Foraging and its consequences in the breeding season of the Blue Tit (*Parus caeruleus*)

De consequenties van voedselzoekgedrag in het broedseizoen van de Pimpelmees (*Parus caeruleus*)

(met een samenvatting in het Nederlands en in het Italiaans)

Proefschrift ter verkrijging van de graad van doctor
aan de Universiteit Utrecht
op gezag van de Rector Magnificus, Prof. Dr. W. H. Gispen,
ingevolge het besluit van het College voor Promoties
in het openbaar te verdedigen
op maandag 11 juni 2001 des middags te 2.30 uur

door

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geboren op 14 juli 1969 te Pavia, Italië

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Printed by	Ponsen & Looijen BV, Wageningen, The Netherlands
ISBN	90-393-2716-5

The research presented in this thesis was carried out at the department of Animal Population Biology of the Netherlands Institute of Ecology – Centre for Terrestrial Ecology, Heteren and was partially supported by a grant of the University of Pavia (1 year) and by a Marie Curie Fellowship of the European Commission (2 years).

To my parents

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Introduction:

Food Availability and Decision Making

FOOD AVAILABILITY: PATTERNS, CONSEQUENCES AND BEHAVIOURAL STRATEGIES IN BIRDS

Food as a limit on reproduction

A dominant feature of the biology of insectivorous forest birds is that food availability changes rapidly in spring. It is commonly believed that food is superabundant during part of the breeding season. However, the existence of food limitations can only be proved by assessing the direct effect of food on reproduction and survival, that is, fitness. This is because organisms have to allocate a certain amount of resources (i.e. energy and nutrients) to reproduction and, at the same time, pay the cost of maintenance and survival. Imagine a bird at the start of the breeding cycle. It has a certain amount of energy reserves stored prior to the reproductive event, plus those resources acquired by feeding during the reproductive event. This total energy (TE) is what the bird has available for reproduction and survival. Note that this definition may also apply to nutrients such as proteins or even specific amino acids. How much will this bird spend on reproduction (Reproductive Effort, RE) and how much on body maintenance and survival (Somatic Effort, SE)? Given that TE=RE+SE and is not infinite, RE has to be traded-off against SE (Figure 1). Suppose that the bird has to spend a certain amount of resource SE* not to incur lower survival and lower future reproductive prospects. That is, SE* is what has to be paid not to decrease one’s residual reproductive value (RRV; Stearns 1992). Clutton-Brock (1984) emphasised the importance of distinguishing the energetic costs of breeding (the cost of breeding, RE) from the costs affecting residual reproductive value (the cost of reproduction). If the amount spent SE is larger than SE*, there is a cost of breeding (RE), but no cost of reproduction, because the reproductive event won’t affect future survival and reproduction. However, the amount (SE-SE*) will not have any fitness benefit, since that energy could be allocated to PE to increase the number or the survival probability of the offspring. In other words, SE-SE* would be waste energy. A strategy where SE < SE* (due to increased RE) is selectively superior to that where SE > SE*, because it allows to increase fitness unless a greater RE disproportionately increases the mortality rate of the breeder. Thus, in order to maximise fitness, the individual has to pay a reproductive cost (SE* - SE). Given that energy and nutrients are obtained from

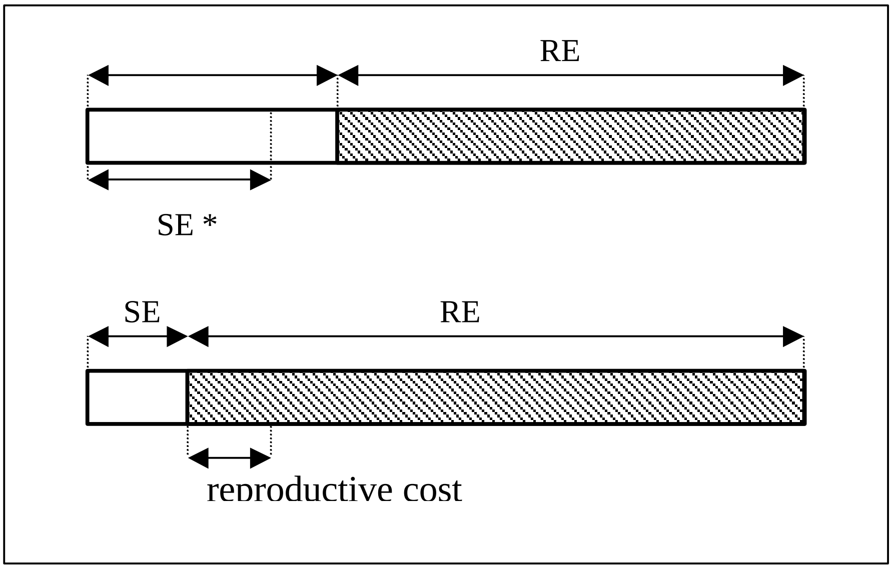


Figure 1. Partitioning of total energy for reproduction in reproductive effort (RE, hatched area) and somatic effort (SE clear area). SE is the somatic energy left after reproduction is completed. SE* is the value of SE above which there is no longer an increase in residual reproductive value. If SE < SE*, the individual pays the cost of reproduction (below), that is, a decrease in future survival and/or fecundity prospects.

food, the bird will be food limited. The extent to which the bird is ‘willing’ to decrease its survival prospects by working harder during the current reproductive event will depend on its life history, particularly on the survival schedules of adults versus juveniles (e.g. Murphy 1968; Pianka & Parker 1975; Ricklefs, 1977; Law 1979; Young 1981).

Food limitation won’t occur for breeding birds only. Parents should provide sufficient respources per offspring to optimise the chances of survival of each young to achieve the maximum number of young possible. Such strategies should commonly result in offspring receiving less than the maximum energy they can use. This creates a parent-offspring conflict (Trivers 1974) and reflects an energy and/or nutritional cost (i.e., food limitation) to the offspring.

Food Limitation: during egg-laying

A number of field studies have shown strong correlations between estimates of natural food availability and various breeding parameters such the date of onset of egg-laying date and the number of eggs. For instance, in the Great Tit *Parus major* Perrins

(1991) has shown that the abundance of *Lepidoptera* larvae (caterpillars) is correlated with the mean clutch size. This suggests that food abundance poses a constraint on the number of the eggs a female may lay. However, more direct evidence for that may come from additional feeding experiments. By supplementing birds with extra food, it is possible to test whether food limits breeding without the confounding effect of other variables that may be correlated with abundance and breeding parameters (e.g., high quality birds may establish territories in food-rich areas, and lay earlier in the season or lay more eggs). The results of these studies have, however, been rather equivocal. In general, enhancing the food supply often results in a small advancement of laying date, but few studies have shown any effect on the size or number of eggs (Martin 1987; Arcese & Smith 1988; Boutin 1990, Aparicio 1994). So far, these experiments have produced mixed results (Arcese & Smith 1988). One reason for that is that study areas and years differ in natural food abundance, and the effect of additional food on laying date or clutch size may be apparent only in poor years or areas (Nager *et al*. 1997). With food availability above a certain saturation point, supplementary food will no longer affect breeding (Boutin 1990; Schultz 1991; Svensson & Nilsson 1995)

Moreover, most studies concentrated on the energy content of the additional food. However, egg formation is not only costly in terms of energy, but also in terms of nutrients such as proteins (e.g. Ricklefs 1974, O'Connor 1984; Bolton *et al*. 1992; Houston *et al*. 1995). Thus protein content of food, rather than energy, may limit egg formation. Poor quality food may fail to enhance reproduction, because it lacks proteins or essential nutrients (Jones & Ward 1976; Ewald & Rowher 1982; Arcese & Smith 1988; Arnold 1994; Bolton *et al*. 1992). Nager *et al*. (1997) suggested that supplying laying Great Tit females with energy was sufficient to advance laying, but the effect of protein supply on egg quality and number remained unclear. Ramsay & Houston (1997) carried out a study where Blue Tits *Parus caeruleus* were given supplementary diets of either fat or a diet containing eggs. Although both diets resulted in an advance of laying date relative to control birds only those females fed egg diets laid larger eggs. Moreover, Providing a diet rich in five essential amino acids resulted in Blue Tits laying more eggs than those receiving the same amount of protein, but without the five amino acids (Ramsay & Houston 1998). This indicates that egg production is limited not only by the total amount of protein that the bird can acquire in nature, but also by the amino acid balance even in a species such as the Blue Tit feeding largely on an animal protein diet.

Food Limitation: during nestling rearing

Variation in the amount of food acquired by nestlings and the predictability of suboptimal food levels comes from two sources. On a broad scale, variation in provisioning may be influenced by environmental factors outside the control of the nestlings or the control of their parents. These sources of *extrinsic variation* may affect food supplies directly (e.g. an excessive drought) or limit the ability of the parents to procure food. An example of the latter case is given by transient weather conditions. Feeding by aerial insectivores, such as the European swift, is extremely susceptible to bad weather (e.g. Lack & Lack 1951). Even in the Great Tit, a few hours of rainfall may induce the parents to reduce feeding frequency, so that a reduction in growth rate can be detected after rainy days (Keller & van Noordwijk 1994).

Another major source of variation arises from the characteristics of the brood, the social interactions among siblings and between parents and offspring. Feeding rates per nestling are known to be inversely related to brood size: the larger the brood, the less food will be delivered to each nestling (Nur 1984a for Blue Tits; review in Martin 1987). *Intrinsic variation* often results from competition among siblings for limited resources and does not affect all chicks equally. Hatching asynchrony creates size hierarchies among chicks within broods, with younger and smaller nestlings usually receiving less food than their older siblings (Werschkul & Jackson 1979; Magrath 1990; Ricklefs 1993). This results from larger chicks obtaining optimal positions within the nest (e.g. Gottlander 1987; McRae *et al*. 1993).

It is important to emphasise that food restriction may also include changes in food quality. While satisfying energy demands, poor quality foods may fail to provide essential nutrients (e.g. amino acids, nitrogen, calcium, and phosphorus) at the time when they are required for growth. Although food can be present in sufficient amounts in nature, parents may have difficulties in finding the right source, particularly when feeding rate is high. Parents feeding experimentally enlarge broods or widowed parents have to bring more feeds per time unit than in natural conditions. To do this, they will bring food items that are usually ignored because of their low protein or water content, even if they are common in the environment (e.g. Tinbergen 1981, Bañbura *et al*. 1994, Sasvári 1996).

Food Limitation: the case of tits and their caterpillars food supply

In seasonal environments, the timing of the breeding cycle becomes crucial to ensure having nestlings when food is plenty. Caterpillars (larvae of *Lepidoptera*) constitute the main nestling food for tits *Parus* spp. (Perrins 1991). However, they are generally available in large numbers for a short period in spring (e.g. van Balen 1973, Perrins 1991). If the period of caterpillar peak availability was predictable in a certain area or habitat, tits could lay their eggs at the right moment to have the nestlings when food levels are at a maximum. However, the caterpillar food peak varies considerably not only between areas, but also between years in the same area (Figure 2; van Balen 1973; Keller & van Noordwijk 1994; Naef-Daenzer & Keller 1999). Therefore tits cannot predict when the best time to raise their young is going to be. A female Blue Tit is expected to have their young in the nest around 30 days after the date of laying of the first egg. By that time, the changing weather conditions in the 30-days period may cause the food peak to be very early (in the case of a warm spring) or very late (in the case of a cold spring), whereas the female has limited options to accelerate and delay breeding after the start of incubation. Therefore, breeding will not always be well matched with the caterpillar peak, so that the 'best' laying date for raising the brood will change among years (van Noordwijk *et al*. 1995).

THE APPROACH TO THE PROBLEM

Food availability and egg laying: food as resource vs. information

In the previous section we have seen that food levels, in terms of both quantity and quality, directly influences the expression of life-history traits, such as clutch size and laying date. The effect of supplementary food on the advancement of laying date

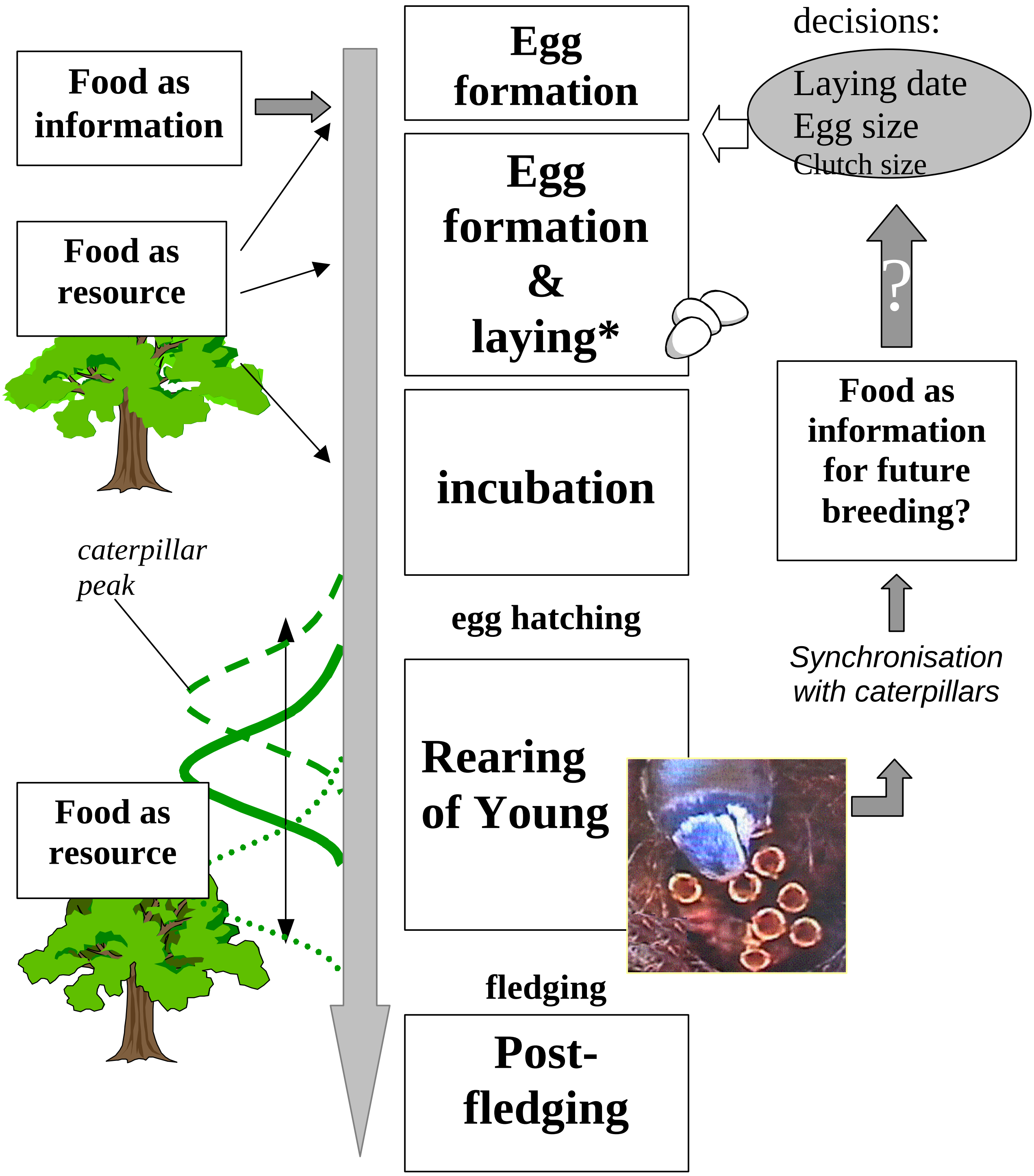


Figure 2. Sequence of the main reproductive events, with the role of food as resource or information. Although this thesis focuses on the effects of food availability on laying and brood rearing, effects are also expected in other phases with high energetic demand (e.g. incubation). * The female bird lays one egg each day. The influence of food on clutch size has not been addressed in this thesis.

allows us to view food in its dual nature (Figure 2). Providing food could cause birds not only to reduce their energetic limitations (food as resource; Perrins 1970), but also to react as if food was an information cue, indicating that the peak of food abundance is near (food as information; Nilsson 1994a; Figure 2). In both cases, food-supplemented female birds would lay eggs earlier than those without additional food.

It has also been suggested that food levels may act as a cue over a much longer time-scale. Birds could use the period of maximum food abundance in the breeding season to better time their next reproductive attempt with the local peak of food abundance (Figure 2). Nager & van Noordwijk (1995) found that Great Tit females changed their laying date from one year to another according to the local environmental conditions. For instance, a certain female laid later than the previous year when all the other females nesting in the same locality laid later that year. Although that may seem obvious, not all females changed their laying date in the same way. Some females advanced or delayed laying date more than could be expected by the behaviour of the other females. This change (delay or advancement) in laying date was correlated with the time lag between caterpillar peak date and the time when the tits had their nestlings the previous year. If a female bred too late relative to the caterpillar peak in one year, the next year she laid the eggs earlier than expected from what the other females did. Similarly, if the female bred too early relative to the caterpillar peak in one year, the next year she laid the eggs later than expected. Thus, it seems that experienced female Great Tits could adjust their laying date according to the past breeding experience in the same locality. The work of Nager & van Noordwijk (1995) showed a correlation between timing of breeding relative to the caterpillar peak and future decisions. Direct evidence for the role of food in timing of the next breeding season would come from manipulating food levels when the birds raise their broods. Females that can have access to additional food will always experience rich food conditions, whatever the time in the season is. Thus, we would predict that they will change their laying date between two years to a lesser extent than those females relying only on the natural food supply.

Food availability and brood rearing

Two sets of general questions may be posed in relation to food limitation. First, we may ask what are the consequences of food limitation on growth of the offspring, and what fitness components of the offspring are enhanced after improving food conditions. In several studies, it has been shown that food supplementation improves the chance of survival, increases growth rates and/or the weight of the offspring before they leave the nest (reviews in Martin 1987; Gebhardt-Henrich & Richner 1998). Yet, there are unresolved questions. For instance, what is the effect of food restrictions on the asymmetry of body traits such as tarsi and flight feathers? In other words, does energy intake play a role in the control of the body asymmetry in the early developmental period? In a recent book on growth in birds, the terms 'asymmetry' or 'fluctuating asymmetry' (i.e., small, stress-induced random deviations from perfect symmetry of bilateral traits) are not even in the subject index (Starck & Ricklefs 1998). This illustrates how little we know about the effect of the environment of the birds early in life on the control of developmental precision. Fluctuating asymmetry has been recognised to influence fitness, both in sexually- and non sexually-selected traits (review in Møller 1997). The approach of the feeding experiments would allow us to investigate the still unclear role of food on these components of fitness.

A second group of questions that may be addressed through food supplementation concerns the response(s) of the parents to high food availability. First, in what way nestlings benefit from the use of an extra food supply? Obviously, this depends on how the parents will partition the supplementary food between the brood and themselves. This is an area that has still to be explored, since previous supplementary feeding experiments were carried out without recording the behaviour of the parents at the nest. Second, if the parents partly feed the nestlings extra-food, one can wonder whether they would change their criteria for the choice of natural prey. Models of Central Place Foraging (CPF; Stephens & Krebs 1986) describe how a bird should select food when it has to carry it to a central place, like a nest (Figure 3). In the case the bird carries only one food item at a time, as for the Blue Tit, we refer to as "single prey loader" models. Central place foraging models assume that the bird spends all its time available searching for food and to feed the brood. This is not

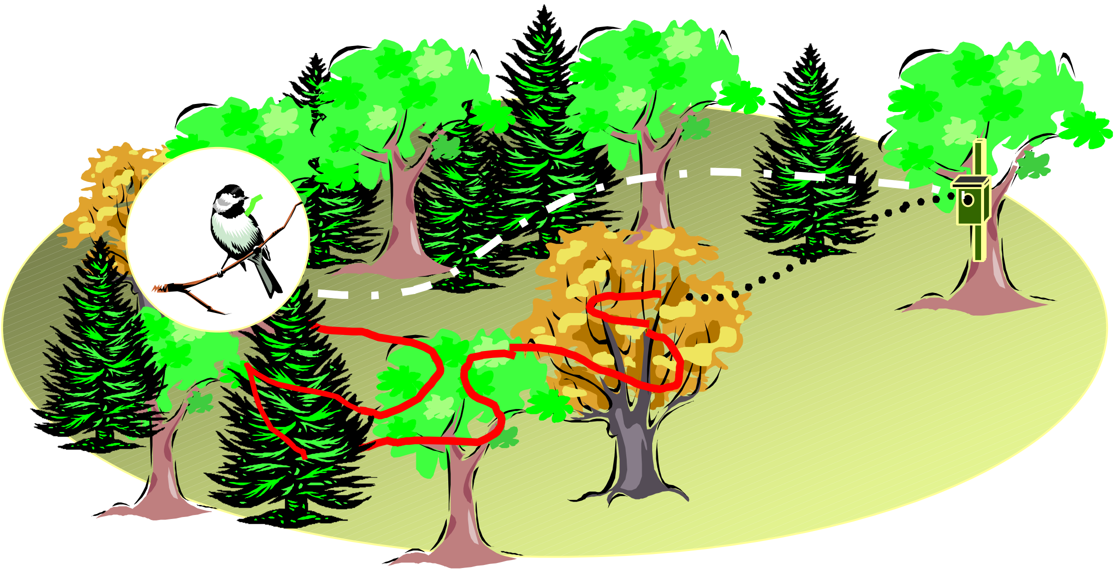


Figure 3. The main events that can be observed during a single food-provisioning cycle in a central-place forager. The bird leaves the nest and reaches the feeding sites (dotted line). Search is performed during a certain time, until prey is found (solid line; presumably the forager eats small items that are encountered during this time lag). Once the food item for the nestlings is found and killed, the forager returns to the nest (broken line). In this situation, the forager has to 'decide' where to go, and what prey to look for (i.e., how selective it has to be). In the case of the Blue Tit, the two-way travel time is much shorter than search time.

what real birds do during breeding. There are a number of duties the parent has to accomplish during the day, such as self-feeding (Martin 1987) and territory defence (Martindale 1982). Moreover, classical CPF models assume that the choice of food type is depending on a number of external variables, including the distance between the nest and the feeding site, and the distribution of size of prey items, but not on variables such as the state of the brood (i.e. hunger level) and of the parent (i.e. energetic requirement). As shown in Figure 3, in each foraging cycle the parent spends some time at the feeding site, looking for food for the offspring. However, it is quite likely that, during its foraging excursion, the parent also eats at least some of the food items encountered. How much time the parent has to spend self-feeding is likely to be influenced by its energy budget. This is because foraging cycles such as the one depicted in Figure 3 are repeated hundreds of times a day, with consequent high costs to the parent. By consuming experimentally-supplemented food, the parents are expected to employ less time self-feeding in the forest. This could lead the parents to use additional time to perform various activities, including food-provisioning. A few studies have emphasised the effects on prey choice of conflicts between food-provisioning and other activities, such as self-feeding (Tóth *et al*. 1998) and nest sanitation (Hurtrez-Boussés *et al*. 1998). These conflicts lead parents to choose different degrees of selectivity. If the parents are released from the time constraint imposed by a certain activity, they increase their selectivity, and bring larger and/or better quality prey. The feeding experiment combined with videotaping at the nest will address the questions of (1) what use the parents make of the additional food, and (2) whether the parents respond to greater food availability by using more time to search for food, and consequently increase their selectivity.

