University of Groningen

The influence of ambient temperature on diet in the Great Tit

Wansink, Dennis; Tinbergen, Joost M.

Published in:
Journal of Avian Biology

Publication date:
1994

Link to publication in University of Groningen/UMCG research database

WILEY

Nordic Society Oikos

The Influence of Ambient Temperature on Diet in the Great Tit
Author(s): Dennis Wansink and Joost M. Tinbergen
Source: *Journal of Avian Biology*, Vol. 25, No. 4 (Nov., 1994), pp. 261-267
Published by: Wiley on behalf of Nordic Society Oikos
Stable URL: http://www.jstor.org/stable/3677272
Accessed: 08/11/2013 06:22

The influence of ambient temperature on diet in the Great Tit

Dennis Wansink and Joost M. Tinbergen

Wansink, D. and Tinbergen, J. M. 1994. The influence of ambient temperature on diet in the Great Tit. – J. Avian Biol. 25: 261–267.

In winter, Great Tits *Parus major* have a mixed diet of insect food and seeds. Field data suggest a dietary shift towards seeds with declining ambient temperatures. We hypothesised that Great Tits increase their preference for seeds with decreasing temperatures to raise their fat intake over time. An experiment was carried out to test whether this dietary shift with temperature exists. Six Great Tit females, held in captivity and acclimatized to winter conditions, had free access to two food types that differed in fat content. The ambient temperature was manipulated during the night, and for both food types the consumption and digestibility were estimated. During the night the energy expenditure was estimated using indirect calorimetry.
Neither the digestibility of fat, nor the energy metabolization was related to ambient temperature. Evening weight, nocturnal energy expenditure, net food consumption and metabolizable energy intake were higher at lower temperatures. The proportion of fat in the diet was independent of the night temperature. There is no evidence that the preference for a fat-rich diet in Great Tits is affected by ambient temperatures.

D. Wansink and J. M. Tinbergen, Netherlands Institute of Ecology, C.T.O., P.O. Box 40, 6666 ZG Heteren. Present address of J.M.T.: Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands.

In classical models of optimal diet choice, differences in profitability are used as the sole factor determining which items are included in the diet (reviews in Krebs and McCleery 1984, Stephens and Krebs 1986). These models predict that the most profitable food type is always taken, and that the inclusion of a lower ranking food type depends on the availability of the former. Yet, several studies on birds have indicated that simple energy maximizing models may not be adequate to explain changes in diet (McLean 1974, Perrins 1979, Tinbergen 1981, Krebs and Avery 1984, Greig-Smith and Wilson 1985, Jordano 1988). Additionally, in an experiment with constant food availability and light conditions over the year, Berthold (1976) showed that Garden Warbler *Sylvia borin* and Blackcap *S. atricapilla* changed their diet over the year. These birds preferred vegetable food during the period of winter moult, and animal food during the periods of migration. This suggests that dietary shifts can be adapted to shifts in nutritional needs of birds.

Great Tits *Parus major* are insectivorous birds that can include seeds in their diet when available (Betts 1955, Balen 1980). The importance of seeds for Great Tits is illustrated by the positive relationship between their winter survival and the beech mast availability (Balen 1980). Within winters, on following days, the number of Great Tits foraging on nuts is higher when ambient temperatures are low (Balen 1980), suggesting a dietary shift. Two hypotheses can be formulated to explain this shift. First, it might be a consequence of temperature effects on the relative availabilities of seeds and insects. Alternatively, it could be an adaptive response to changing nutritional needs. The fat content of nuts is about twice as high as the fat content of insect food; 35 to 40% for beech nuts, 60 to 70% for hazel- and walnuts, less than 10% for insect imagos and 20 to 30% for insect larvae (Holsheimer 1985, J. Mertens unpubl. data). In cold weather it may be important to accumulate enough body fat to survive the night. In Great Tits, as well as in other passerines, evening weights increase with decreasing temperature, reflecting the deposition of body fat (Balen 1967, Newton 1969, Kendeigh et al. 1969, Jenni and Jenni-Eiermann 1987, Lehikoinen 1987, Haftorn 1989, Ekman and Hake 1990). Since the synthesis of body fat is more easily accomplished from fat than from carbohy-

drates or proteins (Mitchell 1962), we would expect a shift towards fatter diet at lower ambient temperatures.

We tested whether captive, winter acclimatized Great Tits respond to a decrease in ambient temperature with a dietary shift towards fat.

