranged from 3.4 to 18.6°C with an average of 10.9°C. Air temperature did not differ between years, but was lower for early broods than for late broods (Table 1). This seasonal pattern corresponded to the pattern observed in the mean daily air temperature measured over 24 hours per day (average daily air temperature per month: June 1991: 8:3°C; July 1991: 11.4°C; June 1992: 7.5°C; July 1992: 12.2°C).

In terms of food availability, mean arthropod biomass at foraging sites was 12.9 mg dry mass per sample. There was no significant difference between female sites and male sites within pairs ($Z = -1.286$, $P = 0.199$; Wilcoxon test), but a 400-fold difference between the best and the worst foraging sites (range = 0.1 – 40.0 mg dry mass per sample). Food availability at foraging sites did not differ between years, neither for male nor female Water Pipits (Table 1). At male foraging sites, food availability did also not differ between early and late broods; however at female foraging sites food availability was higher for late broods than for early broods (Table 1).

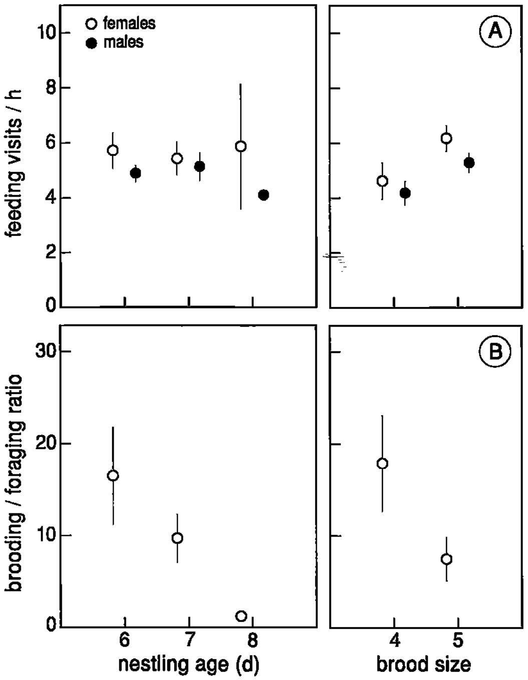

Fig. 1. Feeding rates of females (open symbols) and males (closed symbols) (a) and brooding to foraging ratios in females (b) in relation to nestling age (left) and brood size (right). Shown are means with standard errors.

Air temperature, food availability, brood size and age of nestlings were not correlated (all $P >$ 0.144, -0.016 $< r <$ 0.294). Only age of nestlings and food availability at the feeding sites of female showed a significant correlation (r = 0.412, P = 0.037).

In terms of demand, feeding rates of males and females did not vary with the nestling ages we examined; but they did increase with brood size (Table 2, Fig. 1a), and to such an extent that provisioning rates on a per young basis did not differ between broods of 4 and 5 ($t <$ 1.000, df = 24, $P >$ 0.3 for both sexes). In females, feeding rates also increased with decreasing mean air temperature (Table 2, Fig. 2). Moreover, females significantly decreased the ratio of brooding to foraging, as the nestlings grew older and when broods were larger (Table 2, Fig. 1b). Although food availability showed a considerable pair-to-pair variation (see above), feeding rates of both sexes were not related to food availability. Furthermore, in females the ratio of brooding to foraging was not correlated to food availability. Foraging distances of males and females were not related to any of the four independent variables (Table 2) nor did they correlate with any other dependent variables (all $P >$ 0.180, -0.268 $< r <$ 0.168). Since for nestlings the total, rather than the sex-specific feeding rates matter, we repeated the above analyses with feeding rates pooled and foraging distances averaged over males and females; but the above relationships persisted without exception.

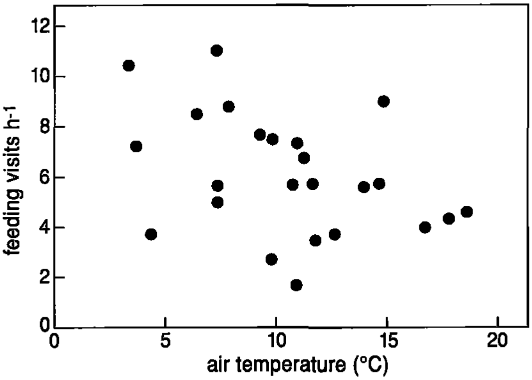

Fig. 2. Female feeding rates in relation to air temperature.

DISCUSSION

Water Pipits rearing 6-8 days old nestling raised their feeding rates in response to their young's increasing food demands which resulted from larger broods and lower temperatures; but feeding rates and foraging distances from the nest and the ratio of brooding to foraging did not vary with prey availability, contrary to predictions (1), (2) and (3) from the Introduction. These findings suggest that even in foraging sites with the lowest arthropod supply, food availability was high enough to not make food a limiting factor for reproduction. Such superabundance of food during breeding is common in grassland habitats (Wiens 1974; 1977a, b; Wiens & Rottenberry 1979; Rotenberry 1980), and its existence in our area is supported by others studies carried out during the same time on the same Water Pipit population: food availability did not affect the number, size and weight of fledglings (Bollmann *et al.* 1997; Brodmann *et al.* 1997b), and only 3% of all young may have died because of starvation (Bollmann 1996). Alternative explanations are that Water Pipits increased their load size with decreasing food availability or extended the length of their daily foraging period. For neither of these possibilities are data available.