THE BLUE TIT PROJECT

The Blue Tit is a sedentary passerine extremely common in the Western Palearctic (Cramp & Perrins 1993). Although it is less known in some aspects than the related Great Tit, it is a good model species for behavioural studies. An extensive literature exists on its feeding habits (Cramp & Perrins 1993). More than the Great Tit, it can easily tolerate the human presence, and various manipulations, including videotaping set up and feeding trays inside the nest box (personal observation).

The study of the consequences of food limitation on breeding in the Blue Tit started in early 1997. The area chosen for the experiments was the National Park “De Hoge Veluwe”, in the central Netherlands. Four hundred nest boxes are scattered in a mixed forest consisting of European Oak (*Quercus robur*), Scots Pine (*Pinus sylvestris*), Birch (*Betula pendula*) and Beech (*Fagus sylvatica*) (more details in van Balen 1973). Studies of tit breeding at the population level started in 1955 (but the emphasis was always primarily on the Great Tit and the Blue Tit took third place after the Pied Flycatcher; Both & Visser, *in press*). This is the first time that the Hoge Veluwe Blue Tit population is studied in detail and extensively colour-ringed.

The experimental approach

The correlation between natural food abundance or availability and breeding parameters or behavioural variables may help address the questions formulated in this project. However, if two variables are correlated, they are not necessarily causally related to one another. A third variable may be involved, and may be the cause of variation in the two variables under study. Suppose that it is found that Blue Tits lay more eggs in territories with more food. It may be concluded that clutch size is limited by food, and that Blue Tits having access to more food are able to lay more eggs. On the other hand, it may also be that high-quality individuals, which lay more eggs, take better territories than the poor-quality ones through some process of competition. This would create a correlation between food abundance and clutch size. To avoid the problem of correlation with third variables, experiments are made where one factor (e.g. food amount) is manipulated. Individual differences can be controlled for by randomly allocating individuals (or nests) to different treatments (e.g. food-supplemented vs. control). In this study, feeding experiments will be carried out together with extensive videorecording of the parental behaviour at the nest. To my knowledge, this is the first time that such a combination is used.

The main disadvantage of supplementary feeding experiments is that the food may be utilised in varying degrees beyond experimental control.

The phenotypic plasticity approach

Phenotypic plasticity occurs when the same genotype (i.e., individual female) expresses different phenotypes (laying dates) in different environments. If temperature, food availability or other factors are involved in the expression of laying date, we would expect the differences between the laying dates in two different breeding seasons to be correlated with the change in the local environmental conditions.

The analysis will reveal whether intra-individual changes in laying date independent of environmental changes depend on the degree of mistiming of the bird in relation to the caterpillar peak in the previous season. The provision of food should cause birds to reduce their change in laying date from one year to another (filled dots, Figure 4). Moreover, if birds use food availability experienced during breeding or some other cue related to it (for instance, work rate during nestling rearing) to fine tune breeding the next year, we would expect food-supplemented females to mistime reproduction the next year, because the additional feeding would, on average, provide the wrong information about the period of maximum food availability in the environment.

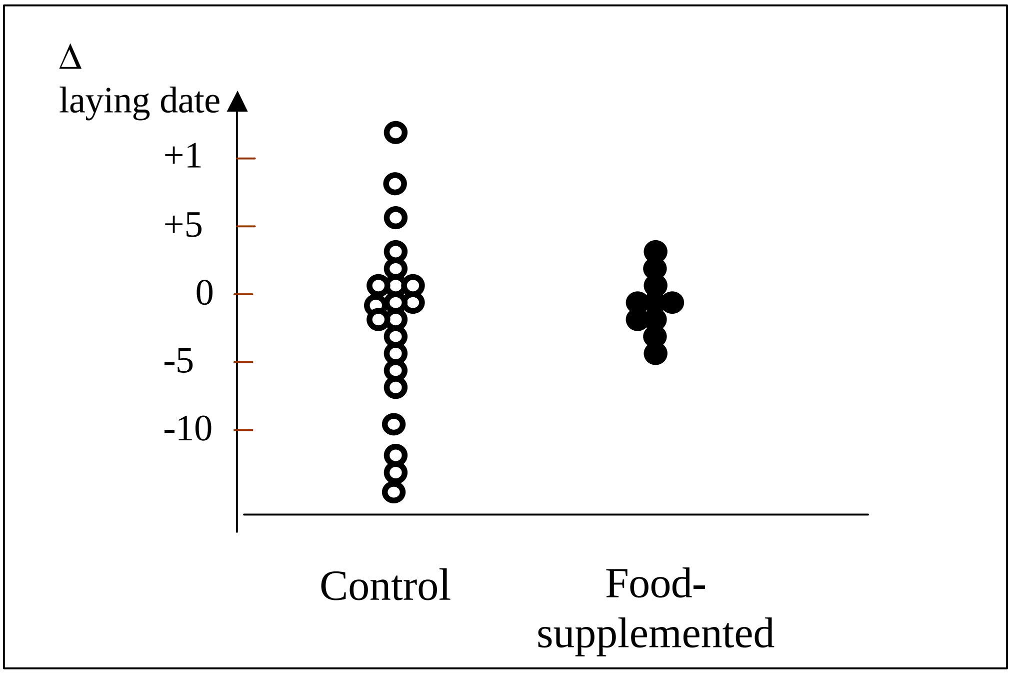


Figure 4. Expected outcome of the additional feeding experiments on the change in laying date in individual females. On the y-axis, the residual of between-year change in laying date from the regression on environmental change (expressed as change in mean of all other females laying in the same locality). As suggested by Nager & van Noordwijk (1995) in Great Tits, birds experiencing low food availability might be more prone to advance or delay laying the next year. In unmanipulated situations, therefore, we expect some variation in laying date change (some birds change laying date much, some others do less). Food supplementation should lead birds not to change laying date much, because they would experience good feeding conditions whatever their actual timing in the previous season is (closed dots).

Outline of the study

Several correlative and experimental studies provide evidence that egg production is affected by food abundance (e.g. Martin 1987). However, the results are far from being consistent, for instance the effect of food abundance on egg size becomes apparent only when ambient temperature is low (Nager & Zandt 1994). An effect of the interaction between food and temperature may be shown by additional feeding experiments in combination with temperature measurements. Food was offered to Blue Tit pairs in the period from nest-building to egg-laying. ***Chapter 2*** will address the question of whether an increase in food availability changes the relationship between temperature and egg size, and between temperature and probability of interrupting laying, i.e. producing laying gaps).

Chapters 3 to 5 analyse the short-term response of parent Blue Tits to increased food availability. Emphasis has been given to the use of videorecording as a tool to detect short-term changes in parental provisioning rate and prey choice. ***Chapter 3*** will show that food provision caused birds to reduce their rate of natural food delivery. However, food-supplemented parents brought larger caterpillars to their chicks than did control parents. The results suggest that parents were time and/or energy limited in the choice of the type and size of prey to deliver to the brood, and that food addition could release this limitation. ***Chapter 4 and 5*** are an attempt to describe the mechanisms behind the results in Chapter 3. There is a positive relationship between the time a bird is staying away from the nest (between-feed interval, BFI) and the size of the prey brought at the next visit (***Chapter 4***). However, when food was provided this relationship changed, and parents brought prey items of size independent of BFI. This suggests that time is limiting prey size only at high feeding rates. In Chapter 3 it is also suggested that parents allocate a certain time to prey search *within* the time available, that is the interval between two feeds (Figure 3). Keeping BFIs equal, the parents probably adjust their search effort according to their state, since they have to trade off foraging against other activities, such as self feeding or resting. ***Chapter 5*** provides further evidence that (1) prey size is depending on feeding rate, and (2) that parents adjust provisioning rate and prey size on a very short time scale. When the chicks stopped begging for food, I detected an increase in the time to the next visit, together with an increase in the size of the larva brought at the next visit. ***Chapter 5*** will also show that male and female parents respond differently to the changes in begging behaviour. The male appeared to be less responsive than the female, in that he kept bringing caterpillars when the chicks were not hungry, while the female returned more often without food or with low-quality food.

Some consequences of the manipulation of food availability on the growth of the nestling are shown in ***Chapter 6***. Food provisioning not only caused nestlings to grow faster, but also appeared to improve the control of developmental precision. Nestlings in food-supplemented broods had more symmetrical tarsi than those in control broods, while asymmetry of their wings was unaffected. This indicates that developmental stability requires energy, and that during early development most of the resource is allocated in the protection of growth of traits important for fledgling survival, such as wing length and symmetry, at the expense of other traits.

Chapter 7 addresses the most intriguing question of this study. Do Blue Tits change their laying date from one year to another in response to the mismatch between their breeding season and the caterpillars in the previous year? Non-environmental changes in laying date of individual females were calculated as the residuals from the regression of change in laying date (i.e., change in individual phenotype), on change in laying date of the females in the same locality (i.e., change in mean phenotype). The results will show that females experiencing additional food during the nestling period laid slightly later than unfed females and mis-timed reproduction the next year. Thus, it may be concluded that the expression of a phenotype (i.e., date of onset of reproduction) depends not only on the current environment but also on past environmental conditions. It is also suggested that these subtle non-environmental changes in laying date may serve the function of fine-tuning breeding with the period of maximum food availability in the next season.

In ***Chapter 8*** I will discuss the main findings of this study. An attempt will be made to bring together the findings in the single chapter in a more general context. Emphasis will be on the extent to which birds are able to reach maximum level of performance (e.g. egg production, offspring condition) without additional food supply.

Chapter 2

Egg laying in the Blue Tit (*Parus caeruleus*): effect of temperature and interaction with food resource

Fabrizio Grieco

ABSTRACT

Egg size and laying interruptions in a Blue Tit population were analysed in relation to changes in temperature within and between three years. A feeding experiment allowed us to study the interaction between the effects of temperature and food consumption on egg-laying. Temperature influenced egg volume in one year of three. The relationship between the two variables was non-linear, i.e. a positive relation was found only at low temperatures. In the other two, relatively warm years, the probability of having laying gaps was negatively influenced by temperature. This was due to the effect of short periods of cold weather.

Egg size variation resulted from the combination of effects of temperature and effects of feeding regimes. Food-supplemented females laid eggs whose volume was less dependent on temperature, even in cold periods. Thus the effect of temperature on egg size changed in different feeding regimes. On the other hand, no evidence was found that good feeding conditions changed the relationship between temperature and the probability of laying interruptions.

Keywords: between-individual variation, egg quality, laying interruptions, within-individuals variation

INTRODUCTION

In birds, egg production and laying are believed to be influenced by ambient temperature. The reason for this is that producing eggs is costly, in terms of energy, nutrients (Perrins 1996, Stevenson and Bryant 2000) and other specific components, such as Calcium (Stlouis & Barlow 1993, Graveland *et al*. 1994) or amino acids (Houston 1998, Ramsay & Houston 1998). In the Great Tit *Parus major*, food demand by females increases up to 40% during laying compared to the pre-laying period (Royama 1966a). The daily costs of egg formation in passerines are estimated to be 40% or more of their basal metabolic rate (Ricklefs 1974, Walsberg 1983). However, recent studies suggest that producing large eggs is more costly at low temperature. Stevenson and Bryant (2000) found an association between high energetic expenditure (DEE) and both low temperatures and the production of large eggs. At low temperature, producing large eggs may cause DEE to increase up to four times the basal metabolic rate. According to this study, temperature is viewed as a constraint on egg production early in the breeding season, which may explain the observed changes in breeding phenology of birds in recent, warmer years (McCleery & Perrins 1998, Forchhammer *et al*. 1998, Crick & Sparks 1999)

The effects of temperature on egg laying may be direct, i.e. low temperature increases the female's cost of body maintenance at the expense of egg formation. Physiological studies indicate that air temperature has large effects on the energetic needs of birds (Haftorn & Reinertsen 1985). Alternatively, low temperature may reduce the response of gonadal growth to the photoperiodic stimulus (Maney *et al*. 1999 and references therein). On the other hand, the temperature effects may be indirect, for instance if low temperature decreases the effective availability of prey that contains the energy and/or nutrients needed for egg formation (Perrins & McCleery 1989).

Effects of temperature have been reported on different life-history traits related to egg production and laying, both in descriptive and experimental studies. Tits *Parus* ssp. laying in colder environments lay at later dates (Kluijver 1952, Perrins 1965, O'Connor 1978, Perrins & McCleery 1989, Nager 1990), while in one study out of three, manipulation of nest box temperature did result in change of laying date in the expected direction (Nager 1992, Yom-Tov & Wright 1993, H.R. Offereins unpubl. data). Egg size and/or mass have been found to be positively correlated with temperature a few days prior to egg-laying (Ojanen *et al*. 1981, van Noordwijk 1984, Järvinen & Pryl 1989, Magrath 1992), while in other cases have not (Nager 1990, Järvinen 1991, Yom-Tov &Wright 1993). In these studies, the effect of temperature was tested not always while controlling for other, confounding variables correlated with temperature, e.g. calendar date. However, experimental manipulation of nest box temperature has shown a clear effect of temperature on egg size in the Great Tit (Nager & van Noordwijk 1992), not in the Blue Tit *P. caeruleus* (Yom-Tov & Wright 1993).

Low temperature may also cause delays in clutch initiation (Meijer *et al*. 1998, Visser & Lambrechts 1999) or interruptions within a laying sequence (Winkel 1970, Winkel & Winkel 1974, O'Connor 1979). Yom-Tov & Wright (1993) demonstrated that an experimental increase in nest temperature caused a drop in the probability of having laying interruptions in Blue Tits.

The different results of studies on temperature and egg quality may be due to the interaction between food resource and temperature. Nager & Zandt (1994) found that Great Tit egg size was smaller when food abundance at the time of egg formation was low. However, the correlation between food density and egg size was evident only when temperature was low. This interaction might be seen the other way round: high food density could reduce the influence of temperature on egg volume or the probability of having laying gaps.

In this study, I have analysed the relationship between ambient temperature, egg volume and laying interruption rate in Blue Tits during three years. A supplemental feeding experiment carried out in a parallel project on Blue Tits provided the opportunity to investigate the interaction between temperature, feeding regimes and egg-laying. By combining temperature patterns and additional feeding experiments in the three years, I have tried to assess the effect of food availability on the relationship between temperature and egg size, and between temperature and laying interruption rate.

METHODS

The study was carried out in the next box population of the Netherlands Institute of Ecology in the National Park “De Hoge Veluwe”, central Netherlands, from 1997 to 1999. The study area comprises four hundred nest boxes in a mixed forest dominated by pine *Pinus* spp. and European oak *Quercus robur* (for details see van Balen (1973)).

Feeding experiments

From half March each year, nest boxes were visited regularly at least twice a week for signs of nestbuilding. Because Great Tits were the subject of other experiments, it was not possible to start supplemental feeding in all potential nest sites. Blue Tit (BT) nest sites were identified by means of (1) the form and structure of the nest (Cramp & Perrins 1993) – but species discrimination is easier at later nestbuilding stages – and, more reliably, (2) observation of minute details of behaviour of birds alarming around the nest boxes (Grieco, in press). More information came from nocturnal inspection of nest boxes, since the females roost in the nest box prior to egg-laying. Of the 101 nests provided with pupae, 96 (95%) turned out to be BT nests. Additional ten BT nests were not discovered and provided with food before laying, since they were built very quickly (usually late in the season).

All Blue Tit pairs were offered fly pupae in fixed daily amounts (25 items/day). To prevent other birds from consuming them, the pupae were placed in a small tray inside the nest box, usually attached at the left inner side. Additional feeding started as soon as there were clear indications for BT nesting. This caused supplemental feeding to start at a variable number of days before laying date (average 8.7±5.9 (SD) days). Nineteen nests (25% of all supplemented nests, n=76) were provided with food less than five days before, or even after the date of laying of the first egg. Given that tits collect energy in the three-four days prior to egg laying (Perrins 1979), for those nests the food addition had probably no effect early in the laying sequence.

Personal observations indicate that the females were visiting the nests more frequently than the males (this is not surprising at least in the pre-laying phase, since nestbuilding is performed by the female), and that the females took most of the pupae.

Previous work on Great Tits showed that females supplemented with fly pupae in a similar experiment laid larger eggs than control females (Grieco & Visser 1997), indicating that part of the additional food was actually eaten by the birds.

Routine fieldwork

Focal nests were visited every day and the number of pupae missing was recorded. Food was replenished up to the standard amount. The only difference in the experimental set up between years was that in 1997 food was provided until the date of laying of the first egg (here indicated as laying date), while in 1998 and 1999 until the first day the female was brooding the eggs or the eggs were found warm.

Eggs were numbered ad measured the day they were laid. A volume-index of eggs was calculated as $0.5 \times l \times b^2$, where l (length) and b (breadth) of eggs were measured with a calliper to the nearest 0.05 mm. This index, here indicated as egg volume, is a good approximation of the measured volume as well as of the fresh weight of Great Tit eggs (van Noordwijk *et al*. 1981).

Data on mean daily temperature were obtained from the KNMI weather station at Deelen Airport, c. 5 km from the study area. For each egg laid, I calculated the average temperature during egg formation of individual Blue Tits as the average temperature of the three days preceding the laying of an egg. This was done because, at least in the closely related Great Tit, the phase of rapid follicular growth lasts three to four days (Walsberg 1983). Mean temperature during laying was calculated for each clutch by averaging temperature of all the three-day periods in the laying sequence (including laying gaps). If not otherwise stated, average temperature will indicate average temperature during egg formation. Calendar date was expressed as April date (1= 1 April, 31= 1 May etc.).

Data analysis

Variation in egg volume was analysed with general linear models. To test the effect of temperature, the individual egg was the observation unit while clutch was considered as factor. Eggs laid after an interruption were excluded from the analysis since they were slightly larger than the average in the sequence. To avoid the problem of the huge number of degrees of freedom in such design where variables are highly correlated (e.g. date and temperature), the effect of each of those variable was tested last against the residual due to within-day variation in egg volume, where day was considered as factor.

For each nest, I also calculated the coefficient of regression of egg volume on mean temperature in the 3-day period preceding laying of each egg. Only the coefficients based on at least five eggs were included in the analysis.

For each day, the laying gap (LG) rate was defined as the proportion of females which interrupted egg-laying on a certain day within their sequences (i.e., between the first and the last egg laid for each female). To have a better estimate of LG rate, only days with more than four females being expected to lay an egg were included. Laying gap rate was analysed with a generalised linear model with binomial error distribution and logit link function, and the effect of predictor variables on the change in deviance was tested with χ^2 tests. Whenever the residual deviance was high compared to the number of degrees of freedom I applied the William's correction for overdispersion (Crawley 1993) in combination with F tests.

I analysed a total of 86 clutches where the incubation stage was reached. Of these, seventy-six belong to nests that were provided with additional food. However, in 14 (18%) of those nests the birds did not accept the food, or average consumption was less than one pupa/day (very low food consumption rates could be due to the action of other, intruder birds; pers. obs.). Those nests were pooled together with the nests not provided with food because of identification errors, and were here considered as nests 'with no food consumption' (n=24), as opposed to those where food consumption was significant (n=62). The three groups of nests (food not provided, food provided but not accepted, food consumed) did not differ in age or body size of the female, laying date, clutch size or average temperature during egg-laying (ANOVA and Kruskal-Wallis ANOVA, all n.s.). The first two groups might be treated as a 'control-like' under the assumption that birds that did not accept food did so because they either they did not see it or because they were scared by the tray. At least the first option is plausible, as shown by some birds in the third group that started eating up the food after ignoring it totally in the preceding days. However, the first two groups did not differ in average egg volume or in LG rate (general and generalised linear models respectively, all n.s.).

Statistical analysis was performed with SAS v. 6.12 (SAS Institute 1989) and GLIM v. 4.0 (Numerical Algorithms Group 1993).

RESULTS

Temperature in the study period

Although March was slightly warmer in 1997 than in 1998 and 1999, the between-years difference in temperature was reversed in April (Table 1). Average values in April were higher in 1998 and 1999 than in 1997 and the long-term average for that month (7.8 °C), yet temperature in those years showed similar patterns with a marked decrease around mid April, when minimum temperature dropped below 0 °C (see Figure 1). The lowest average daily temperature in the period when eggs were laid (usually comprising the second two decades of April and the first of May) was 2.4 °C in 1998, against 3.8 and 3.2 °C in 1997 and 1999, respectively.

Food consumption

Overall, fly pupae were offered in 1236 nest days (234, 466, 536 in the 3 years respectively).

The additional food offered daily was totally consumed in 39.6% of the nest days, while in 22.3% it was ignored. In the rest of the nest days, food was obviously taken in intermediate amounts. Table 2 shows the between-year differences in food consumption rate, in terms of proportion of nests where the fly pupae were taken in significant amounts (see Methods), and in terms of proportion of items taken daily during the experiment. Food consumption differed among years, both in terms of proportion of pairs accepting food and proportion of pupae eaten (proportion of pairs eating $\chi^2_2=8.34$, $P<0.05$; amount consumed $F_{2,58}= 14.49$, $P<0.00001$). Post hoc comparisons show that food consumption was similar between 1997 and 1999, and much higher in those two years than in 1998 (Table 2), both in the whole period of food supplementation and in the period prior to laying date. The proportion of pupae taken increased with date in 1998 and more slightly in 1997 (partial correlations:

Table 1. Temperature data in March and April, for the three study years.

T (°C):	March			April		
	mean	max	min	mean	max	min
1997	7.4	11.5	3.4	7.2	12.2	1.6
1998	6.9	10.7	2.7	9.1	13.0	5.5
1999	6.9	10.8	2.7	9.7	14.5	4.7

Table 2. Food consumption rate during the experiments in the pre-laying period (1997) and pre-laying + laying period (1998, 1999). *) ≥ 1 pupa taken per day. $^{\#}$) includes only nests where ≥ 1 pupa was taken per day. Different letters indicate between-year significant difference after post hoc comparisons (all P<0.005).