Methods

In autumn, several juvenile Great Tits were caught from a wild population in the Netherlands. The birds were kept in outdoor cages $40 \times 50 \times 60$ cm for a month to get used to life in a cage and to the experimental food. Six females kept their body weight at a stable level and accepted the experimental food types. In December 1990 two, and in January 1991 four of these females were used in the experiment.

Experimental procedure

During the experiment the birds were kept on a light regime of 9 hours light and 15 hours darkness. At daytime the birds were housed in the same cages as during the habituation period. The cages were completely closed to prevent spillage of food and faeces. The birds could hear, but not see each other. Ambient temperature was measured with a thermometer inside the cage. The nights were spent in nestboxes $24 \times 12 \times 10$ cm, that were placed in a temperature-controlled cabinet.

By manipulating the night temperature in the cabinet we tried to affect the energetic needs of the birds. The temperature during warm nights was 16°C, and during cold nights -5°C (in December) or -8°C (in January). We did not manipulate the temperature during the day to prevent direct temperature effects on the consistence of the food. Temperatures during the day fluctuated between 15 and 21°C. To exclude possible effects of these fluctuations on diet choice, we used a design with controls. Each experiment took three weeks. All birds started with a week with warm nights. In the second week one bird per pair experienced seven cold nights, while the other bird (the control) experienced warm nights. In the third week the conditions were reversed. This meant that three birds experienced a shift from a "warm" night to a "cold" night (group I), whereas the other three birds experienced both a shift from warm to cold and from cold to warm (group II).

To minimize negative effects of handling, the birds were weighed while in the nestbox. Weighing took place after the birds had entered the nestboxes in the evening, and before they left the nestboxes in the morning.

The food

Food was offered daily in two trays: one containing vegetable fat, the other containing a mixture of ground animal and vegetable food. The mixture had a low fat content (9.8%) and a low energy content (19.9 kJ g^{-1} dry weight). The vegetable fat contained 100% fat with an energy content of 39.5 kJ g^{-1} dry weight. Both food types and water were available ad libitum.

These artificial food types were chosen because the unit effort to acquire them was equal. Both food types could be swallowed immediately; no handling, search or pursuit was needed. Also, control tests indicated that there was no measurable weight change due to evaporation under the experimental conditions. Finally, the birds could not select single items from the mixture because it was homogenized by grinding. This was confirmed by analysis of the fat content of the mixture at the start and the end of the day.

Energy intake and fat consumption

The cages were cleaned daily and the remaining food and faeces were collected, freeze dried and weighed. The net food consumption (CONS), in grams per bird per day, was calculated by subtracting the dry weight of the faeces and the remaining food from the amount of food offered.

To calculate the daily metabolizable energy intake (MEI) and relative fat consumption (RFC) of each bird we measured the energy and fat content of both the food and the faeces. The fat content was determined with a chloroform-water-methanol solvent system (Atkinson et al. 1972). The energy content was measured with a Gallenkamp bomb calorimeter. The faeces of three days were taken together to get a sufficient amount for the analyses. The digestibility of fat (Q_{fat}) and the energy metabolization (Q_{eng}) per three days per bird were calculated, using the formulas:

$$Q_{fat} = 1 - \frac{(\text{g faeces} * \text{proportion fat})}{\text{g fat} + (\text{g mixture} * \text{proportion fat})} \text{ and}$$

$$Q_{eng} = 1 - \frac{(\text{g faeces} * \text{energy content})}{(\text{g fat} * \text{energy cont.}) + (\text{g mixt.} * \text{energy cont.})}$$

Since individual variation in Q_{fat} and Q_{eng} appeared to be low (see Results), the mean values of all birds were used to calculate the fat and energy content of the faeces per day per bird. This made it possible to calculate the metabolizable energy intake (MEI) and the relative fat consumption (RFC) per day per bird.

MEI (kJ d^{-1}) = {(g fat * energy content) + (g mixture * energy content)} * Q_{eng}

$$RFC = \frac{\{\text{g fat} + (\text{g mixture} * \text{proportion fat})\} * Q_{fat}}{\text{g fat} + \text{g mixture} - \text{g faeces}}$$

Table 1. Independent variables used in the regression analyses. Day n is the day following the night the temperature was manipulated.