The good food supply can probably be attributed to the exceptionally good weather conditions during June and July of both study years, 1991 and 1992. Compared with the long term means, temperatures were on average 1.25°C higher, there were 0.73 fewer days with less than 0°C ('ice-days') and snow cover was 7 cm lower (for details see Bollmann 1996). As survival and activity of arthropods is temperature sensitive, these conditions can be expected to have improved food availability through both, higher density and better foraging success. Experimental evidence suggests that Water Pipits find mobile insects faster than resting ones (Brodmann *et al.* 1997a). In spite of this causal link between high temperature, high prey mobility and short searching time, higher temperatures did not increase, but, if anything, decreased the feeding rates of females. This indicates an active parental response to higher nestling food demand under cold conditions.

The lack of a relationship between feeding rates and distances flown to foraging sites, suggesting superabundant food conditions, raises the question why Water Pipits do not produce larger clutches. If clutch size would have been constrained by energetic limitations during egg production or incubation, an increase of clutch size with progressing season would have been expected (Monaghan & Nager 1997), but this was not observed (Bollman 1996; Rauter 1996). Also, within first breeding attempts, there is no evidence that for first breeding attempts hatching success increased or duration of incubation period decreased with progressing season (K. Bollmann & A.R. Schläpfer unpubl. data), which would indicate that incubating females were energetically constrained (Monaghan & Nager 1997). Trade-offs between successive broods within a season which may lead to smaller than 'optimal' broods sensu Lack (1947) seem unlikely, because only 10% of the Water Pipits in our population produced second broods (K. Bollmann & A.R. Schläpfer unpubl. data). Thus, there is no evidence for energetic constraints on clutch size.

As an alternative explanation for the observed egg numbers Bollmann (1996) suggested that in terms of clutch size Water Pipits pursue a bet-hedging strategy in response to high predation rate and decreasing probability of inclement weather with progressing season. On average 28% of the nests lost at least one young due to predation and snowstorms can destroy up to 48% of the active nests (Rauter *et al.*, unpubl. data). The average probability of nest loss due to snow and predation was highest during the first part of the breeding period when Water Pipits undertook their first breeding attempts, and decreased thereafter. This seasonal decrease of probability of nest loss is reflected by larger clutch sizes in the second part of the breeding season compared to the first part of the breeding season (Bollmann 1996).

In conclusion, the observed responses to decreasing food availability do not seem to support the predictions (1)-(3) from the Introduction. We found no evidence for an increase in the ratio of brooding to foraging with decreasing food availability nor an increase in feeding rates (2) and foraging distances (3). This, however, is not to say that parents do not adjust their feeding behaviour to food conditions, because at least three points have to be remembered. (a) For testing the predictions that parents increase load size (4) and/or reduce their own in favour of the nestlings' food intake (5) we have no data. (b) The parental response is likely to vary with the age of the nestlings and the contribution of the mate, because both affect the relative benefits from brooding and feeding. (c) The weather, and hence food conditions, in Alpine environments are rather unpredictable (Franz 1979). Therefore, Water Pipits - and other species with similar habits - may be more food limited and show different responses in other years and even suffer from reduction in reproductive success (cf. Frey-Roos *et al.* 1995). With increasing global warming the probability of 'good' years with higher temperature, earlier snow melt and a longer growing season for plant will increase (cf. Groisman *et al.* 1994; Myneni *et al.* 1997; Menzel & Fabian 1999). This might not only make good food conditions found in our study the rule, rather than the exception; it might also allow birds to nest earlier and rear more broods per year (cf. Crick & Sparks 1999). In the long run, however, global warming may turn out to be disadvantageous. Theoretical simulation studies predict vegetation changes with global warming (e.g. Bartlein *et al.* 1997; Kienast *et al.* 1998). Increased temperatures might elevate the timberline and, thus, reduce the total area of alpine grassland, the main habitat of Water Pipits.

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SAMENVATTING

Om jongen in het nest (nestblijvers) groot te kunnen brengen, moeten oudervogels voldoende voedsel aanslepen. Wanneer het voedselaanbod varieert, zal ook de inspanning die de ouders leveren, variëren: bij een laag aanbod zullen de ouders zich meer moeten inspannen. In deze studie aan Waterpiepers *Anthus spinoletta* is onderzocht hoe de ouders zouden kunnen compenseren voor een laag voedselaanbod. Daartoe is het foerageer-

gedrag van 40 paren gevolgd. De paren kenden rond hun nesten grote verschillen in prooiaanbod: in de rijkste territoria werd 400 maal zo veel potentieel voedsel aangetroffen als in de armste. Toch verschilden de paren niet in het aantal grootgebrachte jongen, of in het gewicht of de grootte van de jongen. Paren in territoria met een laag voedselaanbod bestreken niet meer gebied en brachten ook niet minder vaak per foerageeruur prooien aan. Ook besteedden ze niet meer tijd per uur aan foerageren. Wel werd meer voedsel aangebracht met het ouder worden van de jongen (en de daarmee gepaard gaande grotere vraag om voedsel) en tijdens koude dagen. Hoewel geen gegevens verzameld konden worden over het totaal aantal foerageeruren per dag en over de hoeveelheid aangebracht voedsel per nestbezoek, suggereren deze resultaten toch dat ook ouders in 'arme' territoria nog zoveel voedsel ter beschikking hadden, dat ze niet of nauwelijks harder hoefden te werken dan vogels in rijke territoria. Blijkbaar was er dus in alle territoria ruim voldoende voedsel aanwezig. Alleen koude deed de vogels harder werken: ze lijken dus baat te hebben bij warme zomers. Of het broeikaseffect een positieve bijdrage zal leveren aan het broedsucces van deze soort wordt echter betwijfeld. Klimaatmodellen voorspellen namelijk naast een toenemende kans op warme zomers (goed voor deze soort op korte termijn) ook veranderingen in de vegetatie in de Alpen. De boomgrens zal hoger komen te liggen, wat ten koste gaat van het areaal daarboven gelegen graslanden, de habitat van de Waterpieper in de Alpen. (MFL)

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