	1997	1998	1999
proportion of nests where food was taken* (*n*):			
pre-laying period	0.52 (23)	0.48 (21)	0.86 (22)
overall	0.52 (23)	0.96 (27)	0.92 (26)
Median proportion of items taken per day$^{\#}$ [range] (*n*):			
pre-laying period	0.78 [0.32-1.0] (12) ^{a}	0.19 [0.0-0.94] (19) ^{b}	0.66 [0.0- 0.95] (21) ^{a}
overall	0.78 [0.32-1.0] (12) ^{a}	0.44 [0.17-0.81] (25) ^{b}	0.68 [0.36-0.95] (24) ^{a}

P<0.005 and P=0.08, respectively), but not with average temperature, in any year (partial correlations, n.s.).

Egg volume: effect of temperature and date

Less than 10% of the birds caught each year is known to have bred the preceding season. Consequently, we can treat data from two successive years as independent. There was no significant difference in average egg-volume among years (Table 3; ANOVA, $F_{2,83}$ = 0.21, P>0.80). Neither was there any significant change in egg-volume (here expressed as deviation from mean egg volume in the population and year) of females breeding in two successive seasons (Wilcoxon matched-pairs test,

Table 3. Average (± SD) egg volume and proportion of laying gaps of Blue Tit clutches at the Hoge Veluwe, in the three study years. Mean egg volume was calculated for each of the *n* individual clutches; laying gap rate was calculated for each clutch over the period between the first and the last egg.

Year	Egg volume Mean ± SD (mm^3)	Laying gap rate median [range]	% clutches with at least one gap	*n*
1997	1020.8 ± 99.4	0.07 [0.0- 0.42]	63.3	30
1998	1035.7 ± 85.8	0.0 [0.0- 0.58]	32.1	28
1999	1023.7 ± 87.6	0.0 [0.0- 0.40]	25.0	28

T=13, n=10, $P>0.10$). In none of the study years, egg size correlated with tarsus length or body mass of females at the time they had their chicks in the nest (correlation, all $P>0.05$). Females older than second calendar year did not lay larger eggs than yearling females ($F_{1,70}= 0.11$, $P>0.7$; egg volume expressed as deviation from the population mean).

Clutch, or individual female, contributed a large part of the variation in egg volume (effect of clutch: $F_{83,736} = 20.31$, $p<0.00001$) and explained 65.8% of the total variance. Average temperature in the three-day period preceding laying influenced egg volume, females laying larger eggs in warmer days ($F_{1,101} = 5.94$, $P<0.02$). I also found a nearly significant interaction between year and temperature ($F_{2,100}= 2.86$, $P=0.06$), suggesting that the effect of temperature could be different among years (Figure 1). After repeating the analysis for each year separately, ambient temperature predicted significantly egg volume only in 1997 ($F_{1,35}= 18.26$, $P<0.0001$), while in 1998 and 1999, the effect was far from significant (ANOVA, both $P>0.60$; Figure 2). Date of laying also influenced the size of the egg laid, but only in 1998 ($F_{1,33}= 9.12$, $P<0.005$; for the other years, $P>0.20$).

The strikingly large volume of the eggs laid on 17 and 18 April 1998 (Figure 2) was due to a few females laying large eggs. Given that many females interrupted laying in that period, the mean egg volume increased above the usual range of values. This suggests that females differed in the ability of laying large eggs and without interruptions. Females that had no laying interruptions laid slightly larger eggs than those females that had at least one interruption, but the difference was not significant

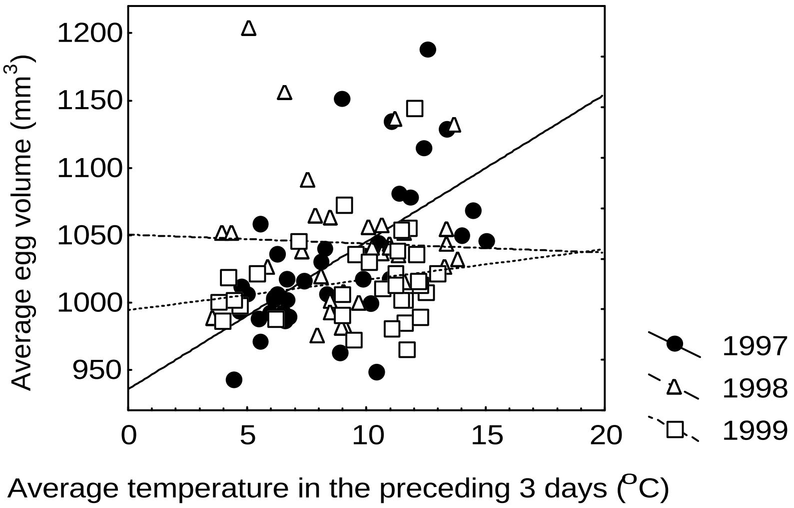


Figure 1. Mean volume of Blue Tit eggs laid on a certain date, in relation to average temperature in the preceding 3-day period, in the three study years.

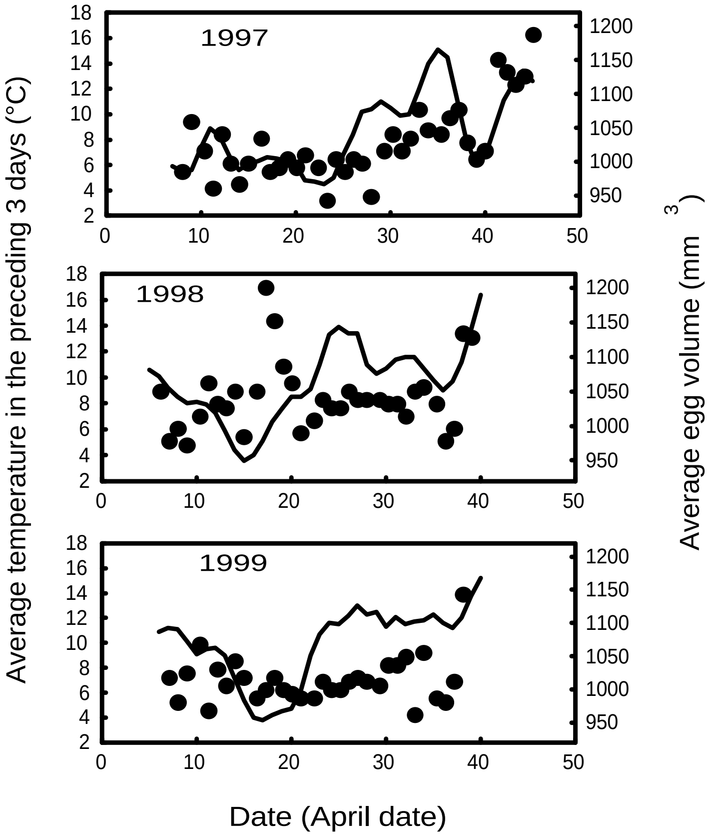


Figure 2. Mean egg volume in Blue Tits (●) in relation to mean temperature in the 3-day period preceding laying (—), in each of the three study years.

(Table 4; $F_{1,80}$= 2.67, P=0.11). However, the interaction between having or not laying interruptions and food consumption was significant ($F_{1,80}$=6.80, P=0.011). This indicated that the difference in egg size between females that had laid with and females that laid without interruptions was affected by whether or not food was consumed. In nests where food was not consumed, females laying without interruptions tended to lay larger eggs than the others (Table 4). The difference disappeared in nests with some food consumption, indicating that consuming extra-food compensated for individual differences in the ability to collect enough resource for egg formation.

Summarising, female Blue Tits laid relatively smaller eggs at lower temperatures only in 1997. The absence of clear influence of temperature in the two subsequent years might have been due either (a) to the average higher temperature, or (b) to the effect of supplemental feeding during egg-laying in those years. However, a between-year difference in egg size was still found at low temperatures. Eggs laid at temperatures lower than 8 °C were on average smaller in 1997 than in the other two years (Figure 1; t_{34}= -2.49, P<0.02; *t*-test, data from 1998 and 1999 pooled), suggesting that food availability, or some unknown factor, led to an increase in egg size. The analysis of egg volume in relation to food consumption (see below) could help establish whether additional feeding had an effect.

Laying gaps: effect of temperature

The proportion of laying interruptions in individual females differed significantly among the three study years, with more laying gaps per day in 1997 than 1998 and 1999 (Table 3; χ^2_2= 7.03, P<0.05). However, the fewer laying gaps in 1998 and 1999 could be accounted for by the marked drop in temperature in short periods of the laying season. I analysed LG rate in individual days in relation to temperature. Average daily temperature seemed to affect LG rate, but if it was tested after entering average temperature during the egg formation period in the model, it was no longer significant (χ^2_1= 0.08, P>0.7). On the other hand, mean temperature over the three-day period was a good predictor of LG rate after controlling for daily temperature (χ^2_1= 8.46, P<0.005). The interaction between year and temperature in the preceding 3-day period was significant (χ^2_2=9.12, P<0.01), therefore I repeated the analysis for

Table 4. Average (+ SD) egg volume (expressed as deviation from the population mean) of Blue Tit clutches laid by females that had laying interruptions and females that did not. Nests are grouped according to whether or not food was taken in significant amounts (see Methods). P values refer to: a) F test in ANOVA; b) *a priori* contrast analysis.

Females	Mean ± SD (mm^3)	*n*	*P*
All nests			
with no gaps	+6.19 ± 76.72	48	
with gaps	-5.14 ± 105.95	36	0.11^a
Food not consumed			
with no gaps	+46.25 ± 69.27	13	
with gaps	-44.27 ± 116.60	11	0.03^b
Food consumed			
with no gaps	-8.70 ± 74.84	35	
with gaps	+12.07 ± 98.47	25	0.37^b

each year separately. Temperature in the egg formation period could not explain variation in LG rate in 1997 (χ^2_1= 0.14, *P*>0.7), but in 1998 and 1999 its effect was significant (1998: $F_{1,17}$= 14.53, *P*<0.001; 1999: χ^2_1= 4.63, *P*<0.05; Figure 3). The largest effect occurred in mid April 1998, when average temperature dropped to about 4°C and over 50% of the females interrupted egg-laying (Figure 3).

Summarising, the effect of ambient temperature on the probability to interrupt laying occurred in the years when there was no effect on egg size. The higher variation in temperature in short periods of 1998 and 1999 made it easier to detect significant changes in laying gap rate.

Effects of supplemental feeding and interaction with temperature

The first question is whether Blue Tits that consumed a significant amount of additional food laid larger eggs than those that either were not provided with or ignored additional food. In 1997 the difference in egg volume between Blue Tits in nests with no food consumption and those exploiting additional food was not significant (average ± SD egg volume relative to population mean: with no food consumption –5.13±110.59 mm^3 (*n*=18), food consumed +7.69±83.80 (*n*=12); $F_{1,28}$=

Table 5. Values (mean ± SD) of regression coefficients *b* of egg volume on temperature in the 3-day period preceding egg-laying, in nests where Blue Tits did not consume additional food and where they consumed a significant part of it (see Methods) in the three study years. The proportion of positive *b*s is also shown. *Includes also pairs not food-supplemented.

year	*b*, Mean ± SD (*n*)		proportion of positive *b*s (*n*)	
	food not consumed*	with food	food not consumed*	with food
1997	13.92 ± 15.10 (18)	-0.52 ± 15.64 (12)	0.83 (18)	0.50 (12)
1998	10.82 (1)	1.21 ± 13.4 (24)	1.00 (1)	0.63 (24)
1999	-13.08 ± 25.2 (4)	-0.49 ± 30.42 (22)	0.50 (4)	0.59 (22)
all	9.09 ± 19.26 (23)	0.21 ± 21.48 (58)	0.78 (23)	0.59 (58)

0.12, $P>0.7$). This result is not surprising since food was offered only until the first egg was laid. However, the first egg, not the second, was slightly larger in females consuming additional food (t_{27}= -1.68, P=0.10). The difference was significant if only the first eggs laid at temperatures lower than 8 °C were included (t_{17}=-2.55, $P<0.02$). Thus low temperature increased the correlation between food availability and egg size.

In 1998 and 1999 the feeding experiment lasted until the onset of incubation, yet the difference in mean egg size between birds exploiting extra-food and the others was not significant (with no food consumption +34.44±74.01 mm^3 (n=6), food consumed -4.22±86.98 (n=55); $F_{1,53}$= 1.08, $P>0.3$; data from the two years pooled). However, this could be due to the small number of birds in the first sample. In none of the three years mean egg volume increased with the average proportion of pupae taken daily (Spearman rank correlation, all $P>0.30$).

Thus, there was no direct evidence that the additional food resources caused a general increase in egg size. Another possibility was that female Blue Tits consuming additional food could lay eggs whose volume was less dependent on ambient temperature than females which were not given additional food or that did not accept it. Given that only in 1997 a sufficient number of nests ‘with no food consumption’ was available, I limited the analysis to this year. The interaction temperature × food consumption was just significant (ANCOVA, $F_{1,350}$= 3.84, P=0.05). This could be due to pseudoreplication because eggs within clutches were likely to be laid at similar

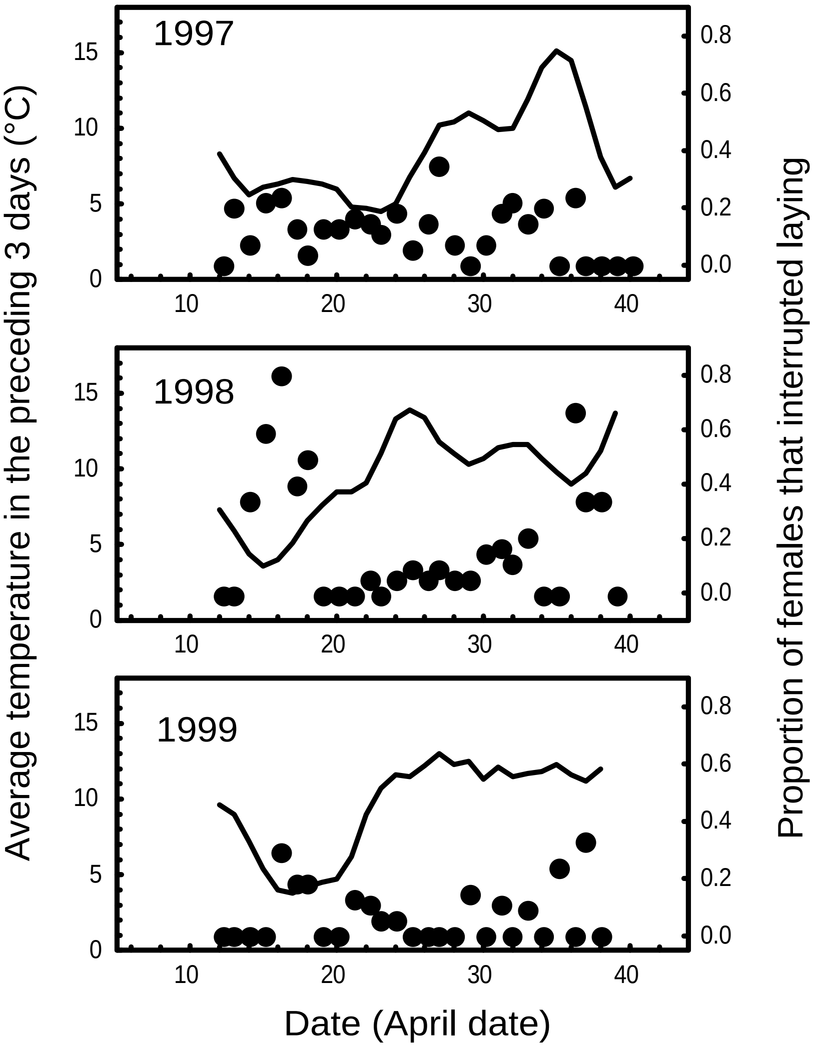


Figure 3. Laying gap rate in Blue Tits (●)in relation to mean temperature in the 3-day period preceding laying (—), in each of the three study years. Laying gap rate is here shown for days when at least two females were expected to lay.

temperatures. For each clutch, I calculated a coefficient (*b*) of regression of egg volume on temperature during the three-day period preceding laying. The regression coefficients were, on average, higher for nests with food not consumed than in nests with some food consumption (Table 5; for 1997: t_{28} =2.53, P<0.02). Egg size increased with temperature during egg formation, but only in those females that did not consume additional food. In food-consuming females, the regression coefficients

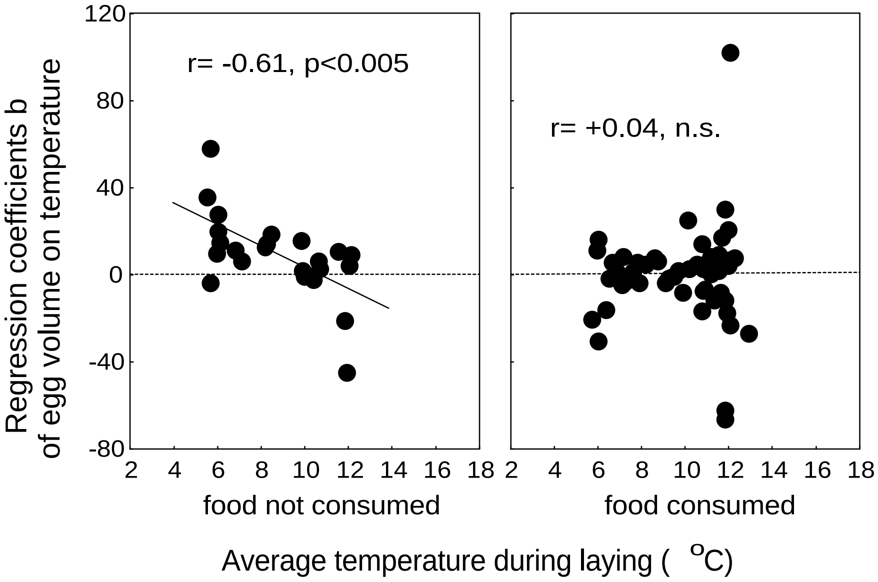


Figure 4. Values of regression coefficients b of egg volume on temperature plotted against the average temperature over the period of egg formation and laying, in female Blue Tits that did not consume supplemented food (including females that were not food-supplemented) and females that consumed at least part of supplemented food.

were unrelated to the mean proportion of food items consumed (Spearman correlation, *P*>0.20 for all years).Table 5 also shows the values for the other two years, where very few pairs belong to the first group.

Could we explain variation in the *b* coefficients *within* feeding groups? Among nests with no food consumption, *b* correlated negatively with the average temperature calculated over the laying period (Figure 4). Thus temperature affected positively egg size within clutches, but only at the lower temperature range. There was not such relationship among nests with some food consumption (Figure 4). The two correlation coefficients differed significantly (*P*<0.005).

Food supplementation could influence the frequency and duration of laying interruptions. Females that consumed some food made as many interruptions within a laying sequence as females that did not, in all years (proportion of laying interruptions in individual laying sequences: Mann-Whitney U test, all n.s.). Moreover, the proportion of laying gaps was unrelated to the amount of food eaten (Spearman correlation, all n.s.). There was no evidence for an interaction between food consumption and temperature (for 1997: $F_{2,32}$= 0.53, *P*=n.s., after correcting for overdispersion; years 1998 and 1999 lack of sufficient number of birds not consuming food). Given that in 1997 food was offered until laying date, the effect could be evident in the very first eggs of the sequence, therefore I focused on the second egg only. Neither the proportion of second eggs that were laid after an interruption, nor the mean duration of such interruptions, differed between females that consumed food and those which did not, at any range of temperature (i.e., below or above 8°C; χ^2 and Mann-Whitney U tests, all n.s.).

Summarising, the interaction between temperature and feeding experiments had an effect on egg size, not on laying gap probability. Blue Tits consuming additional food laid their eggs of size independent of temperature contrary to those that did not consume any, but they did not change the frequency of laying gaps at low temperatures.

DISCUSSION

Egg laying: effect of temperature

Tits lay their eggs in variable environmental conditions (e.g. Kluijver 1952, Perrins 1965, van Balen 1973, Perrins & McCleery 1989). Low temperature affects a laying female either by increasing its cost of thermoregulation or by reducing the density or the availability of natural food. Although several authors have reported a positive correlation of egg size or mass with temperature, the relationship might be non-linear. Van Noordwijk (1984) found that in a cold year Great Tit egg volume was positively related to temperature, while in another, warmer year this correlation disappeared. Nager & Zandt (1994) conclude that egg size was unrelated to temperature over a broad range of moderate to good conditions. The existence of a non-linear relationship between temperature and egg size or, more generally, quality, where the latter no longer increases once some saturation temperature has been reached, may explain the strong influence of temperature on Blue Tit egg size in 1997 (cold year) and the absence of such influence in 1998 and 1999 (warmer years). I could not find any non-linear pattern *within* years, *between* clutches: even in 1997 egg volume increased with temperatures throughout its range (Figure 1). Among the females that did not consume additional food the increase in egg volume with temperature was 0.011 cm^3/°C, very close to that found by Jones (1973) and Nager & Zandt (1994) in Great Tits (approximately 0.01 cm^3/°C in both studies).

A non-linear relationship between temperature and egg size resulted, however, from the analysis of the regression coefficients *b* of egg volume on temperature *within* clutches. These represent the response of the individual female to changes in temperature. Figure 4 shows that, for those females that did not use any extra food resource, this response was dependent on the average temperature the female experienced during the whole period of laying. The slopes of the regression coefficients *b* on temperature were negatively correlated with the average temperature in that period. This means that females experiencing cold weather laid eggs that were positively influenced by temperature, while those laying in warmer days laid the eggs whose volume was more independent on temperature.

Once she has started egg laying, a female Blue Tit may respond to poor weather conditions either (a) by laying smaller eggs or (b) by interrupting egg laying. In both cases, this has consequences on reproductive success. On the one hand, small eggs lead to poorer hatching success, lower offspring survival and/or longer nestling period (e.g. Jones 1973, Schifferli 1973, Järvinen & Väisänen 1983, Nilsson 1990). On the other hand, laying interruptions may delay hatching and therefore fledging of the young, with possible negative effects on their survival and local recruitment (Perrins & McCleery 1989, Perrins 1965, Verhulst & Tinbergen 1991). Slight changes in egg size allow a female to lay the eggs under a wider range of environmental conditions than would be possible according strictly to heritable factors. Laying interruptions, on the other hand, probably prevent the female from laying very small eggs with poor hatching success. In which conditions, therefore, should a female switch from one option to the other?

Blue Tits had more laying interruptions if temperature of the previous three days dropped to around 4°C. Similar threshold temperatures have been found in other studies (Winkel 1970, Winkel & Winkel 1974, Yom-Tov & Wright 1993). However, the time lag between drop in temperature and the effect on laying gap frequency varies among studies. For instance, Blue Tits in an English population made more interruptions when minimum temperature 4 to 5 days before laying was low (Yom-

Tov and Wright 1993). In my study, mean temperature in that period did not correlate at all with laying gap rate (unpubl. data). These discrepancies might reflect actual differences between populations in the speed of response to changes in temperature (see Ojanen *et al*. 1981, Järvinen & Pryl 1989 for similar differences in the time period when temperature correlates most with egg size). Alternatively, they may be due to contingent situations, e.g. birds laying in relatively poorer years or areas may be more exhausted during egg formation and therefore be more dependent on the environmental conditions over longer periods. This would translate in variable time lag between drop in temperature and laying interruption.