1) NT = the average temperature during the night before day n (°C)
2) DT = the average temperature during day n (°C)
3) EW(n-1) = evening weight on the day before day n (g)
4) MW(n) = morning weight on day n (g)
5) AC = dummy variable, 1 in the week after the week with the cold night, 0 in all other weeks
6) IND = 5 dummy variables, that where incorporated in the model together to test for individual differences

Energy expenditure

In a preliminary experiment we had the impression that the experimental birds did not increase their energy expenditure when the temperatures at night were low. Reinertsen and Haftorn (1986) showed that, when ambient temperatures are low, Great Tits may utilize nocturnal hypothermia as an energy saving mechanism. To check whether the birds' energy expenditure was affected by night temperature we measured the O_2 consumption and CO_2 production during the night.

Once per week the nestboxes in which the birds spent the night were connected to a respirometer. The respirometer measured the CO_2 production (VCO$_2$), using a TPA 312 Infra-red analyzer (Telsec Process Analyzers, Ltd.), and the O_2 consumption (VO$_2$), using a S-3A Oxygen analyzer (Applied Electrochemistry, Inc.) in an open-circuit system. Dry air was supplied to the nestboxes at 333 ml min^{-1}. Air flow rates were regulated by mass flowmeters (Brooks Instrument B.V.). The outflowing air was dried over silica-gel. The analyzers were connected via a 3455A Digital Voltmeter (Hewlett-Packard) to a microcomputer, which recorded the CO_2 production and the O_2 consumption at 30-s intervals, both in ml min^{-1}. A series of solenoid valves in the multichannel system made it possible to switch automatically to outdoor air and to two birds sequentially. The outdoor air was measured for 10 min and used for reference. The birds were measured alternately for 15 min. Recordings started a few minutes after the birds entered the nestbox, and lasted until they were released the next morning. Data from the period when the birds were inactive and postabsorptive were used to calculate the mean nocturnal energy expenditure (NEE), using the formula:

NEE (Watt) = 0.270 * VO$_2$ + 0.083 * VCO$_2$
(Romijn and Lokhorst 1961).

Hence, NEE represents BMR + EE$_t$, where BMR is Basal Metabolic Rate and EE$_t$ is the energy expended for thermoregulation.

Statistics

Since we used repeated measurements, paired t-test on the mean performance of individual birds in the different treatments were used to test significance of the overall effect of the experiment.

A multivariate autoregression model was used to analyse variations in body weight and RFC on the temperature at night (NT) in more detail. The autoregression model was used to estimate parameter effects while controlling for the statistical dependence of the repeated measures on the dependent variable.

Other independent variables (Table 1) were added to the model and the significance of each variable's contribution was tested by deletion from the full model using the F-test described by Sokal and Rohlf (1981, p. 633). IND stands for five dummy variables, representing the n-1 experimental birds, that were added to the model together. As this is a correction for the between-individual variation, the remaining variation was purely within-individual.

When proportions were involved, these were first transformed using the arcsine-square-root transformation.

Results
Nocturnal energy expenditure

The temporal pattern of O_2 consumption (VO$_2$) was similar during cold and warm nights (Fig. 1). After the birds entered the nestbox, VO$_2$ decreased and levelled off within 30 min, sometimes before the recordings started. It was very constant throughout the rest of the night until 1.5 h before daybreak, when it increased steadily to its daytime level.

Nocturnal energy expenditure (NEE) was significantly affected by the night temperature (paired t-test on the mean values per temperature (cold vs warm), df = 5, t = 13.11, p < 0.001). The birds expended on average 0.320 ± 0.013 Watt (n = 6) during warm nights and 0.578 ± 0.043 Watt (n = 6) during cold nights.

So, the basic assumption of our experiment, that the energy expenditure of the birds can be manipulated by changing the night temperature, was confirmed.

Body weights

The average body weights of the two groups of birds are given in Fig. 2; there were differences between the two groups. In both groups the mean evening weight increased when the night temperature decreased (paired t-test, df = 5, t = 3.27, p < 0.03). However, the mean evening weight of the birds from group II did not decrease in the third week, when the night temperature was high again. On the other hand, the mean morning weight hardly changed when the night temperature decreased
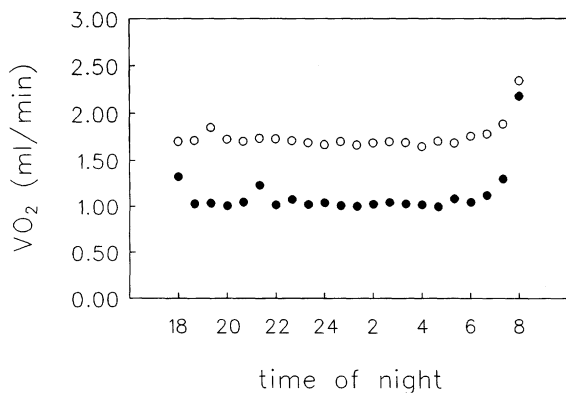
Fig. 1. Rate of O_2 consumption (ml min^{-1}) of one of the female Great Tits during a warm (●) and a cold night (○).