Individual females also differed in the ability to lay their eggs without interruptions. During the cold spells of April 1998 and 1999 a few females continued to lay their eggs while other stopped. Females laying without interruption laid larger eggs than females that had at least one interruption, indicating that the quality of the individual or the territory is an important component in variation in egg volume and sequence. However, the difference in egg volume between females laying with and without interruptions was apparent only when the additional food was not available or not consumed. Therefore, the use of the extra food produced the additional effect of reducing the inter-individual difference in the ability to collect enough resource for egg formation and laying. The ability of producing large eggs and without interruptions is probably a feature of the individual female, yet the two processes are only partially overlapping, as shown by the absence of effects of food supplementation on laying gap rate.

Egg laying: interaction between temperature and food resource

Some evidence was found that supplementing Blue Tits with food changed the relationship between temperature and egg quality. In 1997, the effect of temperature on egg volume was evident only in those females that did not consume additional food. With low temperature, egg size was a more precise estimate of food availability. This result is similar to that found in a study on Great Tits where egg volume at low, not high temperatures, correlated with estimates of natural food abundance (Nager & Zandt 1994). As expected from the experimental set up in 1997, the effect of additional feeding was stronger for the first egg in the sequence (see Nilsson & Svensson 1993a for a similar effect).

Despite the fact that food provisioning reduced the influence of temperature on egg size, I did not find a parallel effect on the incidence of laying interruptions. In 1997, birds consuming additional food in the pre-lay phase did not have fewer laying interruptions in a sequence than those that did not, at any temperature range. This is not surprising, since food was offered until laying date (see Nilsson & Svensson (1993b) for a small effect of supplemental feeding during egg-laying). However, the potential effect of food on laying gap rate was not evident even where it could well be expected, i.e. in the second-laid egg.

Also, the high laying gap rate during cold periods in 1998 and 1999 despite provision of food during laying seems to indicate that the influence of low temperatures on laying interruptions does not operate purely through energy reserves in the female's body, as suggested by the minimal amount of energy invested in the phase of yolk deposition that is more sensitive to temperature (Yom-Tov & Wright 1993).

In conclusion, the different patterns of egg volume observed in the three study years may be ascribed to the combination of the non-linear effects of temperature (whatever the proximate mechanisms are, i.e., constraints of thermoregulation vs. food availability), with the effects of experimentally increased food availability. On the other hand, the probability to make laying interruptions appears to be primarily a function of temperature changes.

ACKNOWLEDGEMENTS

This paper benefited from comments by Arie van Noordwijk and Rüdi Nager. Thanks to Kate Lessells for valuable suggestions about the statistical analysis of egg volume. Leonard Holleman provided the fly pupae for the experiment, while Christel Mols wrote a Dutch summary. This study is part of my PhD project at the Netherlands Institute of Ecology, Department of Animal Population Biology, funded by the University of Pavia with a Postgraduate Scholarship and the European Commission with a Marie Curie Fellowship (n° ERBFMBICT 971939).

Chapter 3

The trade-off between provisioning rate and prey size in breeding Blue Tits (*Parus caeruleus*): effects of an additional feeding experiment

Fabrizio Grieco & Arie J. van Noordwijk

ABSTRACT

Classical central place foraging models assume that prey choice is independent of the energy demand of the foraging parent and the brood. Field data, however, suggest that, everything else being equal, a forager changes its selectivity depending on its condition and that of the brood (e.g. hunger level). We reduced the energy requirement of parent Blue Tits (*Parus caeruleus* L.) by supplementing them with insect larvae during the offspring-rearing period. The adults consumed most of the food offered, but delivered a small (15%) proportion of it to the brood. Thus, the parents presumably spent less time self-feeding in the trees, and had potentially more time to spend provisoning the offspring. The rate at which the parents delivered natural prey was lower in nests with extra-food supply than in controls. In usually supplemented nests, temporary removal of the extra-food supply caused an increase in provisioning rate to the offspring. The magnitude of the effect differed among years, was larger for older nestlings and in large broods than in younger and smaller broods, and larger in male than female parents. Food-supplemented pairs collected larger larvae than controls. In control nests, prey size was smaller if the parents had to feed larger broods. However, supplemented parents delivered large prey even when feeding large broods, suggesting that prey choice was more constrained when brood demand was greater. Also, food-supplemented parents could probably better regulate prey size according to the age of the nestlings.

A model that takes into account the effects of parental energy requirement on minimum acceptable value of prey for the offspring explains the changes in size of delivered prey observed in this study. When the parent gets extra-food, it can save time that otherwise would be spent in self-feeding. This way, more time will be allocated to food search, and selectivity can increase as long as it results in a net rate of energy intake of the brood comparable to that in unmanipulated conditions.

INTRODUCTION

The synchrony of food availability and requirements is a major determinant of life histories. In altricial birds the period when parents provide food for nestlings, birds with large brood sizes, such as Blue Tits, have to find several times the amount of food needed for self-maintenance and moreover, they have to transport much of this food to the nest. Thus, the period of nestling provisioning is both crucial in the life history and very interesting, because one can expect that birds work very close to their limits in this period. The problems that a bird faces in bringing food to the nest are the subject of Central place foraging theory (Orians & Pearson 1979; Stephens & Krebs 1986). In organisms that usually bring one prey items at a time to the central place (single-prey loaders, Orians & Pearson 1979) the foraging behaviour is best explained by a prey choice model (Lessells & Stephens 1983) contrary to the original view of a patch residence time model (Orians & Pearson 1979). A simplified model where handling times are the same for all prey types solves for the rate-maximising "minimum acceptable prey size" (Lessells & Stephens 1983). This value affects the within-patch search time because it determines the proportion of prey to ignore. According to this model, foragers make the choice of a minimum acceptable prey size, or more generally, prey value, which implies a choice of delivery rate of food to the central place. This is because minimum acceptable prey value determines both load size (the larger the minimum acceptable prey value, the larger the average prey value) and the time taken to deliver a meal (the larger the minimum acceptable prey value, the more choosy the forager, and consequently the longer the average search time; Lucas 1983, 1985).

In the 'classical' models of optimal diets and central place foraging the optimal strategy is a function of extrinsic factors like encounter rates and profitability of prey types, travel distances and loading effects. The decision to accept or ignore a prey item does not depend on the food requirement of the brood, or on the condition of the parent. If one of the two latter varied, these models would not predict any change of the optimal foraging strategy, e.g. the type and/or size of prey delivered to the nest. The parent would simply dedicate more time to foraging. A model by Houston (1987) suggests that prey selectivity can change when the energy budget of the parent is taken into account. Houston (1987) assumed that the parents could fulfil their energetic needs by eating all the prey items that were not above the critical value of prey to be taken to the nest. Depending on the need it has to fulfil, the parent is expected to change the range of type and size of items that can be eaten while looking for nestling food. This process is likely to work in tits *Parus* spp.. Tóth *et al*. (1998) observed an increase in body weight of adult Great Tits *Parus major* in some visits to the nest, suggesting that they had spent some time self-feeding in the previous foraging bout. They found that, after some self-feeding, the female, not the male, brought smaller loads to the nest than when she was only foraging for the offspring. They concluded that the effect of self-feeding was apparent only in the female because of greater time constraints imposed by long brooding. Thus, there is the potential to test whether prey choice is affected by the parent's state.

Theoretical Background

In this study, we wish to investigate the consequences on prey choice of changes in the energy requirements of the parent. To do this, we observe prey choice in adult Blue Tits *Parus caeruleus* that were supplemented with insect food while they were raising their broods. To give some idea of such effects we outline a very simplified model of central place foraging. It is assumed that the parents have to hunt on prey whose size is distributed exponentially with average value 1/u:

$$\text{Probability (Prey of energy value} > x) = \exp(-ux)$$

The forager has to look for prey with size larger than X_p to cover its energy costs and brings back to the nest the first item larger than X_f it encounters. The main assumption is that the parent has first to fulfil a certain need (E_n) to cover the costs of the foraging cycle and presumably other costs (e.g. territory and nest defence), then use some time to look for the offspring's food (review in Martin 1987). The time the parent is expected to spend to find one of the food items for self-feeding is

$$T(X_p) = \exp(-uX_p) / r,$$

where r is the encounter rate of the prey. If the parents keeps X_p as critical prey value, it will find, on average, an item of value X_p+1/u. The parent will cover the energetic need

E_n by spending $T_p= (E_n/ (X_p+1/u)) * T (X_p)$, where the first term of the product is the expected number of items that fulfil the parent's need. For a single-prey loader like the Blue Tit, the expected time spent for finding a food item for the offspring larger than X_f is

$$T_f = \exp(-uX_f) / r$$

Thus the total time spent in a foraging cycle is $T_t = T_p + T_f + \tau$, where τ is travel time. We assume that τ is constant, since in Blue Tits travel time is not a good predictor of total time T_t; Smith & Sweatman 1974; Naef-Daenzer & Keller 1999; Naef-Daenzer 2000; F. Grieco, unpublished data).

Figure 1a shows the total time used for a foraging cycle against the critical size of prey for the offspring. The total time used for foraging increases exponentially with selectivity, because the parent has to use more time to look for the item to be brought back. If, however, the parent's energetic need is lower, the curve will be lower than the original one. This is because it will spend less time for self-feeding, assuming that it does not reduce X_p. (however, in presence of high need the parent can reduce X_p so it will eat all prey encountered, but the 'gain' in time is limited by the encounter rate of prey). Figure 1a suggests that the parent can maintain the same visit rate (i.e., T_t), by increasing its selectivity. This has implications on the energy delivery to the brood. The net energy rate to the young when critical prey value X_f is used is

$$N(X_f) = (Xf +1/u - \tau M_t – (T_p+T_f)M_f – C) / T_t$$

where M_t and M_f are the rates of energy expenditures during flight and foraging respectively, and C is the cost of accelerating at the start and decelerating at the end of the foraging cycle. Figure 1b shows an example of the effect of decreased parental requirement on the energy intake of the brood. A reduction in E_n causes the parents to deliver more energy per time unit if everything else stays the same. However, the parent can deliver the same N as before by choosing larger prey for the offspring, i.e. increasing X_f. This model suggests that, when the parent is 'freed' of the time constraint on self-feeding, it can deliver food at the same or even higher rate by increasing selectivity.

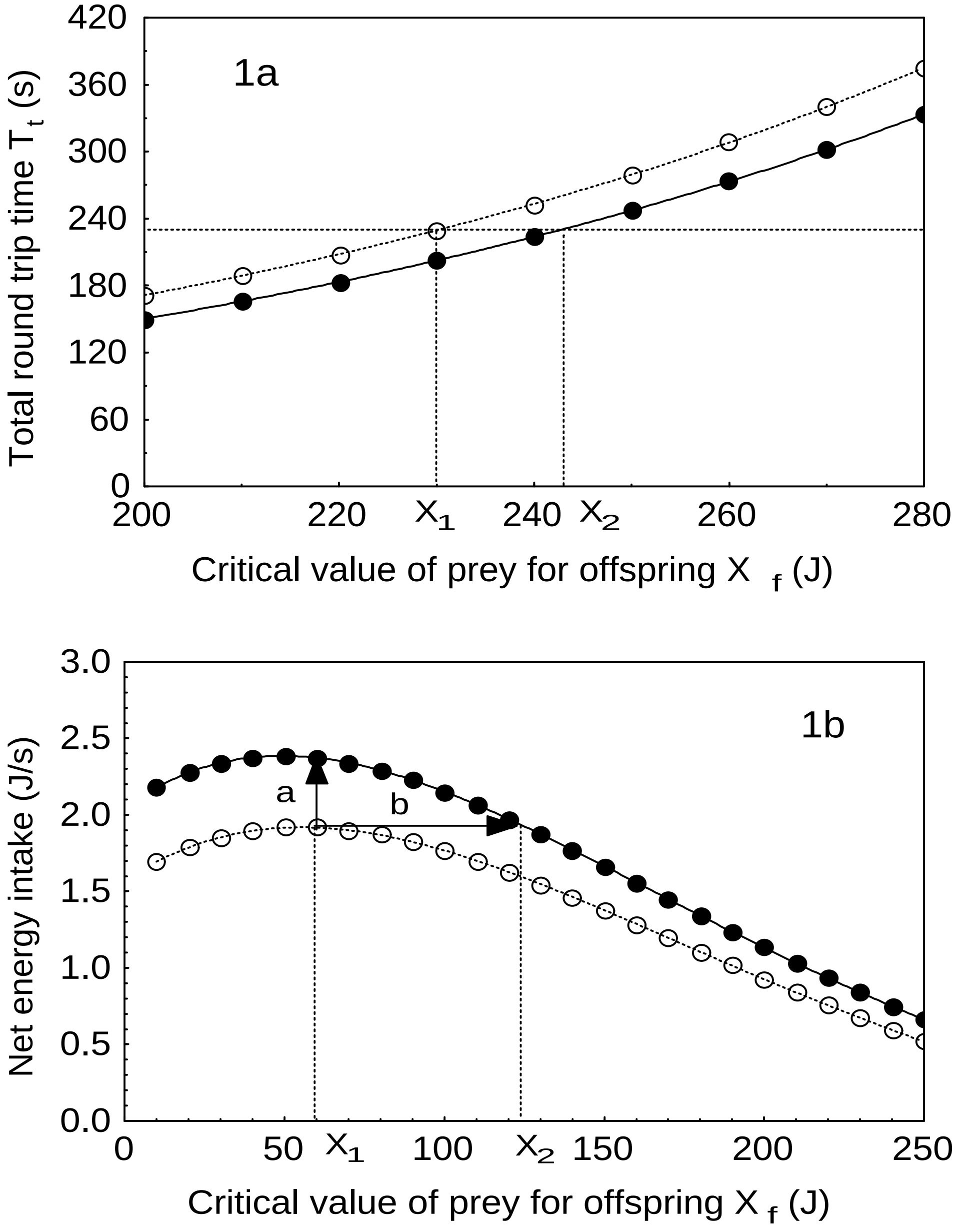


Figure 1. (a) Schematic relationship between the total time spent in a foraging cycle (round trip travel time + time spent searching for food items) and the critical value of prey for the offspring. The critical value for prey eaten by the parent is assumed to be the minimum in the range considered. The two lines represent time and prey size options available to parents with different costs. Closed dots: full foraging and flight costs. Open dots: 10% of flight and foraging costs. (b) Net rate of energy intake of the brood in relation to critical size of prey taken to it, when the parents have different energetic requirements. X_1 and X_2 represent critical prey values that allow parents in different state to deliver equal amount energy to the nest per time unit. The two arrows indicate possible effects of manipulation on prey selectivity. Open dots: requirement to cover flight + foraging + acceleration/deceleration costs; Filled dots: 10% of the previous case. Parameters: X_p= 10; encounter rate r= 0.05 items/s, average size of prey 1/u=100 J; E_{n1} =cost of one foraging cycle (flight + foraging + acceleration and deceleration); E_{n2} = 0.1*E_{n1}; travel time τ=10 s; travel cost (10×BMR) M_t= 2.1 J/s; foraging cost (3×BMR) M_f= 0.63 J/s, acceleration/ deceleration cost C=1.7 J (see Houston 1987); BMR=0.21 J/s (Bryant & Tatner 1991)

STUDY AREA AND METHODS

The study was carried out on a population of Blue Tits breeding in nest boxes in the Hoge Veluwe National Park, The Netherlands, from 1997 to 1999. The study area comprises four hundred nest boxes in a mixed forest dominated by pine *Pinus* spp. and European Oak *Quercus robur* (for details see van Balen (1973)).

Feeding experiments

Mealworms (*Tenebrio molitor*, family *Tenebrionidae*) and larvae of wax moth (*Galleria mellonella*, family *Pyralidae*) were offered to Blue Tit parents during breeding, from the day of egg hatching of their brood to the day of fledging of the young. At early chick ages (day 0 to 6), food consisted of a mixture of the two species, while afterwards it was composed of mealworms only. We decided to give about one half of the amount corresponding to the estimates of daily food consumption of nestling Blue Tits (Gibb & Betts 1963). The food amount daily offered to the adults increased linearly from day 0 to day 10, then levelled off around 20 g for a 12-chick brood. Adjustments in food amount were made for smaller and bigger broods. The larvae were placed in small trays (5.5×3.5×4.5 cm) inside the nest boxes to prevent other birds than the focal adults to consume them. Half of the nest boxes were food-supplemented, while the other half were not and served as control. Food-supplemented and control boxes were chosen randomly in order to have the same range of hatching date. If eggs in two or more clutches hatched on the same date (blocks), different treatment levels were assigned to an equal number of boxes. However, if at any date the treatment level had to be assigned to an odd number of broods, at the next hatching date one additional box was given the treatment that was underrepresented in the previous block. Effort was made to assign different treatment levels to boxes in similar habitats.

All the nest boxes were checked daily for egg hatching and food was replenished in the supplemented ones, according to the amount scheduled.

Observations at the nest

In 1997, parental provisioning activities were observed in three nests that were usually food-supplemented. The observer stood at a distance of about 25 m from the nest and counted the number of feeding visits. By using a binocular, he also tried to assess whether the adults entered the box with a natural prey item or with an extra-food item. It was assumed that the parent fed the young extra food when it left the nest with an item, reached a branch in the neighbourhood, killed and prepared the item and finally returned to the nest within short time (usually between 10 and 30s). In three usually supplemented nests, observations were made in two subsequent 1-hour sessions, one with additional food being kept in the usual tray, and the other after food was removed (or vice versa). The next morning, the sequence was reversed (first with no food, then with food, or vice versa) to reduce possible effects of time of the day on feeding rates.

Videotaping

In 1998 and 1999 we filmed parental food provisioning at 39 nests, one or two times each, between day three and day 13 after egg hatching. Video cameras Sony CCD-TR825E were placed facing down from the top of the nest box. A wooden box covered the video camera during filming, while a small lamp provided additional light inside the nest. To have the birds more habituated to the video camera and the artificial light, a dummy wooden box with a small lamp was placed on the box at least one hour prior to filming. All videotaping sessions (n=75) started in the morning between 08:00 and 12:00 and lasted 90 minutes.

Hi8 videotapes were copied to extra-high grade VHS tapes and the latter were analysed. The adults could be identified from colour ring combinations. If they had not yet been ringed, they could be identified from individual (not sexual) morphological features (e.g. irregularities of the head and face plumage). In such cases, final identification of sexes was done by comparing plumage features in the videos made before and after the date of ringing. As an estimate of parental provisioning rate (PPR), we considered the number of natural feeds delivered by the adults in the last hour of filming. Prey items were classified as larvae, spiders, other adult arthropods, pupae, and unidentified items. In this paper, we focus on size of larvae, which accounted for 68% of all natural prey items. Prey size (PS) was defined as the width of the larva’s head capsule relative to bill width, both measured on the screen with a calliper at the nearest 0.1 mm. Size was measured in 66.7% (n=2240) of the larvae delivered to the nest. Additional information was collected in 1999 about the colour of caterpillars (the vast majority of the larvae delivered). Caterpillars were divided into 'green', 'brown', and 'others' (e.g. black and white), according to their predominant colour. 'Green' and 'brown' types formed more than 96% of all caterpillars delivered.

For 15 nests of 1999, the behaviour of the parents while foraging on trees was observed during the filming sessions at the respective nest boxes. The time spent foraging was estimated by measuring the time during which birds moved along branches at small and fast hops (see ‘searching movements’ in Remsen & Robinson 1990), apparently looking for prey. The time spent flying between branches was excluded from this count. Since the stopwatch of the observer was synchronised with the time counter of the video camera, it was possible to relate foraging time to the total time away from the nest.

Data analysis

Individual nests were treated as observation units. Whenever two sessions per nest were available, one of them was chosen at random for the analysis. Parental provisioning rate and prey size were analysed using general linear models in Statistica 5.5 (StatSoft 1999). The significance of each variable was tested after all other significant variables and interactions were included in the models. In all analyses nestling age, calendar date (expressed as April date, e.g. 1=April 1st, 31= May 1st) and brood size were treated as covariates.

RESULTS

Consumption of supplementary food

During the three years of study, adult Blue Tits utilised the whole daily amount of additional food offered in 468 (67.7%) of 691 nest-days. In 21 nest-days (3.0%, all in 1997) birds did not use any. During videotaping in 1998 and 1999, the adults took on average 16 items per hour (range 0 - 49). Extra-food utilisation rate increased with age of nestlings (r_s=+0.45, n=39 video sessions, P<0.005, Spearman rank correlation), but not with brood size (P>0.1). However, the adults delivered to the nestlings only 15% (range 0-100%) of food items taken from the tray, and took the rest out of the box while exiting (usually one in a visit). Hence, we assume that most of the food was eaten by the parents (F. Grieco, personal observations). The proportion of extra-food given to the young increased with nestling age (r_s=+0.41, n=37, P<0.02), not with brood size (P>0.10). Thus, age of nestlings influenced both the rate at which the adults used supplemented food and the amount fed to the nestlings.

Parental provisioning rate

In 1997, Temporary removal of extra-food caused a marked increase in visit rate by adult Blue Tits that were usually supplemented. For three nests, and in a total of six pairs of observation sessions (with and without supplemental food) the number of natural feeds in one hour was always lower when food was present than when food was removed (Fig. 2; paired t-test on averages per nest; t_2= 16.45, P=0.004). When food was present, the parents fed the nestlings 1 to 6 (mean 3.7) larvae offered. The higher PPR observed when food was removed was independent of whether the observations were made before or after the sessions with food being present (Fig. 2). Thus, the availability of additional food, not the sequence of observations, caused a drop in natural provisioning rate.

More evidence for an effect of the feeding experiments on food-provisioning behaviour came from videotaping at the nest in 1998 and 1999. Male Blue Tits brought more feeds than females (17.6±9.5 vs. 12.4±8.6 items/hour respectively; Table 2). Visit rate increased with age of nestlings (Fig. 3) and brood size and decreased with date. In both years, supplemented parents made fewer natural feeding visits than controls, controlled for nestling age, brood size and date (Table 2).

While the positive effect of age and number of chicks was obvious, the negative effect of date on PPR was more indirect. Early in the season, caterpillars were much smaller than later, thus, everything else being equal, more prey items per time unit were needed.