(paired t-test, df = 5, t = 0.06, ns), but it increased in the third week for group II, an indication that body fat was deposited (Lehikoinen 1987, Haftorn 1989). As a result, overnight weight changes differed consistently with night temperature (paired t-test, df= 5, t = 3.48, p < 0.02, warm nights: − 1.08 g, cold nights − 1.60 g).

To analyse the effect of the sequence of the cold and warm periods we used an autoregression model to control for the statistical dependence of the data. To do so we regressed the evening weights (EW) on the temperature in the previous night (NT), the day temperature (DT), the morning weight (MW) and a dummy variable that was 1 in the week after a cold night and 0 in all other cases (AC). We controlled for statistical dependence by including the evening weight of the night before (EW-1) and the evening weight of two nights before (EW-2) and for individual differences (IND). The result indicates that both NT and DT were associated negatively with EW (Table 2). This result means that within individuals, and
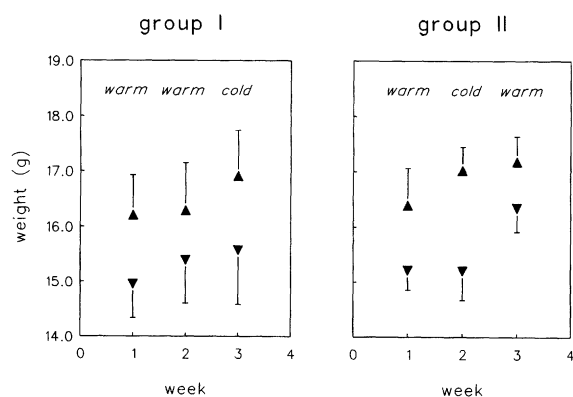
group I   group II

Fig. 2. Mean morning (▼) and evening weights (▲) of two groups (I and II) of three Great Tit females under different night temperature regimes. Warm is 16°C (all birds) and cold is −5°C (one bird in each group) or −8°C (two birds in each group). The vertical lines are the standard deviations.

Table 2. First order autoregression model explaining variation in evening weight (EW) as a function of evening weight on the previous night (EW-1), individual differences (IND), morning weight (MW), night temperature of the previous night (NT) and day temperature (DT) and the sequence of the warm and cold weeks (AC). Given are the coefficients of the independent variables in the final model, and the significance of their contribution to the model as tested by deletion from the full model.

	Estimate	(Delta) deviance	F	p
Null model		50.812		
Constant	5.984			
EW-1	0.728	12.77	$F_{1,76} = 148.4$	<0.001
EW-2		ns		
IND		1.504	$F_{5,76} = 3.50$	<0.01
MW		ns		
NT	−0.00866	0.702	$F_{1,76} = 8.70$	<0.01
DT	−0.0862	1.094	$F_{1,76} = 12.71$	<0.001
AC		ns		
Residual deviance		6.5416		

independently of the EW-1, EW is associated with these variables. No effect of AC was apparent. The interactions between NT and DT with IND were not significant.

The morning weights (MW) were analysed in a similar way. MW was regressed on the temperature in the previous night (NT), the day temperature (DT), the evening weight of the day before (EW-1) and the dummy variable (AC). We again controlled for individual differences (IND) and for statistical dependence by including the morning weight of the day before (MW-1) and the morning weight of two days before (MW-2). The result was that EW and AC were associated with MW, but not DT and NT (Table 3). No interactions with IND were found

Table 3. First order autoregression model explaining variation in morning weight (MW) as a function of the previous morning weight (MW-1), individual differences (IND), the evening weight on the previous day (EW-1), night temperature (NT) and day temperature (DT) of the previous day and the sequence of the warm and cold weeks (AC). Given are the coefficients of the independent variables in the final model, and the significance of their contribution to the model as tested by deletion from the full model.