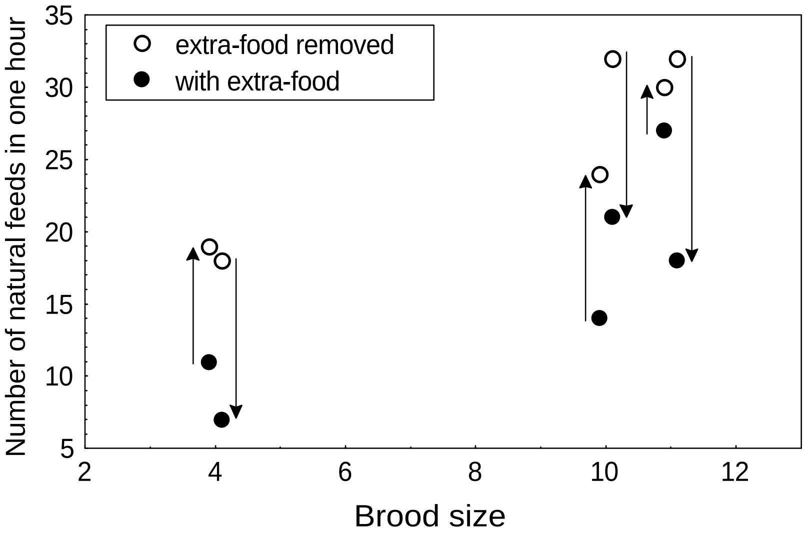


Figure 2. Change in rate of provisioning of natural food in usually supplemented Blue Tits that were temporarily deprived of additional food in 1997. Each of the three nests (with chicks being 6, 16 and 17 days old respectively) was observed four times, i.e. twice with food present and twice with food removed. The arrows indicate the temporal sequence of the observation sessions in each pair (with food - with food removed).

There was an interaction between year and treatment (Table 2), the effect of supplemental feeding on PPR being greater in 1998 than in 1999 (Table 1). The interaction between parental sex and treatment was also significant, indicating that males reduced PPR more strongly than females (Table 2, Fig. 3).

Table 1. Parental provisioning rate and mean size of larvae delivered by food-supplemented and control Blue Tit pairs, in 1998 and 1999. Prey size is expressed as size of larvae relative to the bird's beak size. Values are calculated with one data point for each nest (see Methods). Sample sizes are indicated in brackets.

	Number of feeds / h ± SD		Mean relative prey size ± SD	
Year	Control	Supplemented	Control	Supplemented
1998	38.8 ± 12.4 (9)	17.4 ± 6.3 (9)	0.71 ± 0.10 (9)	0.75 ± 0.14 (9)
1999	33.5 ± 19.2 (11)	26.1 ± 10.6 (10)	0.83 ± 0.11 (11)	0.90 ± 0.13 (10)
1999 (Green)			0.82±0.15 (9)	0.89±0.13 (7)
1999 (Brown)			0.93±0.12 (8)	1.10±0.11 (8)

Table 2. Results of ANCOVA on the number of feeds in one hour of Blue Tits, in the years 1998 and 1999. Results from final models are shown. Full models included year, experimental treatment, parental sex, chick age, date, brood size and all two- way interactions.

Variable	Sum of Squares	$F_{1.66}$	P	Direction of effect
Treatment	374.360	9.22	0.003	Suppl. < Control
Parental sex	461.091	11.36	0.001	Females < Males
Chick age	1252.112	30.84	<0.00001	Young < Old
Date	234.839	5.78	0.019	Late < Early
Brood size	197.443	4.86	0.031	Small < Large
Year × Treatment	368.578	9.08	0.004	a)
Parental Sex × Treatment	224.983	5.54	0.022	b); Fig. 3
Treatment × Chick age	467.164	11.51	0.001	c)
Treatment × Brood size	353.863	8.72	0.004	d)
Residual	2679.731			

a) effect of treatment larger in 1998. b) effect of treatment larger in males.
c) effect of chick age, coefficients: control, 2.31 ± 0.40, $F_{1,35}$= 33.0, P=0.00001; food-suppl., 0.99 ± 0.47, $F_{1,31}$= 4.38, P=0.045.
d) effect of brood size, coefficients: control, 2.10 ± 0.60, $F_{1,35}$= 12.27, P= 0.001; food-suppl. –0.11 ± 0.48, $F_{1,31}$= 0.04, P=0.83.

Males and females increased PPR with age of nestlings (Fig. 3) and brood size (Table 2), however the effect of these two variables was much larger in control than food-supplemented nests, as shown by the significant interactions between chick age and treatment, and between brood size and treatment (Table 2). Food-supplemented males seemed not to increase PPR with chick age (Figure 3). This was because in some nests of 1998 supplemented males fed the brood very frequently while the females spent more time brooding than controls (temperature in the breeding season was slightly colder in 1998 than in 1999). However, the interaction treatment × parental sex × chick age was not significant ($F_{2,63}$= 2.48, P=0.09).

Prey size

The average size of larvae brought to the nest did not differ between male and female Blue Tits ($F_{1,58}$= 0.11, P=0.74; but see Blondel *et al.* 1991 for a between-sex difference

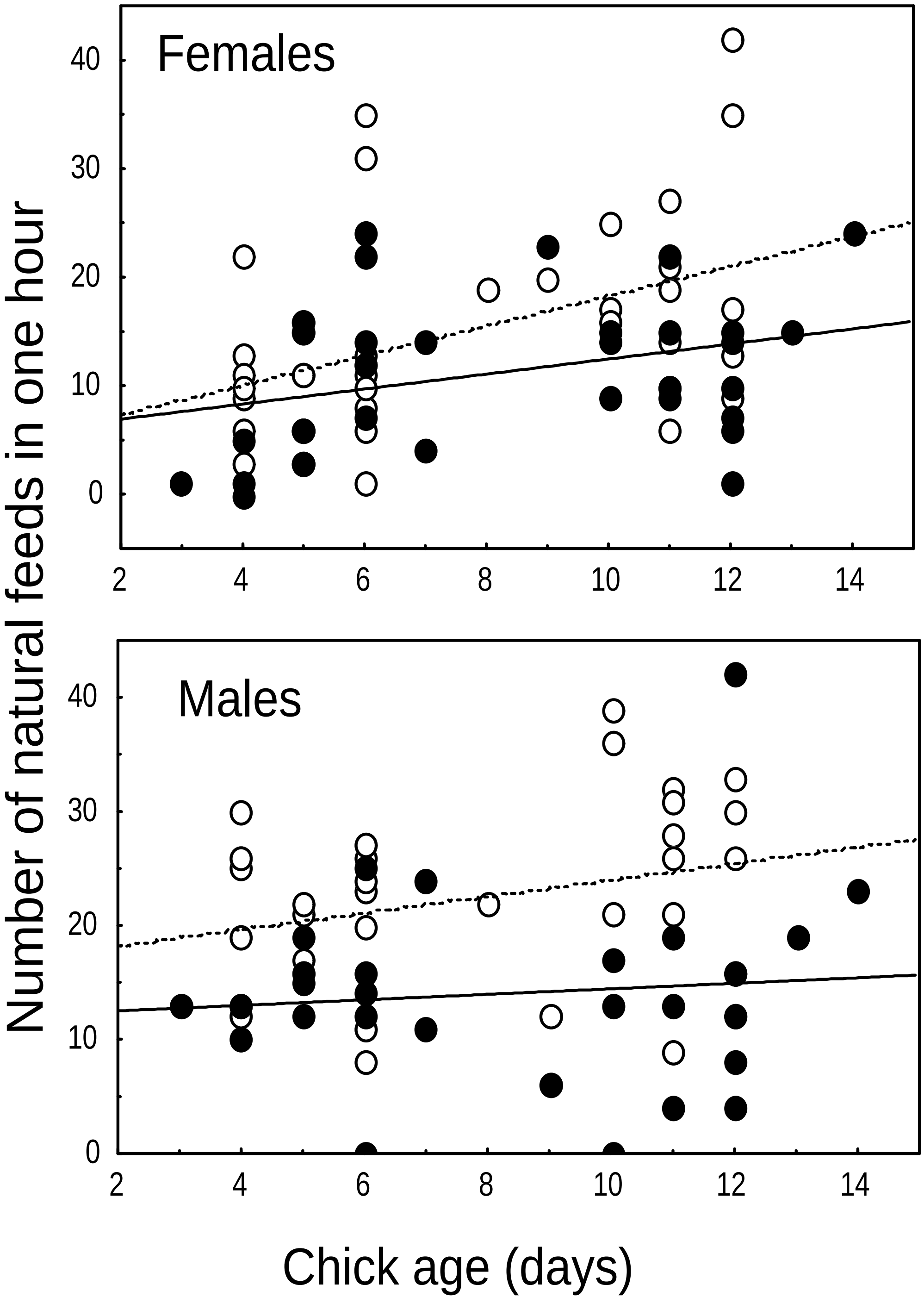


Figure. 3 Parental food-provisioning rate (natural feeds only; see Methods) in relation to age of the brood, in female and male Blue Tits that were supplemented with food (closed dots, solid line) and in controls (open dots, dotted line). More than one data point per nest is shown.

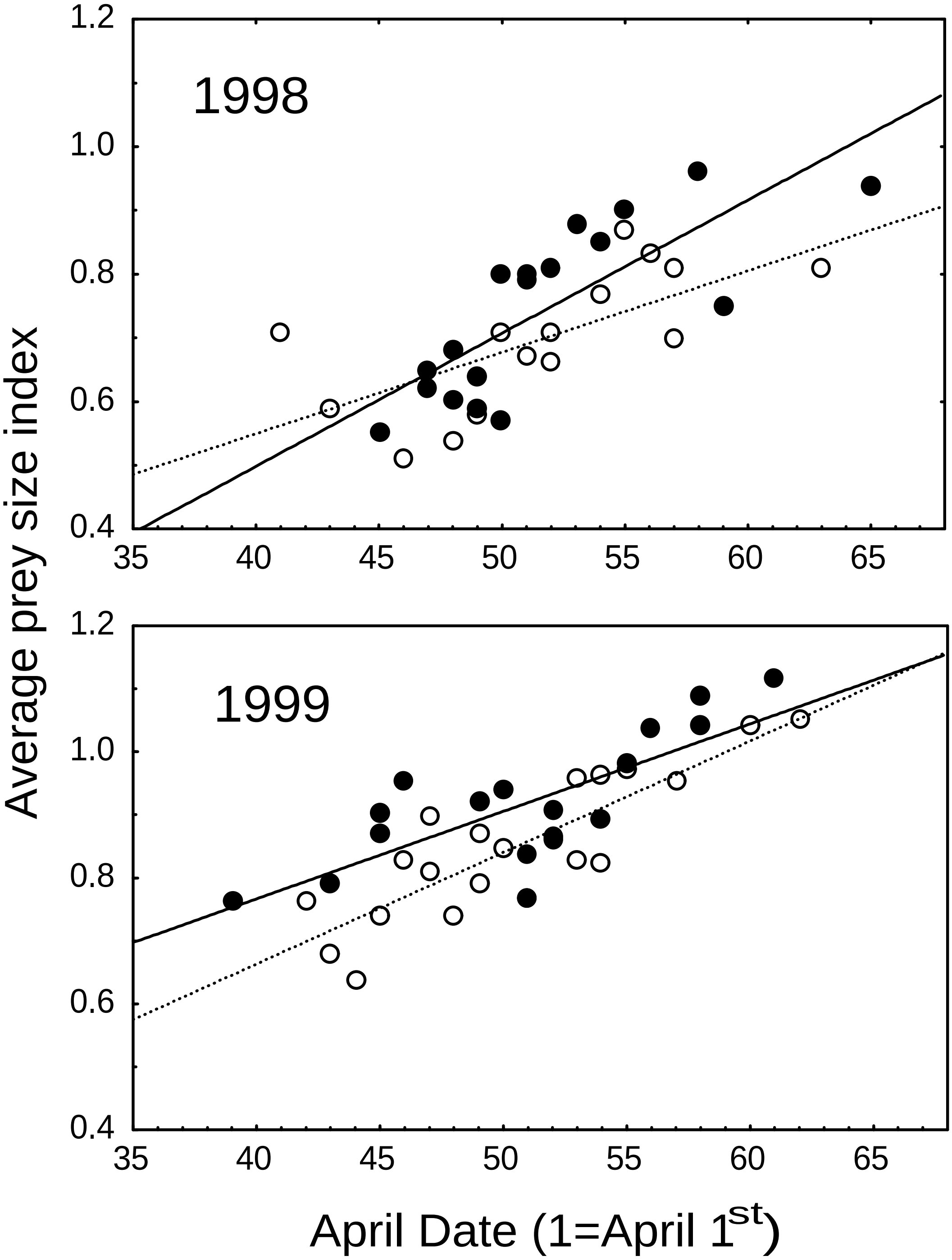


Figure 4. Average size of larvae (natural feeds only; see Methods) brought by Blue Tit parents in relation to date in 1998 and 1999. Date is expressed as April Date (1= April 1st). Open dots, dotted lines: control. Closed dots, solid lines: food-supplemented. More than one data point per nest is shown.

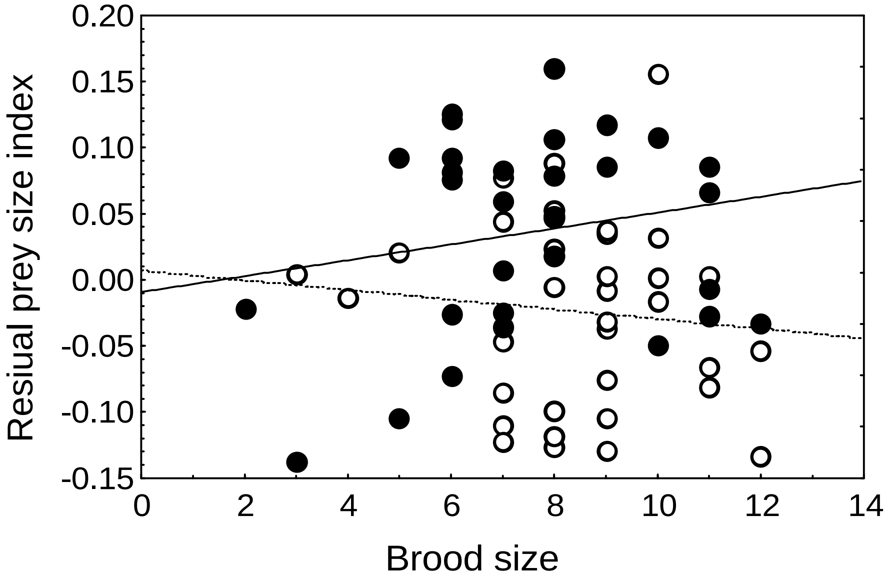


Figure 5. Average size of larvae (natural feeds only; see Methods) brought by Blue Tit parents in relation to brood size. Prey size is expressed as the residual from the its linear regression on date (each year has its specific regression equation: 1998, PS= -0.143 + 0.017*date, R^2= 0.55; 1999, PS= 0.056+0.016*date, R^2= 0.66). Open dots, dotted lines: control. Closed dots, solid lines: food-supplemented. More than one data point per nest is shown (statistical details are given in Table 3, with one data point per nest).

in prey size), therefore we used the prey size averaged over the two parents in each session. The results of the analysis are shown in Table 3. There was a significant effect of year of study, larvae being larger in 1999 than in 1998, perhaps reflecting the different environments that parents experienced in those years (Table 1). Prey size increased both with date and age of the nestlings (Table 3). Although date and nestling age were correlated, including the latter in a regression model with date (R^2= 0.608) increased significantly the proportion of variance explained (R^2= 0.693, P=0.0043). The increase in prey size with date reflected the development of caterpillars in the forest, while the effect of nestling age suggests that Blue Tits selectively collected large prey items at later nestling ages. Supplemented pairs delivered larger larvae than controls did, early as well as late in the season (Fig. 4).

Although brood size did not influence significantly prey size, we found a significant interaction between treatment and brood size. Controlling for other confounding variables, unmanipulated pairs collected smaller larvae when they had to feed more chicks (Table 3, Fig. 5), suggesting that the size of meals had to be traded-off against an increased feeding rate in large broods. On the contrary, food-supplemented parents delivered prey independent of brood size (Table 3, Fig. 5). There was also a significant interaction between treatment and chick age (Table 3). This was due to food-supplemented parents delivering larger items as the chicks grew, while prey size delivered by control parents was relatively independent of chick age (Table 3, Fig. 6).

Table 3. Results of ANCOVA on the mean relative size of larvae (additional food items excluded) delivered by parent Blue Tits to their nestlings, in 1998 and 1999. Results from final models are shown. Full models included year, experimental treatment, chick age, date, brood size and all two-way interactions.

	Sum of Squares	$F_{1,29}$	P	Direction of effect
Year	0.104	24.17	<0.0001	1998 < 1999
Treatment	0.039	9.03	<0.01	Control < Suppl.
Chick age	0.039	8.92	<0.01	Young < Old
Date	0.040	9.31	<0.005	Early < Late
Treatment × Chick age	0.035	8.07	<0.01	a); Fig. 6
Treatment × Brood size	0.036	8.36	<0.01	b); Fig. 5
Residual	0.125			

a) effect of chick age, coefficients: control, +0.002 ± 0.007, $F_{1,14}$= 0.06, P>0.80; food-suppl. +0.024 ± 0.007, $F_{1,12}$= 11.59, P=0.005.
b) effect of brood size, coefficients: control, –0.024 ± 0.011, $F_{1,15}$= 4.87, P=0.043; food-suppl. + 0.013 ± 0.006, $F_{1,12}$= 4.54, P=0.054.

In 1999 supplemented pairs delivered relatively more 'green' caterpillars than control pairs (medians of proportion of 'green': supplemented 0.91 (range 0.44-1.0, n=9), control 0.39 (0.0-1.0, n=10); $F_{1,17}$ = 8.74, P=0.015). If 'green' caterpillars were on average larger than 'brown' ones, that could produce the observed difference in average prey size. However, within videotaping sessions, the size of caterpillars brought was not different between the two colour categories (average ± SD : 'green' 0.89±0.14; 'brown' 0.92±0.21; t_{15}= 0.52, NS, paired t-test). Moreover, within colour groups, there were still differences in size of larvae between supplemented and

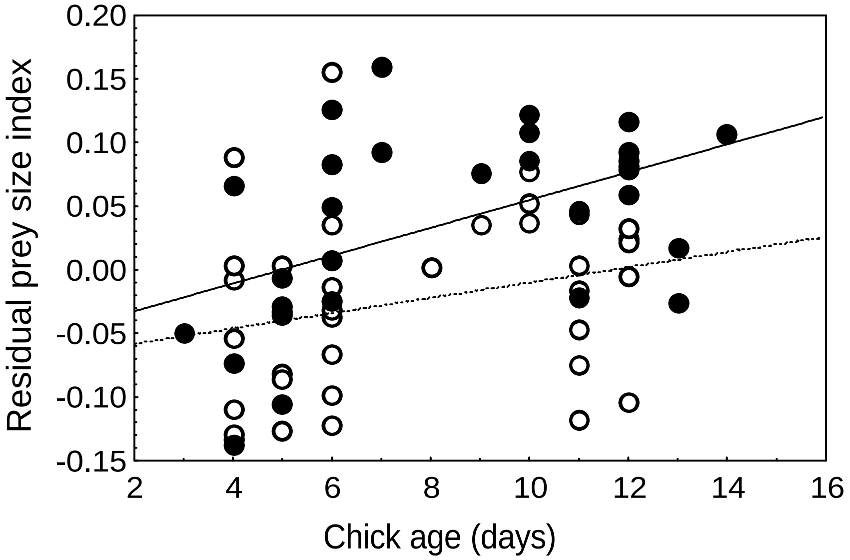


Figure 6. Average size of larvae (natural feeds only; see Methods) brought by Blue Tit parents in relation to age of the chicks. Prey size is expressed as its residual from its year-specific regression on date (see Fig. 4). Open dots, dotted lines: control. Closed dots, solid lines: food-supplemented. More than one data point per nest is shown (statistical details are given in Table 3, with one data point per nest)

control nests, at least for brown caterpillars ('green': $F_{1,13}$ =3.52, P=0.08; 'brown': $F_{1,13}$ =7.27, P=0.018; Table 1). Within *Operophtera brumata*, one of the most frequent species, items delivered by supplemented parents were larger than those delivered by control parents, but the difference was no longer significant (mean PS index: supplemented 0.88 ± 0.14 (n=9); control 0.78 ± 0.15 (n=6); $F_{1,11}$ = 1.92, P=0.19 after controlling for date and chick age).

Food supplementation and Search time

There was a strong positive correlation between search time and the time gap between feedings (r= +0.92, n=15 nests, P=0.0004). This indicates that the duration of the single feeding excursion T_t, which reflects visit rate, was strongly dependent on search time (T_p+T_f in our model). However, food-supplemented parents spent more time searching for food than controls even at similar visit rates. Table 4 compares the median time spent searching in a single foraging excursion with the total time spent away from the nest. Parents provided with additional food spent more time searching

Table 4. Median [range] (*n*) of time spent foraging by control and food-supplemented parent Blue Tits in 1999. Note the longer time spent foraging by supplemented parents while the total time spent away from the nest remained unchanged.

	Control	Food-supplemented
Estimated foraging time (s) *	29.4 [19.7 – 54.7] (6)	37.5 [9.6 – 160.0] (9)
Average time spent away (s) #	56 [37 – 77] (6)	54 [19 – 173] (9)

* measured with a stopwatch; # measured with the video camera counter.

than controls (Table 4; effect of treatment on log-transformed search time: $F_{1,12}$ =16.02, P=0.002, controlled for total time away). This suggests that search time could also vary within a certain visit rate, depending on the state of the parent.

DISCUSSION

Effects of the parent's state on provisioning strategies

In this study, we have shown that parent Blue Tits with an additional food supply reduced their rate of natural food provisioning to the offspring and, at the same time, delivered larger larvae than those delivered by control parents. The model we have outlined in the introduction provides an explanation for changes in size of prey brought by a central place forager following changes in the energy requirement of the forager itself. The use of an extra food resource by the parent results in a reduction in its own energetic demand, so that the parent may spend less effort and time in self-feeding. A trade-off between time devoted to self-feeding and that devoted to food provisioning is likely to work in tits and can produce changes in provisioning strategies. Tóth *et al.* (1998) demonstrated that when female Great Tits made significant self-feeding they reduced the size of meals brought to the nest. More generally, prey size would change when compromises are made between food provisioning and a number of parental and non-parental activities. Female Blue Tits in highly parasitized nests spend much time in nest sanitation, presumably make shorter foraging excursions and bring a smaller proportion of caterpillars. In contrast, males, which do not participate in nest sanitation, do not change their prey spectrum. This has been interpreted as evidence that the parents adaptively change search time and selectivity as time constraints become greater (Hurtrez-Boussès *et al*. 1998, J. Blondel, personal communication). The ability to increase the time devoted to the search for offspring food has dramatic consequences on the rate at which the parent can bring energy to the brood. Naef-Daenzer & Keller (1999) showed that the time employed to find a prey item was inversely related to the general abundance of prey in the tree canopy. When caterpillars were at the maximum density, Great and Blue Tits could find prey within 2 minutes, against 5-6 minutes when they were foraging before or after the period of peak density. Search time was also depending on caterpillar size, which indicates that when caterpillars are small the bird takes more time to find them (Naef-Daenzer, Naef-Daenzer & Nager 2000). This clearly demonstrates that there are important time constraints on the energy flow to the nest. If the parent has to eat a greater amount of food to fulfil some energy demands, it will spend more time in the feeding sites. By maintaining a constant selectivity X_f, the parent will deliver the same amount of food in a longer time period (Fig. 1a). This allows for the possibility that the parent with low energetic demand can potentially increase its search time (and therefore selectivity) for the single prey item that has to be brought to the brood. As a result, it could deliver larger prey in the same time lag as the former (Fig.1b). We wish to point out that, when the parent is released from the need to spend long time in self-feeding, it does not necessarily reach the maximum rate of energy delivery attainable (arrow a in Fig. 1b). That way, food-supplemented parents could be able to bring more food than actually needed by their brood. Our results suggest that the parents with extra-food worked in the right part of the curve (arrow b in Fig. 1b), delivering larger food items than controls, at a similar or slightly higher (if food in the environment was limiting) rate of net energy intake. Once the parents could satisfy the requirement of their brood, they could reduce visit rate and increase feeding efficiency (i.e. the same amount of energy being delivered in shorter time).

Notice that the chicks also obtained part of the extra-food by the parents, therefore they may have needed even less food than control chicks. This suggests that the potential switch in prey selectivity was even greater than that caused if only the state of the parents had been manipulated.

The model presented here cannot explain changes in prey size when only the state of the brood changes. Lifjeld (1988) temporarily increased hunger level of Pied flycatcher (*Ficedula hypoleuca*) broods. The parents responded by increasing feeding frequency but delivered smaller loads to the brood. The author concluded that the parents attending hungry nestlings presumably adopted a strategy that could reduce the time gap between deliveries and thereby minimising the risk of starvation of the brood. This could be achieved by reducing travel time or search time (Houston & McNamara 1985a, 1985b). Also, a more comprehensive model should identify the conditions in which the parents use the extra-time to deliver more feeds per time unit instead of increasing selectivity when they get additional food (arrow a vs. b in Fig. 1b; Markman, Pinshow & Wright 1998).

Changing prey selectivity or differential depletion?

The difference in the diet of nestlings of the two experimental groups could reflect different degrees of prey depletion in the respective territories. By exploiting the extra-food supply, the adults might have depleted their feeding sites less quickly than in unmanipulated conditions, and consequently would have brought to the nest, on average, larger food items. The effect of depletion, therefore, could not be distinguished from that of increased food selectivity of the parents. Unfortunately we do not have data on density and size distribution of prey in the home ranges of Blue Tits, therefore this possibility cannot be excluded. However, two facts suggests that prey depletion did not play a major role in this system. First, the effect of food addition on size of delivered larvae was already apparent at the very beginning of the breeding season (see left side of Fig. 4). In that phase, all the data points represent nests that were filmed when the brood was a few days old, that is, when an effect of depletion was unlikely, also given the small extra-take of control parents early in the nestling stage (about 10 additional feeds/h, not of all being larvae; Fig. 3).

Second, there are important short-term changes in the size of larvae delivered during filming, especially in unmanipulated nests. Such changes often occur from one visit to the next (Grieco, in press), and can be due to prey depletion only if they reflect abrupt switches of the forager between sites of different prey size distribution. However, such changes in prey size are strongly associated with changes in duration of the foraging trip (Grieco, in press). If the parent makes longer foraging excursions, it will be more likely to take a large larva. This could well be due to the forager reaching feeding sites that are less depleted and located further away at the same time (Andersson 1981; Naef-Daenzer 2000). But the changes in foraging trip duration are so marked (e.g. 1 minute; Grieco, in press) that cannot simply be due to changes in foraging distance. Furthermore, observations of parents during their foraging trips indicate that the total time spent away is a predictor of search time, not travel time (this study; see also Naef-Daenzer & Keller 1999). Thus, small prey brought by control parents is more likely to result from allocation of shorter search time, rather than the more frequent use of poor feeding sites.

If finding large prey takes time, it has to be traded-off against the increased provisioning rate required when brood demand increases. In unmanipulated nests, the parents brought smaller larvae when feeding large broods, after controlling for other confounding variables. Apparently, when the rate of provisioning is high the parents cannot spend much time in any foraging excursion to find large food items. However, parents with extra-food supply delivered large larvae even when feeding large broods. This has to be considered together with the fact that those parents did not increase natural visit rate, thus they did not presumably reduce their average search time when feeding large broods. They could deliver larger prey because they could make, on average, longer foraging excursions than controls. These results indicate that the magnitude of the constraint on prey selectivity increases with brood demand.

The effect of the interaction between treatment and nestling age could be explained in a different way. While control parents delivered prey whose size was independent of nestling age, food-supplemented parents delivered larger prey as the nestlings grew older. It is possible that time saving following food addition allowed the parents to fine-tune the size of prey according to the age of the offspring (van Balen 1973).

Finally, we wish to suggest that changes in prey selectivity could also occur in terms of prey type, which was not taken into account in this model. Parent birds have often been reported to collect less preferred prey types when their condition or that of the offspring change (Sasvári 1986; Bañbura *et al*. 1994, 1995). Food-supplemented parents delivered more green and fewer dark caterpillars relative to controls. Thus, when the parents worked less hard they ignored prey types that would otherwise be collected. Components of the nestling diet are not equally preferred (Prop 1960; Tinbergen 1960; Royama 1970). Prey choice experiments on in aviaries has suggested that Blue Tits prefer pale-coloured caterpillars to darker ones (J. Blondel, personal communication). A possible explanation for that is that green caterpillars may be preferred as a source of carotenoids important for plumage coloration (Slagsvold & Lifjeld 1985; Eeva, Lehikoinen & Rönkä 1998).

An open question

We found that Blue Tits provided with additional food spent more time searching for natural food ($T_p + T_f$ in our model) even if the total time between visits T_t was the same as for control parents (Table 5). Our model assumes that the forager can increase selectivity X_f by increasing the time needed to find a food item for the offspring T_f at the expense of the time needed for self-feeding, T_p. These findings suggest that the total search time $T_p + T_f$ does not have to stay constant given a certain T_t. Further modelling work will address the question of how different food resources can produce patterns of different allocation of search time within a certain duration of the foraging excursion.

ACKNOWLEDGEMENTS

We thank the board of the National Park ‘De Hoge Veluwe’ for permission to carry out this research. Piet Drent provided the larvae for the feeding experiment. Discussions with Shai Markman and comments by Jacques Blondel, Bruno Massa and Beat Naef-Daenzer improved the manuscript. This study was partially funded by the European Commission with a Marie Curie Research Fellowship to F. G. (n° ERB FMBICT 971939).

Chapter 4

Trade-offs during parental food provisioning in breeding Blue Tits (*Parus caeruleus*): the relationship between provisioning rate and prey size

Fabrizio Grieco

ABSTRACT

The relationship between provisioning rate and size of prey delivered to the nest was investigated in parent Blue Tits under different food conditions. Provisioning rates and nestling diet were studied by videotaping at the nest, while food availability was experimentally manipulated. When time limits prey selectivity, one would predict an increase in prey size with the time spent away from the nest by the parent. This was confirmed by the within-day, positive correlation between the size of larvae brought to the nest and time since the last visit. The time interval between deliveries was a good predictor of searching time as measured during direct observations of the parent foraging in the tree canopy. In unmanipulated conditions, a significant positive relationship was more likely at high provisioning rates, suggesting that periods of intense feeding limits the size of prey delivered.

Food-supplementation changed the relationship between prey size and time since the last visit. Parents with access to extra-food reduced the number of natural food deliveries and made longer foraging excursions. The size of prey brought was independent of time spent away from the nest. This suggests that, below some value of visit rate, prey size is no longer constrained by duration of the foraging excursion.

Since the adults consumed most of the additional food themselves, the experiment changed the parents' time and effort for self-maintenance. This might have relaxed the time budged for feeding the young, which resulted in increased searching time and more selective foraging.

INTRODUCTION

From foraging theory we gather that the size of prey that a forager takes to a central place (e.g. a nest) is expected to determine the time the forager needs to search for it (review in Stephen & Krebs 1986). Many birds are single-prey loaders (Orians & Pearson 1979), which means that the forager brings back only one food item per trip. Lessells & Stephens (1983) pointed out that the single-prey model is a diet choice model, in that the forager chooses the prey size, or more generally value, that maximises its net energy intake. In a simplified model where handling time is negligible, the forager rejects all prey below a critical value, called ‘minimum acceptable prey value’, and takes the first item above this value it encounters. The prey value is related to search time, i.e. the more selective the forager, the longer it will have to forage until an acceptable item is found.

In central-place foragers, it is reasonable to assume that search time per food item is strongly correlated with the time spent away from the nest, because most of the time between feedings is spent searching for prey (Smith & Sweatman 1974; Naef-Daenzer & Keller 1999). Thus, the slower the visit rate, the longer the time between two subsequent feeds, and the longer the time spent searching for a food item. (it is, however, possible that when feeding frequency decreases, relatively more time is spent in non-food searching activities, so that search time won’t change, but that’s not in the scope of this paper). In a wide range of feeding conditions, the time interval between two subsequent parental visits shows significant variation, even in a short time scale (Gibb & Betts 1963; Royama 1966b; van Balen 1973; Naef-Daenzer & Keller 1999). The analysis of the sequence of feeding events indicates that the parents alternate phases of intense feeding with phases when they stay longer time away from the nest (e.g. Fig. 1). These changes in feeding rate are mediated by the interaction between the parent and the offspring, feeding rate generally increasing with the level of food-begging of the offspring (Bengtsson & Rydén 1983; Leonard & Horn 1996; Ottosson *et al*. 1997; Burford *et al*. 1998; Price 1998; Grieco, in press). Changes in search time should be associated with changes in the average size of prey brought to the nest. If the parent has to reduce the time between visits, for instance in presence of predators around the nest (Martindale 1982), we expect a decrease in its food selectivity (Lucas 1983, 1985; Houston & McNamara 1985b).

In tits *Parus* spp. time limitations occur frequently, depending among other things on the density of insect food available in the territory. Naef-Daenzer & Keller (1999) have shown that the foraging bout length of parent Great and Blue Tits increased exponentially with decreasing prey biomass. During the period of peak abundance of caterpillars, the parents took 2-3 minutes to deliver a prey item against 5-6 before and after the peak. Searching time was significantly reduced when the birds returned to the foraging site where the preceding food item was found. Search time is also depending on caterpillar size, which indicates that when caterpillars are small the bird take more time to find them (Naef-Daenzer *et al*. 2000). This suggests that the total food abundance, size and clumped distribution of prey within the canopy put severe time constraints on the energy flow to the nest. The question I now wish to answer is to what extent variation in time limitation affects prey choice in Tits. From studies of food-provisioning behaviour in Tits we know that there is an inverse relationship between size, or weight of food loads, and provisioning rates (Gibb & Betts 1963; Royama 1966b; van Balen 1973), which would imply a positive correlation between prey size and time between subsequent food deliveries. Such correlations resulted from variation in the data *between* nests, or at most *within* nest, *between* days (Royama 1966b). This has been interpreted as the result of variation in food quality between days and between territories. Smaller average prey size due to habitat characteristics or time of the season would cause parents to increase the number of feeding visits, assuming that the total amount of food delivered is kept constant (van Balen 1973). Although this interpretation sounds plausible, the causal relationship could also work the other way round. Part of the variation in size of food items delivered *within* a day or a shorter time lag would reflect changes in prey selectivity due to the different times available to parents for food-searching. Figure 1 suggests that an increase in the time between two subsequent visits (between-feed interval, BFI) is associated with a consistent increase in prey size. Such changes are smooth, thus they are unlikely to reflect a switch of the forager from a feeding site to another with different prey size distribution.

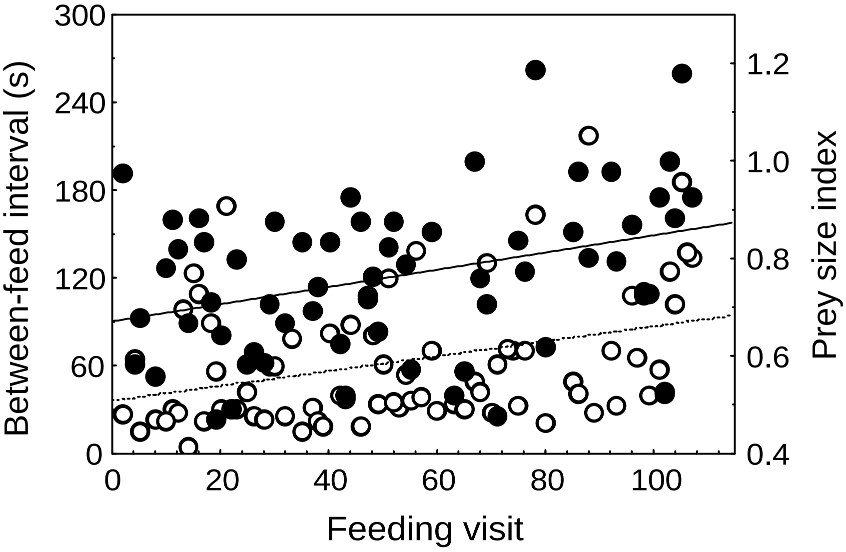


Figure 1. Sequence of feeding visits of Blue Tit parents to their brood and changes in time since last visit (open dots; between-feed interval, see Methods) and size of the larva brought at that visit (filled dots). The trend of increasing BFI and prey size with time since the start of filming is not consistent across nests. In some nests, BFIs and prey size decrease with time from the start of filming, while in others there is no clear trend in any direction.

The aim of this study was to investigate whether a relaxed time budget would result in parents delivering larger prey items. First, I have explored the relationship between the time spent away from the nest and the size of prey delivered to the brood. This was done by looking at the variation in both variables in 1.5-hour periods. This relationship was predicted to be positive (Fig. 2), with steeper slopes (size more dependent of time) when average visit rate is higher (e.g. in parents feeding large broods). This is because parents working harder should alternate periods of intense feeding (short intervals between visits) with periods of less intense feeding (longer intervals). In an extreme case, of course, the parents should show no change in prey size if they always fed the brood at a very high rate, but this is less likely to occur in caterpillar-rich habitats. The relationship is likely to be non linear (Fig. 2), because prey size should not increase above a certain limit either set by the environment (i.e., the size distribution of prey) or by the parent's preference (very large prey are not optimal for the nestlings as well as very small prey). Second, to test whether the parents could change prey size when searching for longer time, I attempted to reduce the work rate by the parents by offering them additional food. The food addition

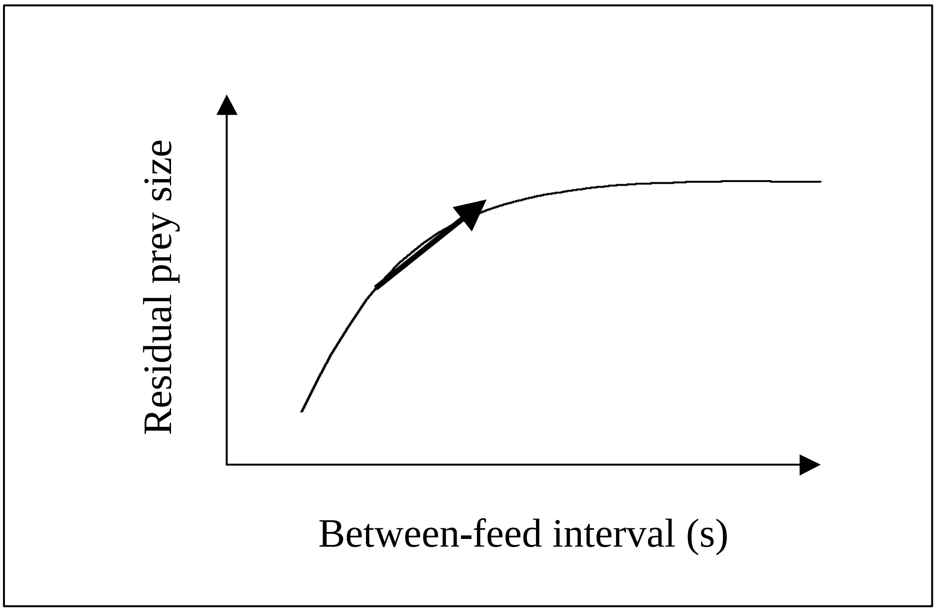


Figure 2. Schematic representation of the possible relationship between prey size independent of time of the season and time spent by parents away from the nest (between-feed interval, BFI). Prey size does not increase further above some value of time spent away from the nest.

should result either in (1) parents giving extra-food to the nestlings, or (2) parents consuming the extra-food themselves, or both (Figure 3). In case (1), the parents will decrease their visit rate through mechanisms of regulation (see above). This will cause an increase in between-feeds intervals. In case (2), the parents consume the food themselves, hence they could save time otherwise spent for self-feeding (Martin 1987). However, two scenarios are possible. In the first, the extra-time is devoted to bring additional feeds (see Markman *et al.* 1998), so that the average time between feedings won't change (path 2a in Fig. 3). In the second, the parents make longer feeding excursions (i.e., longer BFIs; path 2b in Fig. 3). An increase in prey size would be apparent only when the between-feed interval time increases significantly (paths 1 and 2b), assuming that this is accompanied with an increased search time. The increase in average BFI should also lead to a less positive correlation between prey size and time spent away, following the arrow in Fig. 2.

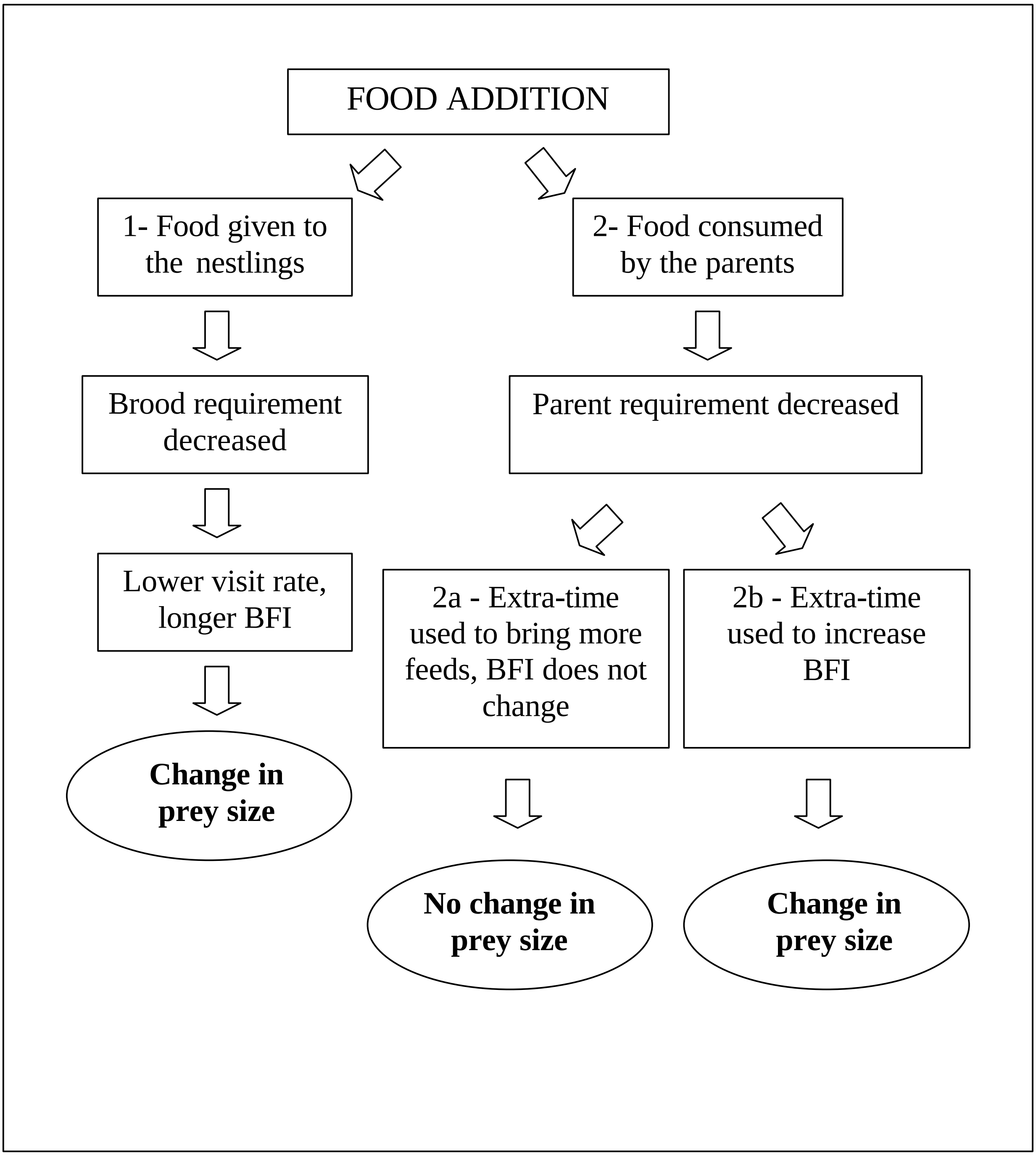


Figure 3. Possible consequences of food supplementation of parent Blue Tits on feeding frequency and prey size. White arrows indicate the chain of behavioural processes that might lead to a change (or no change) in the time gap between food deliveries, and associated change in prey size (ovals). In all cases, it is assumed the extra-time is not used in other activities than foraging for the offspring.

STUDY AREA AND METHODS

The study was carried out on a population of Blue Tits breeding in nest boxes in the Hoge Veluwe National Park, The Netherlands, in the breeding seasons 1998 and 1999. The study area comprises four hundred nest boxes in a mixed forest dominated by Pine *Pinus* spp. and European Oak *Quercus robur* (for details see van Balen (1973)).

Feeding experiments

Mealworms (*Tenebrio molitor*) and larvae of wax moth (*Galleria mellonella*) were offered to adult Blue Tits from the day of hatching to the day of fledging of their young. Food consisted of a mixture of the two species in the first six days after hatching (day 0 to 6), and only mealworms afterwards. The quantity of food supplied each day corresponded to about one half of the daily brood requirement (Gibb & Betts 1963). For a 12-chick brood, it increased linearly from 1.0 g at day 0 to 20 g at day 10, and then levelled off until fledging date. Adjustments in food quantity were made for smaller and bigger broods (c. 1 g per additional nestling). The larvae were placed in small trays (5.5×3.5×4.5 cm) inside the nest boxes so as to prevent birds other than the focal adults from consuming them. Feeding trays were replenished each day according to the scheduled amount. Half of the nest boxes were food-supplemented, while the other half (with a feeding tray as well) were not and served as a control. Food-supplemented and control boxes were assigned randomly within pairs in order to have the same range of hatching dates. Effort was made to assign different treatment levels to boxes in similar habitats.