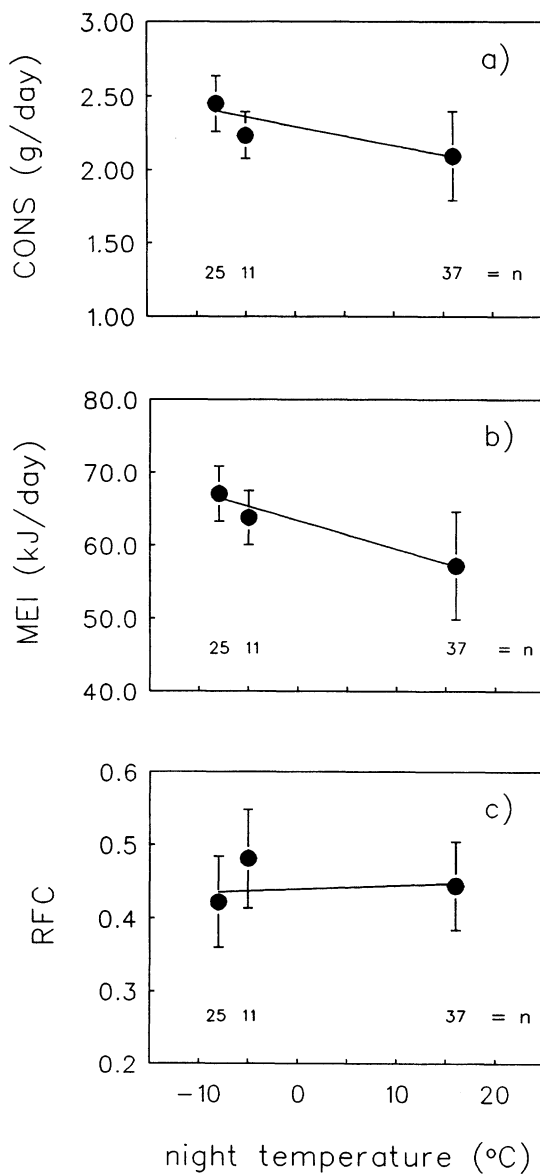|	Estimate	(Delta) deviance	F	p
Null model		52.708		
Constant	3.124			
MW-1	0.442	2.28	$F_{1,76} = 26.35$	<0.001
MW-2		ns		
IND		1.849	$F_{5,76} = 21.36$	<0.001
EW-1	0.313	1.620	$F_{1,76} = 18.72$	<0.001
NT		ns		
DT		ns		
AC	0.516	1.256	$F_{1,76} = 14.52$	<0.001
Residual deviance		6.577		

Fig. 3. Simple regressions of the Net Food Consumption (a), the Metabolizable Energy Intake (b), and the Relative Fat Consumption (c) of six Great Tit females on the temperature at night (NT). Shown are the means and standard deviations of all birds at the three different night temperatures (-8, −5 and 16°C). N = number of observations (bird-days). The regression equations are respectively: CONS = 2.297 − 0.013 NT (r^2 = 0.264, df = 71, p < 0.001), MEI = 63.37 − 0.388 NT (r^2 = 0.374, df = 71, p < 0.001), and RFC = 0.44 + 5*10^{-4} NT (r^2 = 0.009, df = 71, p = 0.434). Although statistical evaluation of RFC on NT was based on arcsine-square-root transformed data, the figure is based on untransformed data.

to be significant. These results strongly suggest that increasing the night temperature after a cold week affected the morning weights differently than decreasing the night

temperature (significance of AC). Therefore we restricted our analyses of the dietary shift to the two weeks with a shift from warm to cold nights (weeks 2 and 3 for group I, and weeks 1 and 2 for group II).

Consumption, energy intake and diet

The net food consumption (CONS) increased with decreasing night temperatures (paired t-test, df = 5, t = 3.04, p < 0.03, Fig. 3a).

The digestibility of fat (Q_{fat}) and the energy metabolization (Q_{eng}) were not different among individuals (p = 0.956 for Q_{fat}; p = 0.985 for Q_{eng}). Within individuals Q_{eng} was not different between weeks with cold nights and weeks with warm nights (paired t-test, df = 5, t = -1.67, ns). The average value of 0.847 was used in all calculations (see Table 4). Q_{fat} was also not affected by the temperature at night (paired t-test, df= 5, t = -1.75, ns), and we used the overall mean (0.921; Table 4) to calculate the relative fat consumption (RFC) per day per bird.