All the nest boxes were checked daily from the expected hatching date to the date of fledging of the young. The adults were caught and colour-ringed when the chicks were seven days old.

Videotaping and direct observations

In 1998 and 1999 parental food provisioning was filmed in 41 nests, once or twice each (total 75 sessions), between day three and day 13 after egg hatching. Video cameras (Sony CCD-TR825E) were placed facing down on the top of the nest box. A wooden box covered the video camera during filming, while a small lamp provided more light inside the nest. To have the birds more habituated to the set up, a dummy wooden box with a light was placed on the nest box one hour prior to filming. All videotaping sessions started in the morning between 8:00 and 12:00 and lasted 90 minutes. The food-provisioning rate in presence of video cameras (35.9±16.3 feeds/h for unmanipulated pairs) was similar to that gathered from observations at the nest without video cameras in 1997, and within the natural range in caterpillar-rich habitats (ref. in Cramp & Perrins 1993).

Hi8 videotapes were copied to extra-high grade VHS tapes and the latter were observed. The adults could be identified from colour ring combinations. If they had not yet been ringed, they could be identified from individual (not sexual) morphological features (e.g. irregularities of the head and face plumage). In such cases, final identification of sexes was done by comparing plumage features in the videos made before and after the date of ringing. Sex identification could also be done through behaviour, i.e. only females brood the young and clean up the nest.

Definitions. Between-feed interval (BFI) was the time lag between two successive feeding visits. In food-supplemented parents, only visits with natural food items were considered. Prey items were classified as larvae, spiders, other adult arthropods, pupae, and unidentified items. For larvae, which were about 68% of all prey items, prey size (PS) was defined as the ratio between the width of the larva's head capsule and bill width, both measured on the screen with a calliper to the nearest 0.1 mm. Size was measured in 66.7% of the larvae brought to the nest (n=2240). The size of larvae delivered to the nest increased linearly with date as a result of their growth during the season. In both years, the quadratic term of date did not significantly improved the model of prey size (all video sessions: ΔR^2= 0.005, $F_{1,71}$= 0.99, P=0.33; see also Naef-Daenzer *et al*. 2000). To express prey size independent of date, I calculated the residual of PS from its linear regression on date (residual prey size, RPS). This value was calculated separately for the two years (regression equations: 1998, PS= -0.143 + 0.017*date, R^2= 0.55; 1999, PS= 0.056+0.016*date, R^2= 0.66).

For some nests in 1999 the behaviour of parents was observed during filming sessions. Every time the parent left the nest for a foraging excursion, I measured the time during which the parent moved along branches with small hops (see ‘searching movements’ in Remsen & Robinson (1990)). This was defined as search time. The time spent flying among branches was excluded from search time measurements. The stopwatch of the observer was synchronised with the time counter of the video camera, so that search time could be related to the between-feed interval.

Data analysis

Individual nests were treated as observation units. Whenever two sessions per nest were available, one was chosen at random for analysis. Residual prey size was analysed with general linear models in Statistica for Windows 5.5 (StatSoft 1999). Log-transformed between-feed interval was treated as covariate. To test for between-nest difference in the slope of the regression line of prey size on BFI, I tested the interaction nest × log (BFI) on residual prey size. For each nest, I calculated the slope of the regression line of RPS on log (BFI), and tested the difference of such values between treatment levels.

RESULTS

Food consumption

Food consumption was total (i.e. 100% of the mass daily offered) in 468 (67.7%) of the 691 nest feeding days. The parents totally ignored the larvae in just 21 (3%) of the nest feeding days. During videotaping in 1998 and 1999, the adults took on average 16 items per hour (range 0 - 49). However, the adults delivered to their young only 15% (range 0-100%) of food items taken from the tray. This proportion increased with nestling age (r_s=+0.41, n=37, P<0.02), but not with brood size (P>0.10).

Prey size and time away from the nest

I found an association between residual prey size (i.e. prey size independent of date) and between-feed interval. The interaction between nest and log transformed BFI was significant ($F_{39,690}$= 1.67, P=0.007), indicating that nests differed in the slope of the regression of prey size on BFIs. Food-supplemented nests showed lower slopes

(0.004±0.057, n=21) than controls (0.042±0.055, n=20), indicating that prey size increased less strongly with time spent away from the nest (Fig. 4; $F_{1,39}$= 4.67, P=0.037; brood size, nestling age and date of filming being not significant). Yet, in neither the two groups the average slope was significantly different from zero (one sample t test, both P>0.40). In control nests, however, positive slopes were more then expected by chance (15 of 20, 4 significant (all positive); Goodness of fit test, χ^2_1= 5.00, P=0.025; Fig. 4). Note that the significant regression coefficients lay in the upper left corner of the graph, indicating that the regression line of prey size against BFI was steeper at higher visiting rates (Fig. 4). On the other hand, food-supplemented nests showed negative and positive slopes in similar proportions (9 and 12 (1 significant) of 21 respectively; Goodness of fit test, χ^2_1= 0.43, P=0.51; Fig. 4). The higher regression coefficients in control nests could be due to the greater number of prey items with which the regression lines were calculated (control birds brought on average more feeds than supplemented birds). Thus, control nests would be more likely to show significant positive regression lines. However, there was no relation between those regression coefficients and the number of prey items used (r=0.23, n=41, P=0.15). In addition, regression lines were steeper in control nests even when the comparison was restricted to nests with similar numbers of feeds (e.g. between 10 and 30 items: t_{24}= 3.07, P=0.005).

Food supplementation resulted in an increase of the interval between two natural feeding visits (Fig. 4; effect of treatment $F_{1,33}$= 4.13, P=0.05 after controlling for chick age, date of filming and brood size; three food-supplemented nests were excluded since the female fed the chicks without the contribution of the male). Of the three nests attended only by the female, two showed very short BFIs (Fig. 4). These two nests contained nestlings less than six days old at the time of filming. Hence, the female had to spend a significant proportion of time brooding the nestlings while she had to feed the brood on her own. This might explain the very high BFI despite of food supplementation. In addition, the high feeding rate of those females can explain the absence of positive correlation between prey size and BFI. Those females very rarely left the nest unattended for more than two minutes, therefore variation in BFI and prey size was very low.

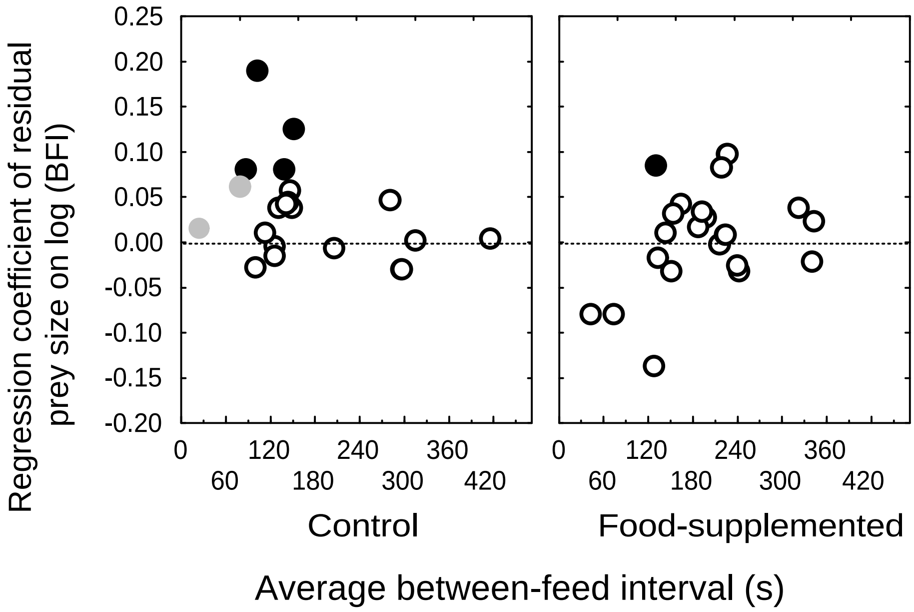


Figure 4. Coefficients of regression of residual prey size (see Methods) in relation to the average time between two subsequent natural feedings. In three food-supplemented nests only the female fed the chicks during videotaping. Between-feed intervals were much shorter than in the rest of food-supplemented nests (lower left corner of the graph). Black dots indicate statistically significant regression coefficients (P<0.05); shaded dots indicate 0.05<P<0.1.

Food-supplemented parents brought larger larvae than controls to the brood (Table 1; effect of treatment on average PS: $F_{1,33}$= 4.57, P=0.04 after controlling for year, chick age and date of filming). The effect of treatment was even larger if we consider only nests where at least 10 larvae were measured ($F_{1,29}$= 9.03, P<0.005 after controlling for year, chick age, date of filming and interactions treatment × brood size, treatment × chick age). As we have previously seen, prey size was no longer related to the time since the last visit when extra-food was offered to the parents. Thus, food manipulation caused prey size to shift in the direction expected from Figure 2.

Table 1. Size of prey brought to the nest by parent Blue Tits. Prey size (PS in Methods) is the ratio of larva's head size to the bird's beak width. Sample sizes are given in brackets.

Year	Control	Food-supplemented
1998	0.71 ± 0.10 (9)	0.74 ± 0.13 (11)
1999	0.83 ± 0.12 (11)	0.95 ± 0.12 (7)

Between-feed intervals and search time

There was a strong positive correlation between search time and between-feed interval (Fig. 5; *r*= +0.92, *n*=15 nests, *P*=0.0004). This indicates that the large variation in BFI, which reflects provisioning rate, was due to variation in search time. However, there was no relationship between the BFI and the remaining time within BFI (=BFI-search time) (*r*= +0.26, *n*=15, *P*=0.34). In addition, residual prey size was still positively correlated with search time (*r*= +0.643, *n*=10, *P*=0.045), not with remaining time within BFI (*r*= -0.241, *n*=10, *P*=0.50). If we assume that travel time was the main component of this remaining time, it follows that travel time could not explain the large variation in between-feed intervals (Fig. 4), nor the variation in the deviation of prey size from that expected at a certain date.

DISCUSSION

Differential prey depletion or change in selectivity?

A within-nest, within-day positive association between size of prey and time spent away from the nest before delivering the item could result from the different degree of prey depletion of feeding sites at different distances from the nest. Feeding sites closer to the nest are more exploited than those located further (Naef-Daenzer 2000). As a result, those sites would contain prey in lower density (Andersson 1978; 1981; Naef-Daenzer 2000), as well as smaller average size, since tits tend to catch large caterpillars among those available (Gibb & Betts 1963; Tinbergen 1960; Naef-Daenzer *et al*. 2000). If the time between two feeds reflected the distance from the nest, this would lead to a positive correlation between the former and the size of larvae.

However, there is some evidence that BFIs did not reflect travel time. First, the range of BFIs was large (from 30 s to more than 6 minutes, see Fig. 4). Blue Tits forage very close to their nest, usually within 20-25 m (Smith & Sweatman 1974; Naef-Daenzer 2000; author's personal observation). Intuitively, the round-trip travel time for such distances could not produce the observed variation in BFI. More importantly, the time between two visits was a good predictor of search time, not the

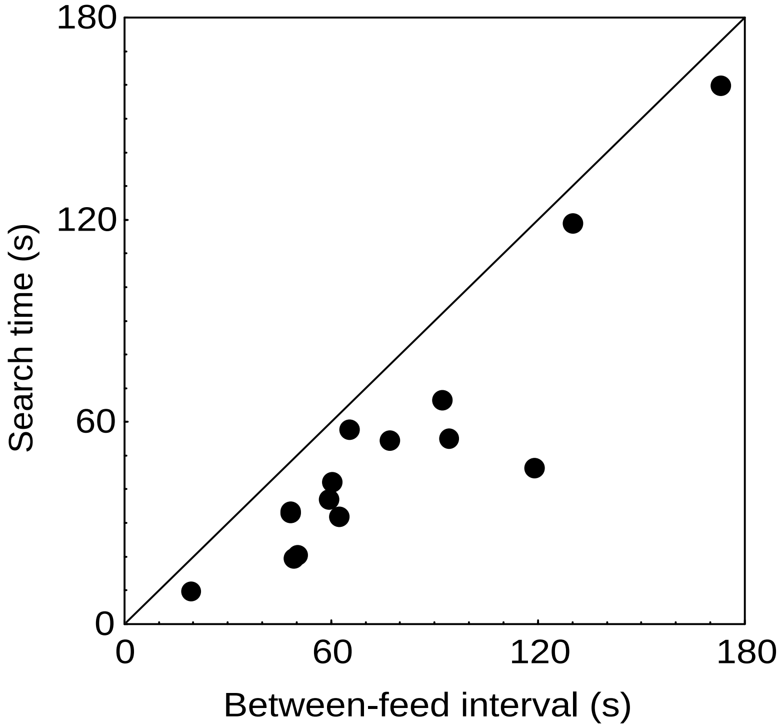


Figure 5. Time spent searching for food before a single visit in relation to the time since the last visit. The full line indicates the identity line (obviously search time cannot exceed the total duration of the round trip nest – feeding site – nest). Each data point represents the average for a nest where between-feeds intervals were recorded on video while the parents were watched during foraging.

remaining time within BFI, which included travel time. Similarly, Naef-Daenzer & Keller (1999) found that the distance of the foraging site from the nest could not explain duration of feeding intervals. Thus, variation in prey size observed in my study could be better explained by variation in food-searching time. Adjustments in search time, which reflect adjustments in selectivity, are made on a very short time scale, for instance in response to changes in begging behaviour of the nestlings (Grieco, in press). Thus, what appear as partial preferences in a static representation of prey choice (e.g. small as well as large larvae brought to the nest) are instead dynamic foraging rules that change rapidly (e.g. small larvae brought during intense feeding, followed by larger items being brought during less intense feeding; see McNamara & Houston 1987).

Food-supplementation and effects on foraging strategy

Blue Tit parents receiving additional food used it to feed the young but mostly as their own source of energy. This might have potentially produced all effects on provisioning rate as expected in Fig. 3. Nestlings in food-supplemented nests were given a significant proportion of the larvae offered, and were more satiated than control nestlings (Grieco, in press). Therefore, a reduction in visit rate (and the consequent longer BFIs) might have been brought about through path 1 of Fig. 3. On the other hand, most of the food was consumed by the parents themselves, indicating that the experiment also modified the state of the parent, and presumably reduced the time and the effort for self-maintenance. Thus, it is likely that the observed increase in BFI, and the larger size of delivered prey, resulted from the mechanism suggested in path 2b of Fig. 3.

I have shown that parent Blue Tits adopted a strategy that allows delivery of larger food items. Food-supplemented parents stayed for longer time away from the nest, and delivered large larvae to the brood (F. Grieco & A. J. van Noordwijk, unpublished; this study). According to what was predicted, they shifted prey size to a range where it no longer increased with duration of the foraging trip. This provides evidence that delivering large prey to the nest can only be achieved by performing longer foraging excursions, confirming the interpretation of natural short-term variation in prey size (e.g. Fig. 1). The results also show that the relationship between prey size and between-feeds time is not linear, i.e. above a certain value of BFI, if the parent spends longer periods of time searching for food it cannot find larger larvae. Alternatively, the upper limit of prey size is set by the preference of the parent for a certain range of sizes that matches the requirement of the offspring (van Balen 1973, Perrins 1979).

The view that relaxed time budget may reduce the constraints on selectivity can also explain changes in nestling diet reported in some other experimental work. Hurtrez-Boussès *et al.* (1998) reduced the density of ectoparasites in Blue Tit nests. Female, not male, adult Blue Tits spent less time in nest sanitation, but made longer foraging excursions and delivered larger prey (J. Blondel, personal communication). Such effect was not seen in males, which do not clean the nest. This leads to the conclusion that within nest variation in prey size is determined by the forager’s time budget. In a study of Pied flycatchers (*Ficedula hypoleuca*), hunger level of broods was experimentally increasing by replacing 2 well-fed young with 5 hungry young (Lifjeld 1988). The parents responded by taking on average smaller prey, indicating that they increased feeding rate at the expense of prey selectivity. However, in both works the authors did not relate the between-feeds interval to prey size.

The key question, of course, is what mechanism is involved in the change of selectivity, both within nest (i.e. short term variation in feeding frequency and prey size) and between nests (effect of food addition). Classical central-place foraging models would not predict any change in foraging strategy (i.e., selectivity) of the rate-maximising single prey loader, since they do not depend on the state either of the parent or of the offspring (Orians & Pearson 1979; Lessells & Stephens 1983; Stephen & Krebs 1986). These models are only concerned with the rate at which energy is delivered to the brood. Therefore, whether the parents ignore or eat the items falling below the minimum acceptable prey size for the offspring (Lessells & Stephens 1983) does not influence the optimal strategy. Houston (1987) has shown that, as soon as the parent's energy budget is brought into a model, the energy that the parent gets from items below the critical prey size becomes important, and can produce different optimal degrees of selectivity. Thus, food supplementation may have changed the parents' state and therefore a shift in critical prey size, with longer BFI as natural consequence of the change in selectivity.

On the other hand, this mechanism cannot explain changes in selectivity when the state of the parent has not changed, for instance in the case when parents feed the young with extra-food but they do not eat it themselves (path 1 in Fig. 3) or in the work by Lifjeld (1988) where hunger level of the brood, not body condition of the parents, was experimentally varied. One of the possible mechanisms behind such changes is involved in the variation of time gaps between deliveries to minimise the probability of starvation of the brood. According to models by Houston & McNamara (1985a) for non-central place foragers, if the forager faces an increased probability of food deprivation it should accept all encountered prey items which represent a net energy gain. This would be obtained by reducing selectivity. In the context of central place foragers, this class of models suggests that the parent could adaptively change feeding rate according to the state of the brood. To reduce the time between food deliveries, the parent could either (1) make shorter foraging trips or (2) forage for shorter time, and therefore reduce food selectivity.

ACKNOWLEDGEMENTS

I thank the board of the National Park 'De Hoge Veluwe' for permission to carry out this research. Piet Drent provided the larvae for the feeding experiment. Discussions with and comments by Jacques Blondel, Patsy Haccou, Jeffrey Lucas, Arie van Noordwijk, Tracey Parrish, Marcel Visser and two anonymous referees improved the presentation. This study was partially of a PhD project funded by the European Commission with a Marie Curie Fellowship (n° ERB FMBICT 971939).

Chapter 5

Short-term regulation of food-provisioning rate and effect on prey size in Blue Tits (*Parus caeruleus*)

Fabrizio Grieco

Animal Behaviour, in press

ABSTRACT

The short-term regulation of parental provisioning rate (PPR) in Blue Tits was investigated by videotaping the parents at the nest. An additional feeding experiment allowed a comparison between the behaviour of parents raising their brood under normal and supplemented feeding conditions. Videotaping revealed that parents changed their PPR as an immediate response to the absence of chicks' food-begging behaviour. When chicks did not beg for food, the parents solicited them with a particular call (feeding call, FC) to make them open their beak. Parents significantly increased the time away from the nest immediately after performing feeding calls. Provisioning rate returned to the usual levels as soon as chicks started begging again, but supplemented parents took a shorter time to do so compared with controls (i.e., parents not provided with additional food). Changes in PPR had effects on both type and size of prey brought to the brood. Females often responded to low brood demand by returning to the nest without food. Food-supplemented parents, not control, took larger larvae when they stayed longer away from the nest. This suggests that parents in the supplemented group could use more time to reach good feeding sites or, more probably, increase their prey selectivity. Blue Tits continually monitored the begging behaviour of the offspring and responded accordingly by adjusting their feeding rate, with immediate consequences for prey choice.

INTRODUCTION

Life-history theory predicts that parental effort is regulated so that the costs and benefits of current reproduction are balanced to maximise lifetime reproductive success (Stearns 1992; Roff 1992). Parents must make decisions throughout the breeding cycle about how much effort to put in reproduction and how much in self-maintenance. When the offspring are well fed, it does not pay to maintain a high feeding effort; conversely, hungry offspring need an increased feeding rate. In birds, a number of observational and experimental studies found a relationship between chick demand and parental effort, primarily in terms of parental provisioning rate (PPR; e.g. Henderson 1975; Bengtsson & Rydén 1983; Hussell 1988; Stamps *et al.* 1989; Dijkstra *et al.* 1990; Yasukawa *et al.* 1993; Leonard and Horn 1996; Price and Ydenberg 1995). Experimental manipulation of brood size causes changes in feeding rate (Nur 1984; Smith *et al.* 1988; Wright & Cuthill 1990; Conrad and Robertson 1992; Rytkönen *et al.* 1996). Food-begging behaviour of nestlings appears to be the main signal that parents use to assess the current need of the offspring. Besides the debate on whether begging behaviour is an honest signal of need (Godfray 1991, 1995; review in Kilner and Johnstone 1997), parents do respond to begging levels. Experimental manipulations of begging intensity using recorded vocalisations have often shown an increased provisioning rate relative to unmanipulated situations (Harris 1983; Bengtsson and Rydén 1983; Ottosson *et al.* 1997, Burford *et al.* 1998; Price 1998). Most of the studies above do not report the exact moment when the parents react to the artificial or natural stimulus. In other studies, however, there is evidence for an immediate response by the parents. Captive zebra finches (*Poephila guttata*) increased the frequency of regurgitation as soon as begging calls were played (Muller & Smith 1978). In a study on tree swallows *Tachycineta bicolor*, parents responded to increased begging intensity by immediately reducing their time to the next visit to the nest (Leonard and Horn 1996).

Besides visiting rate, size and type of food items are also important components of provisioning effort. If a parent bird is able to deliver large food loads to the nest, fewer foraging bouts per unit time are needed to meet the brood's requirements. This is of course strongly influenced by the quality of both the territory (e.g. Royama 1966, van Balen 1973) and the forager. However, prey size is also related to the time budget of the forager. In order to obtain a larger item, thereby to increase selectivity, more time is needed as more small items will be ignored during the foraging bout (see Lessells & Stephens 1983 for central-place foraging). Selectivity is also reflected in the type of prey brought to the nest. This is due to the fact that nutritional quality of available prey types is not uniform across the environment. For instance, prey types that are common in the environment and lead to maximisation of energy gain may not be the ones that serve as protein source (e.g. Krebs & Avery 1984). Therefore, if foraging time is limiting, as in most cases in nature, parents may find it difficult to find the food type that maximises the long-term growth of the offspring. Indirect evidence for this comes from switches in prey type following experimental manipulation of brood size (e.g. Tinbergen 1981; Bañbura *et al*. 1994; Wright *et al*. 1998). Models of Lucas (1983; 1985) predict an increase in selectivity with foraging bout duration, and some field and laboratory studies support this (e.g. Martindale 1982; Lucas 1987). Changes in prey choice as response to changes in prey density, time constraints and satiation are very rapid (Lucas 1990), suggesting that they could be detected in parents responding to different levels of begging of the brood.