The metabolizable energy intake (MEI) increased with decreasing night temperatures (Fig. 3b, paired t-test, df = 5, t = -3.65, p < 0.02).

The relative fat consumption (RFC) was not affected by the night temperature (Fig. 3c, paired t-test, df = 5, t = 0.52, ns). Since it is known that fatter birds, e.g. Greenfinches *Carduelis chloris*, increase their fat reserves less (Ekman and Hake 1990) we again used an autoregression model to test for effects of morning weights on the relative fat consumption (RFC). The variance in RFC was significantly explained by RFC-1 ($F_{1,58}$ = 50.67, p < 0.001), but not by morning weight or other variables. Individual differences in RFC explained part of its variation ($F_{5,54}$ = 8.65, p < 0.001). There is no indication that NT affected RFC.

These results are based on analyses of all days of the week. However, after the shift in night temperature we may expect a period of time in which the birds get used to the new situation. Analysis of the dependence of CONS, MEI and RFC on NT, excluding the first or the first three days after the temperature shift, did not affect the above mentioned results. So, we can say that acclimatization after the temperature shift did not play a rôle.

In summary, the increase in energy intake, to compensate for the increased nocturnal energy expenditure at

Table 4. Assimilation efficiency of fat (Q_{fat}) and energy (Q_{eng}) per three days per bird. Given are the mean values and their standard deviations (± sd) of six Great Tit females, for weeks with cold nights (-8 and −5°C) and weeks with warm nights (16°C). n = number of 3-day samples.

	Cold (mean ± sd)	n	Warm (mean ± sd)	n	Both (mean ± sd)	n
Q_{fat}	0.912 ± 0.017	11	0.926 ± 0.021	20	0.921 ± 0.020	31
Q_{eng}	0.832 ± 0.024	9	0.853 ± 0.019	19	0.847 ± 0.023	28

lower ambient temperatures, was achieved by an increase in food consumption and not by a shift to a fatter diet.

Discussion

No significant effect was found on the relation between the relative fat consumption (RFC) and the night temperature (NT). Since the goal of the study was to estimate this relationship we will elaborate on the precision of this result by estimating the power of the test used. The paired t-test estimated the difference between the warm and the cold group to be statistically indistinguishable from 0 (mean difference + 0.0219, se 0.0219). If we assume the estimate of the variance of the distribution of the difference between the groups to be independent of its mean, a power curve can be calculated by comparing the normal distribution of the differences for H_0 (mean = 0) to a number of alternative hypotheses (mean = 0.02, 0.04 etc.) at a significance level of 0.05. We then calculated the difference that could be detected with a power of about 0.8. Back-transformation of the arcsine-square-root transformed coefficient at average RFC (0.4) gave an estimate of the difference of 0.05. Small differences thus should be detectable with the test used. Hence, we can safely conclude that the Great Tits in our experiment increased their food consumption with decreasing ambient temperature, but did not change the fat content of their diet.

That the tits in our experiment had a mixed diet is remarkable. Based on the most simple optimalisation models we would expect that the tits would exclusively eat one of the two food types and not a mixed diet. The logic behind this is that one type will always have the highest profitability. Judging from the high energy return of fat (Bairlein 1985, Zwarts and Blomert 1990, this study) we expect that, in an ad libitum situation, vegetable fat should be the preferred food, and should therefore be taken exclusively. Yet, we found that the tits took both food types in a stable proportion. This suggests that a mixed diet is advantageous to the birds.

There are two models that may explain such a partial preference. Pulliam (1975) suggested that essential nutrients could play a role in the determination of the diet. His model predicts a constant intake rate of the item with the essential nutrients, while the intake rate of the alternative item (higher in energy content) depends on its availability. A different model was put forward by Rapport (1980). His model suggests that diets reflect an optimal mixture of complementary nutrients given their relative availabilities.

According to both models the mixture of ground animal and vegetable food is expected to have an essential nutrient not present in the vegetable fat. Protein is a likely candidate. Birds need a minimum amount of protein per day for maintenance, which varies between 7 and 30 per cent of the diet, depending on the bird's physiological state and the quality of the protein (Fisher 1972, Robbins

1983). According to the producer, the mixture contained 18.8% protein. During weeks with warm nights the diet contained on average 67.0% mixture (by weight) and during weeks with cold nights 69.1%. In other words, about 12.8% protein was consumed, and because the digestion of protein is never complete (Fisher 1972, Bairlein 1985) probably less was retained. Although we cannot with certainty identify protein as the nutrient that makes the mixture attractive to Great Tits, it seems plausible that the birds showed a partial preference to guarantee their protein intake.

An increase in energy expenditure for an animal living on a mixed diet would lead to a dietary shift under Pulliam's hypothesis, but not under the hypothesis of Rapport. In our experiment with Great Tits, energy expenditure was increased by manipulation of the ambient temperature at night. If Great Tits were energy maximizers subject to a nutrient constraint we would expect a shift in fat consumption with decreasing temperatures. Against this expectation, their diet did not change with temperature manipulation, favouring the model of Rapport. However, it is possible that by manipulating the temperature at night we not only altered the energy requirements of the birds, but also the requirements for specific nutrients or vitamins. Since we have no data on the physiological state of our birds at different ambient temperatures, further experiments are needed to discriminate between Rapport's and Pulliam's model.

Several authors have noted a preference for seeds high in fat content during periods of fat deposition in birds (Kear 1962, Fry 1967, Greig-Smith and Wilson 1985, Thompson et al. 1987). In experiments with winter acclimatized House Finches Carpodacus mexicanus Sprenkle and Blem (1984) found that finches fed a diet low in fat were unable to maintain body weights at low temperatures and died, whereas finches fed a diet with a high lipid level survived, indicating that a fatty diet has survival value. The fact that our experimental birds had a high relative fat consumption during weeks with warm nights (45%), and no dietary shift occurred with decreasing ambient temperature is at variance with the observations on beech nut consumption in the field. Balen's (1980) postulation that beech mast is an emergency food only taken when insect food is scarce does not correspond with the high relative fat consumption of our experimental birds. Our results predict that seeds will also be taken when insect food is readily available. There are two possible explanations for the field observations. First, Balen (1980) only recorded the number of birds foraging under beeches and not what they did elsewhere. Thus, it is possible that the birds increased their consumption of nuts as well as of insects. However, there are indications that the availability of arthropod prey decreases with decreasing ambient temperatures (Avery and Krebs 1984) and this may force the birds to eat more nuts. Secondly, it is possible that Great Tits are constrained in the consumption of beech nuts by one or more other factors. These factors could be the risk of predation during the search

266

for nuts on the ground (Nilsson 1979, pers. observ.), social interactions (Drent 1983, De Laet 1985, Ramenofsky et al. 1992), or the presence of a toxic substance in beech nuts (cf. Greig-Smith and Wilson 1985).

References

Atkinson, T., Fowler, V. R., Garton, G. A. and Lough, A. K. 1972. A rapid method for the accurate determination of lipid in animal tissues. – Analyst 97: 562–568.

Avery, M. I. and Krebs, J. R. 1984. Temperature and foraging success of Great Tits *Parus major* hunting for spiders. – Ibis 126: 33–38.

Bairlein, F. 1985. Efficiency of food utilization during fat deposition in the long-distance migratory Garden Warbler, *Sylvia borin*. – Oecologia 68: 118–125.

Balen, J. H. van 1967. The significance of variations in body weight and wing length in the Great Tit, *Parus major*. – Ardea 55: 1–59.

– 1980. Population fluctuations of the Great Tit and feeding conditions in winter. – Ardea 68: 143–164.

Berthold, P. 1976. Animalische und vegetabilische Ernahrung omnivorer Singvogelarten: Nahrungsbevorzugung, Jahresperiodik der Nahrungswahl, physiologische und ökologische Bedeutung. – J. Ornithol. 117: 145–209.

Betts, M. M. 1955. The food of the titmice in oak woodland. – J. Anim. Ecol. 24: 282–323.

Drent, P. J. 1983. The functional ethology of territoriality in the Great Tit (*Parus major* L.). – PhD Thesis, University of Groningen, Groningen.

Ekman, J. B. and Hake, M. K. 1990. Monitoring starvation risk: adjustments of body reserves in Greenfinches (*Carduelis chloris* L.) during periods of unpredictable foraging success. – Behav. Ecol. 1: 62–67.

Fisher, H. 1972. The nutrition of birds. – In: Farner, D. S. and King, J. R. (eds.). Avian Biology, Vol. II. Academic Press, New York, pp. 431–469.

Fry, C. H. 1967. Lipid levels in an intra-tropical migrant. – Ibis 109: 118–120.

Greig-Smith, P. W. and Wilson, M. F. 1985. Influences of seed size, nutrient composition and phenolic content on the preferences of bullfinches feeding in ash trees. – Oikos 44: 47–54.

Haftorn, S. 1989. Seasonal and diurnal body weight variations in Titmice, based on analyses of individual birds. – Wilson Bull. 101: 217–235.

Holsheimer, J. P. 1985. Voeding van kooi- en volièrevogels. – Thieme, Zutphen.

Jenni, L. and Jenni-Eiermann, S. 1987. Body weight and energy reserves of bramblings in winter. – Ardea 75: 271–284.

Jordano, P. 1988. Diet, fruit choice and variation in body condi-

tion of frugivorous warblers in Mediterranean scrubland. – Ardea 76: 193–209.

Kear, J. 1962. Food selection in finches with special reference to interspecific differences. – Proc. Zool. Soc. London 138: 163–204.

Kendeigh, S. C., Kontogiannis, J. E., Mazac, A. and Roth, R. R. 1969. Environmental regulation of food intake by birds. – Comp. Biochem. Physiol. 31: 941–957.

Krebs, J. R. and Avery, M. I. 1984. Chick growth and prey quality in the European Bee-eater (*Merops apiaster*). – Oecologia 64: 363–368.

– and McCleery, R. H. 1984. Optimization in behavioural ecology. – In: Krebs, J. R. and Davies, N. B. (eds.). Behavioural ecology; an evolutionary approach. 2nd edition. Blackwell, Oxford, pp. 91–121.

Laet, J. F. de. 1985. Dominance and anti-predator behaviour of Great Tits *Parus major*: a field study. – Ibis 127: 372–377.

Lehikoinen, E. 1987. Seasonality of the daily weight cycle in wintering passerines and its consequences. – Ornis Scand. 18: 216–226.

McLean, S. F. 1974. Lemming bones as a source of calcium for Arctic sandpipers (*Calidris* spp.). – Ibis 116: 552–557.

Mitchell, H. H. 1962. Comparative nutrition of man and domestic animals. Vol. 1. – Academic Press, New York.

Newton, I. 1969. Winter fattening in the bullfinch. – Physiol. Zool. 42: 96–107.

Nilsson, S. G. 1979. Seed density, cover, predation and the distribution of birds in a beech wood in southern Sweden. – Ibis 121: 177–185.

Perrins, C. M. 1979. British Tits. – Collins, London.

Pulliam, H. R. 1975. Diet optimization with nutrient constraints. – Amer. Nat. 109: 765–768.

Ramenofsky, M., Gray, J. M. and Johnson, R. B. 1992. Behavioral and physiological adjustments of birds living in winter flocks. – Ornis Scand. 23: 371–380.

Rapport, D. J. 1980. Optimal foraging for complementary resources. – Amer. Nat. 116: 324–346.

Reinertsen, R. E. and Haftorn, S. 1986. Different metabolic strategies of northern birds for nocturnal survival. – J. Comp. Physiol. B 156: 655–663.

Robbins, C. T. 1983. Wildlife feeding and nutrition. – Academic Press, New York.

Romijn, C. and Lokhorst, W. 1961. Some aspects of energy metabolism in birds. – In: Proc. 2nd Symp. Energy Metabolism. Agricultural University, Wageningen, pp. 49–58.

Sokal, R. R. and Rohlf, F. J. 1981. Biometry. 2nd ed. – Freeman, New York.

Sprenkle, J. M. and Blem, C. R. 1984. Metabolism and food selection of eastern House Finches. – Wilson Bull. 96: 184–195.

Stephens, D. W. and Krebs, J. R. 1986. Foraging theory. – Princeton University Press, Princeton, New Jersey.

Thompson, D. B., Tomback, D. F., Cunningham, M. A. and Baker, M. C. 1987. Seed selection by dark-eyed juncos (*Junco hyemalis*): optimal foraging with nutrient constraints? – Oecologia 74: 106–111.

Tinbergen, J. M. 1981. Foraging decisions in starlings (*Sturnus vulgaris* L.). – Ardea 69: 1–67.

Zwarts, L. and Blomert, A.-M. 1990. Selectivity of Whimbrels feeding on Fiddler Crabs explained by component specific digestibilities. – Ardea 78: 193–208.