During a study of foraging in Blue Tits *Parus caeruleus*, I extensively videotaped the parents at the nest to collect data on provisioning rate and prey choice in different feeding conditions. This gave the opportunity to monitor changes in provisioning rate and prey quality and/or size after changes in parent-offspring interactions. In this paper, I have focused on the instances when the chicks did not beg for food rather than to changes in begging intensity. I have tried to answer the question of whether parents react immediately to the absence of begging by increasing the time spent away from the nest and thereby slowing down PPR. I have then looked at whether a reduction of provisioning rate was accompanied by changes in type and/or size of meals brought to the nest. Moreover, a supplemental feeding experiment was carried out where Blue Tit parents were offered insect food during the nestling-rearing phase. The parents could therefore eat the supplemental food or give it to the young. In any case, this was expected to increase the time available to the parents for searching natural food for the offspring (Martin 1987), with two possible outcomes were predicted. The rate at which the parents feed the offspring might increase, as reported by Markman *et al*. (1998) for sunbirds. On the other hand, the number of total feeds might not change or even decrease, with a consequent increase in the time gap between two feeding visits. This could potentially reduce the time constraints on food selectivity (Lucas 1983, 1985), and therefore show effects on size and/or quality of food brought to the nest (Hurtrez-Boussès *et al*. 1998). The feeding experiment provided the opportunity to establish whether parents modify their response to the begging behaviour according to the food resources they experience during brood raising.

METHODS

This study was carried out in 1998 and 1999 on the Blue Tit population breeding in nest boxes in the Hoge Veluwe National Park, central Netherlands. The study area comprises of 400 nest boxes located in a mixed forest dominated by European Oak *Quercus robur*, and conifers *Pinus* spp. (van Balen 1973).

Feeding Experiments

Mealworms (*Tenebrio molitor*, family *Tenebrionidae*) and larvae of wax moth (*Galleria mellonella*, family *Pyralidae*) were offered to adult Blue Tits during breeding, from the day of hatching to the day of fledging of the young. Food consisted of a mixture of the two species in the first six days after hatching, and only mealworms afterwards. The quantity of food supplied daily corresponded to about one half of the brood’s daily requirement as reported by Gibb & Betts (1963). For a 12-chick brood, it increased linearly from 1.0 g at day 0 to 20 g at day 10, and then levelled off until fledging date. Adjustments in food quantity were made for smaller and bigger broods. The larvae were placed in small trays (5.5×3.5×4.5 cm) inside the nest boxes so as to prevent birds other than the focal adults from consuming them. Feeding trays were replenished each day according to the scheduled amount. Half of the nest boxes were food-supplemented, while the other half (with a feeding tray as well) were not and served as a control. Food-supplemented and control boxes were chosen randomly within pairs in order to have the same range of hatching date. Effort was made to assign different treatment levels to boxes in similar habitats.

All the nest boxes were checked daily from the expected date of hatching to the date of fledging of the young. The adults were caught, sexed and colour-ringed when the chicks were seven days old.

Videotaping

Parental behaviour during provisioning of offspring was filmed in 39 nests (18 in 1998 and 21 in 1999), once or twice each, during the time the chicks were three to 13 days old. Of the 75 birds filmed (three males were never filmed as they presumably abandoned the nest), 10 (five females and five males) were filmed in both years. Of these, six were under different treatments in the two years (e.g. control in 1998, food-supplemented in 1999). Even for the four birds that were in the same treatment group in both years, the effect of pseudoreplication should be negligible as the main analysis of provisioning rate was done on breeding pairs (values were averaged over the two adults in each pair). A video camera handy cam SONY CCD-TR825E was placed facing down from the top of the open nest box. During filming, a wooden box covered the video camera and a small lamp placed behind it provided more light in the nest. To have the birds more habituated to the video camera and the light, a dummy wooden box with a small light turned on was placed on the nest box one hour prior to filming. All videotaping sessions (n=75) started in the morning between 0800 and 1200 hours and lasted 90 minutes. In none of the years the starting time of videotaping significantly explained variation in either number of feeds brought in one hour or size of prey. Hi8 videotapes were copied to extra-high grade VHS tapes and these were observed. The adults could be identified from colour ring combinations. If they had not yet been ringed, they could be identified from individual (not sexual) morphological features (e.g. irregularities of the head and face plumage). In such cases, final identification of sexes was done by comparing plumage features in the videos made before and after the date of ringing. Sex identification could also be done through behaviour, i.e. only females brood the young and clean up the nest. Furthermore, the video camera boosted the between-sex difference in blue colour of the bird's crown, probably due to its higher sensitivity to near-UV radiation than the human eye (for ultraviolet sexual dimorphism in Blue Tits see Andersson *et al*. 1998; Hunt *et al*. 1998). For each visit, I recorded the time when the adult entered and left the nest box. Prey items were classified as insect larvae, arthropods (including adults and pupae), and unidentified items. The latter were divided into 'large' and 'small', according to whether they were larger than the bird's beak width. The size of larvae was estimated from the screen by the size of their head relative to the width of the bird's beak. During a feeding visit, the parent gave a short, low-pitch call (feeding call, FC) if the chicks did not beg for food, with the apparent aim of making them open the beak. By imitating this call the observer could make the chicks open their beaks when opening the nest box. The feeding call has previously been investigated in several passerines, including the great tit (Messmer & Messmer 1956; Khayutin & Dmitrieva 1978), but not the Blue Tit. The FC was scored without detail on per-visit frequency. In a very few cases (27 out of 3325 visits) the prey taken to the nest was so large relative to the chicks' gape that feeding them was difficult, causing the parents to give FCs even if one or more chicks had opened their beak. Those instances were excluded from analysis. In only one visit the parent did not give FCs when the chicks did not beg for food, and left the nest with the prey in its beak. In that instance, it is likely that the adult was scared by the video camera.

Definitions

Between-feed interval (BFI) was the time lag between two subsequent feeds, i.e. the difference between the time the parent entered the nest box and the time it had left the box in the previous visit. In a small proportion of visits (8 %, quartiles 0.0 – 26.2%) food-supplemented parents fed the offspring extra-food items previously taken from the tray. These visits carried no information about the time taken to capture and deliver natural prey, therefore were excluded from the analysis. Feeding call rate was the proportion of all feeding visits (including those with extra-food in supplemented nests) that the parent gave at least one FC. Extra-food visits were included in this calculation because FC-rate was meant to reflect the general level of satiation of the brood.

For FC-visits, I considered three adjacent between feed-intervals (Fig. 1): B, immediately before the visit, A1, immediately after the visit, and A2, after the first visit where the chicks resumed begging behaviour. Usually A2 followed A1 immediately as in Fig. 1, however if the chicks were well fed they resumed begging a few visits later, causing A2 to be located further. In such instances the parent performed FCs in two or more subsequent visits, thus some BFIs could be considered as occurring both immediately before and after an FC visit. These ambiguous intervals were excluded from calculations. Although these were 40.9% of all BFIs that could be considered of type A1 (n=357), including them as A1-type BFIs in the analysis did not change the results qualitatively (second paragraph in the Results section), as shown by preliminary analysis of the 1998 data set.

For any videotaping session, and for each parental sex, I calculated the mean of intervals B, A1and A2. In an additional analysis, I also considered three adjacent intervals after A2 (A3, A4 and A5). These were all characterised by the absence of feeding calls by the parents at the visit concerned.

Data Analysis

To test whether FC visits by male and female parents were distributed independently along the sequence of visits in a video session, I considered only visits that were followed by a visit by the other parent. Successive visits by one parent were therefore ignored. For each session, I counted the non-FC visits by one parent that were followed by (i) a non-FC visit and (ii) an FC visit by the other parent. The same was done for FC visits by the first parent. Only those nests with 10 or more FC-visits (n=6 nests) were included in the analysis. The counts produced a 2×2 table for each session, where the proportion of counts of a certain event (e.g. giving an FC after the other parent gave one) were considered as probability that the event would occur. Changes in proportions were tested with a Chi-square test. A combined test used the P-values relative to each of the n tables according to the formula: $P_c = -2 \Sigma \log_{10} P$ (Sokal & Rohlf 1997). The combined P_c was then compared with critical Chi-square values with 2n degrees of freedom. FC-visits were much less numerous than non-FC visits. To have greater numbers in the tables, counts from different sessions were summed up for each nest. This could be done since the proportion of FC-visits followed by FC-visits by the other parent did not change with chick age (r=-0.09, P=0.72, n=17 sessions with 5 or more FC visits).

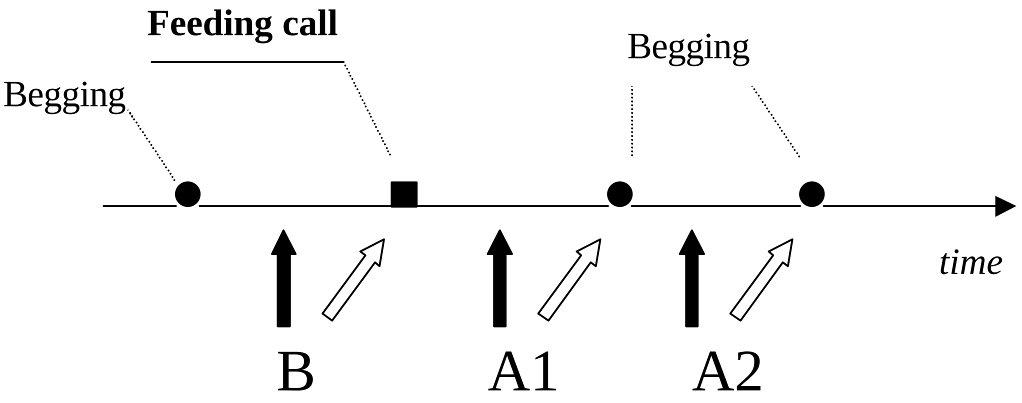


Figure 1. Sequence of visits by parent Blue Tits and behavioural variables in relation to chick-feeding behaviour. Dots represent parental visits when the chicks were begging for food, the square represents a visit when the chicks did not beg and the parent gave a feeding call. The main analysis refer to the between-feed intervals immediately before an FC visit (B), the interval after an FC visit (A1) and the next if chicks resumed begging (A2). If feeding calls were given in more subsequent visits, the related A1 intervals were ignored. Arrows indicate the between-feed interval (black arrow) and the prey brought at the end of it (white arrow). Intervals A3 to A5 immediately follow A2 and were used in a secondary analysis.

Between-feeds intervals and prey size were analysed with general linear models as in Statistica v. 5.5. for Windows (StatSoft 1999). The individual bird or nest were treated as the observation unit. When two sessions per nest were available, one of them was chosen at random and included in the analysis. The size of larvae delivered to the nest increased markedly with date because of their growth during the season (F. Grieco & A. J. van Noordwijk, unpublished data). To express prey size independent of date, I calculated the residual of prey size (RPS) from its regression on date. This was done for the two years separately (regression equations, 1998: PS= -0.143 + 0.017*date, R^2= 0.55; 1999: PS= 0.056+0.016*date, R^2= 0.66). Values of BFIs were right-skewed distributed, therefore they were log-transformed prior to analysis, while FC rates, expressed as proportions, were arcsine-transformed. Date, chick age and brood size on the day of filming were treated as covariates, and were excluded from the model if their effect was not significant. To test for within-nest changes in BFIs and RPS in the sequence B - A1 - A2, I used repeated measures analysis of variance, where the sequence of intervals B, A1 and A2 was the repeated measures factor. Planned comparisons were used to test for changes between pairs of variables (e.g. B vs. A1). Changes in prey type along the sequence B - A1 - A2, were tested with Chi-square tests on prey type counts. The data set also included a few visits with no prey (especially for female parents). Given that a certain prey type may reflect the use of a particular feeding site, the data from individual birds did not represent statistically independent data points. For each session and for each parent, I numbered all intervals of a certain type (B, A1 and A2) from 1 to *n* (where *n* was the number of intervals available). One of the *n* intervals was chosen by generating a random number between 1 and *n*. I then considered the type of prey (or 'no prey' if that was the case) brought at the end of the interval concerned. In this way the prey item brought by the individual parent was represented once for each BFI type.

Ethical Note

Permission to catch the birds was obtained by the National Park “The Hoge Veluwe” and by the Ringing Station of the Netherlands. The videotaping set up did not cause any breeding pair to abandon the nest. The parents returned to the nest within 502±428 (SD) s (range 189 – 2167 s) from the start of filming. The food-provisioning rate in presence of video cameras (35.9±16.3 (SD) feeds/h for unmanipulated pairs) was similar to that gathered from observations at the nest without video cameras in 1997, and within the natural range in habitats rich in caterpillars (Gibb & Betts 1963; Nur 1984; Cramp & Perrins 1993)

RESULTS

Rate of Feeding Calls

Parents gave feeding calls in a small proportion of feeding visits (Table 1). Feeding call rate calculated over a 1.5-hour time decreased strongly with age and number of chicks (ANCOVA: effect of chick age, $F_{1,34}$= 29.17, P<0.00001; effect of brood size, $F_{1,34}$=14.74, P<0.001). A similar decline of FC rate with nestling age was reported in the great tit (Bengtsson & Rydén 1981). This could be a consequence of the higher food requirements in older and bigger broods. After controlling for chick age and number, food-supplemented parents gave, on average, slightly more FCs (Table 1; ANCOVA, effect of treatment: $F_{1,34}$= 4.41, P=0.04). An interaction between treatment and brood size was found (ANCOVA: $F_{1,34}$= 5.01, P=0.032), indicating that the effect of increasing number of chicks on FC rate differed between the two treatments. Separate analysis of FC rate revealed that the effect of brood size was highly significant in control broods (ANCOVA: $F_{1,17}$= 19.94, P=0.0003), and not significant in supplemented broods ($F_{1,16}$= 1.19, P=0.29). Thus, food supplementation reduced the influence of brood size on the rate at which parents solicited the chicks, which was inversely related to how often the chicks begged for food.

Male and female parents did not give feeding calls independent of each other. For each nest, I considered only visits by a parent that were followed by a visit by the other one, regardless of the order (male after female or *viceversa*). Counts of visits with or without FCs, and for the first and the second parent produced a 2×2 table for each nest. When the first parent did not give an FC, the probability that the other gave one was 0.10 (quartiles: 0.07 - 0.14). Conversely, this probability was 0.47 (0.21 - 0.54) when the first parent did give an FC (n=6 nests, number of visits ranging 10 to 109 in any category). The difference was significant (combined test, χ^2_{12}= 25.4, p=0.013).

Feeding Calls and Time Away From the Nest

I first looked at whether parents significantly increased the time spent away from the nest immediately after the visits where they gave a feeding call. In a model with experimental treatment, parental sex, repeated measures factor (sequence of intervals in the order B - A1 - A2) and their interactions as explanatory variables there was no effect of parental sex on the duration of feeding intervals (repeated measures ANOVA: $F_{1,36}$= 1.05, P=0.31). Therefore, BFIs of each type were averaged over the two parents. There was a significant difference in the average duration among the three types of BFI under consideration (effect of repeated measures factor; $F_{2,54}$= 9.65, P=0.0003). In particular, the duration of BFI increased markedly after the parent gave an FC (B vs. A1 in Fig. 2; ANOVA planned comparison: $F_{1,27}$=31.47, P<0.00001), indicating that the parents slowed down their PPR immediately after the chicks showed no food-begging behaviour. Feeding intervals became shorter after the chicks resumed begging (A1 vs. A2 in Fig. 2; ANOVA planned comparison: $F_{1,27}$=

Table 1. Total feeding visits, visits where the parent gave feeding calls and feeding call rate in the two experimental treatments.

	Visits	FC-Visits	Feeding call Rate* Median (quartiles)	*n*
Control	1043	102	0.058 (0.000; 0.248)	20
Food-supplemented	766	125	0.063 (0.050; 0.280)	19

*Feeding call rate is calculated for each nest, over a 1.5-h videotaping session. When two sessions were available for a nest, one was chosen randomly and included in the calculations. *n*= number of nests.

5.36, P=0.028), so that the parents returned to levels of PPR comparable to those before giving FCs (B vs. A2; ANOVA planned comparison: $F_{1,27}$= 2.39, P=0.13).

On average, food-supplemented parents stayed away from their nest as long as control parents (repeated measures ANOVA: $F_{1,27}$= 0.88, P=0.36). However, there was a difference in the way parents of the two experimental groups responded after giving FCs, as suggested by the interaction between treatment and repeated measures factor ($F_{2,54}$= 6.43, P=0.003). Control parents increased BFIs more than supplemented parents after giving FCs (Fig. 2). This was due to the BFIs of type B being much shorter in control than supplemented nests (ANOVA planned comparison: $F_{1,27}$= 7.34, P=0.011). The difference reflected the lower provisioning rate in food-supplemented parents found in previous work (Grieco 1999, F. Grieco & A. J. van Noordwijk, unpublished data).

When the chicks resumed begging, control parents stayed away from the nest for long time, so that A2 was as long as A1 (ANOVA planned comparison: $F_{1,27}$= 0.54, P=0.47), but still longer than B ($F_{1,27}$= 16.24, P=0.0004; Fig. 2). On the contrary, food-supplemented parents returned to the nest sooner, so that type-A2 BFIs were similar to those of type B (Fig. 2; ANOVA planned comparison: $F_{1,27}$=2.40, P=0.13). Thus it appears that food-supplemented parents resumed the usual high feeding rate much sooner than controls. This was confirmed when I extended the analysis to three more intervals after A2. Table 2 shows comparisons between the B interval and each of those after A2. For control nests, A3 intervals were

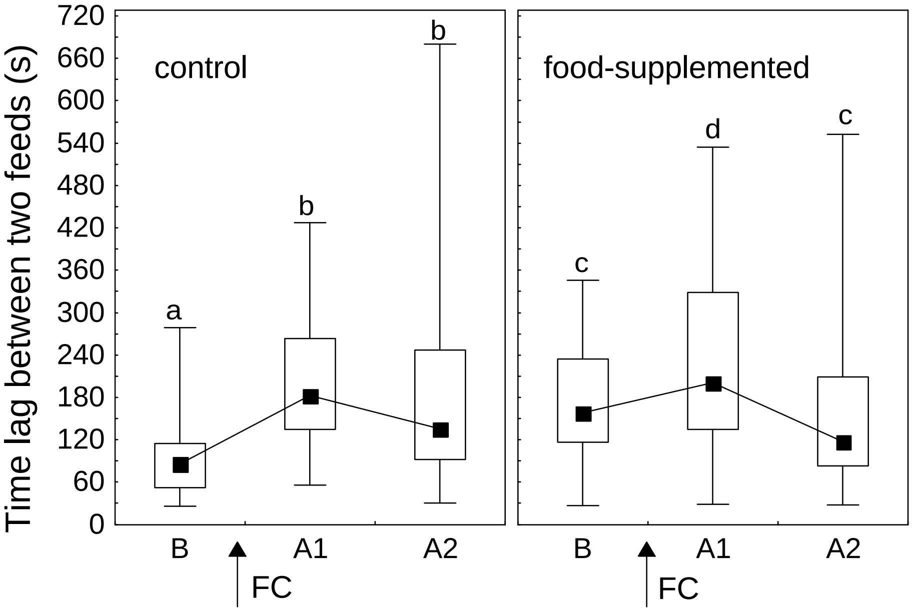


Figure 2. Duration of between-feed intervals at three visits by the parents (see black arrows in Fig. 1). (B) BFI before a visit where the parent gave the feeding call, (A1) BFI after an FC visit, and (A2) BFI for the first visit after the one where the nestlings resumed begging. Nests were included where BFIs of all three types were available. Filled squares: medians; boxes: 25%-75% ; bars: range. Different letters on bars indicate significant differences between samples in planned comparisons: a-b, $p<0.0005$; c-d, d-c, $p<0.05$.

still longer than B, and even A4 tended to be so. This suggests that control parents returned to the usual provisioning rates after the third or fourth visit after an FC visit. Food-supplemented parents, on the other hand, did not change the time away from the nest in that sequence, confirming that they had returned to the high feeding frequency earlier on.

Effects on Prey Type and Size

Figure 3 shows the type of prey items delivered immediately before and after giving feeding calls. During the visits when the parents gave FCs, the parents always brought a meal to the nest. In most instances this was a larva (row B in Fig. 3). The nestling diet differed among the three types of BFIs, but only in female parents (Chi-square test: females, $\chi^2_6= 17.57$, $P=0.007$; males, $\chi^2_6= 8.14$, $P=0.23$; after grouping counts of

Table 2. Comparisons of duration of between-feed intervals (in seconds) between immediately before giving a feeding call (B) and each of three intervals after A2. Changes are the differences between A3, A4 and A5 and B (positive values indicate that the interval concerned is longer than B). Matched pairs *t*-tests are performed on log transformed values.

	Control			Food-supplemented		
B	Change ± SD (*n*)	*t*	P	Change ± SD (*n*)	*t*	P
A3	+152 ± 232 (16)	-4.59	0.0004 ***	-29 ± 117 (13)	1.22	0.25
A4	+209 ± 330 (14)	-2.04	0.06	+77 ± 283 (10)	0.25	0.81
A5	+77 ± 195 (13)	-0.40	0.70	+56 ± 265 (8)	0.26	0.80

small and large unidentified items). After giving FCs, females took relatively fewer larvae, more unidentified items and more often no items at all than before (B vs. A1 in Fig. 3; Chi-square test: χ^2_3= 14.28, P=0.003). After the chicks started begging again, females tended to bring more larvae and other arthropods and fewer items that were not identified, but the difference was not significant (A1 vs. A2 in Fig. 3; Chi-square test: χ^2_3= 7.47, P=0.06).

The reduced feeding effort after an FC visit also led to rapid changes in the size of prey delivered. The size of larvae was not affected by parental sex in a model with treatment, parental sex and repeated measures factor and their interactions as explanatory variables, therefore the average value of RPS for each nest was used. There was a general tendency of RPS to increase after the parent gave an FC (Fig. 4), but I found no within-subject change in prey size along the sequence of feeding visits (repeated measures factor: $F_{2,38}$= 1.09, P=0.35). The greater variances in prey size brought at the end of intervals A1 and A2 (Fig. 4) was due to the higher proportion of large items that were underrepresented in the B sample. For instance, larvae with RPS greater than 0.1 were brought by 32.3% and 26.9% of the pairs at the end of A1 and A2 intervals respectively, and by only 12.1% of the pairs at the end of B intervals. This suggests that the reduced feeding effort could somehow lead birds to have access to larger larvae. Food-supplemented parents brought slightly larger larvae than controls, but the difference was not significant (repeated measures ANOVA:

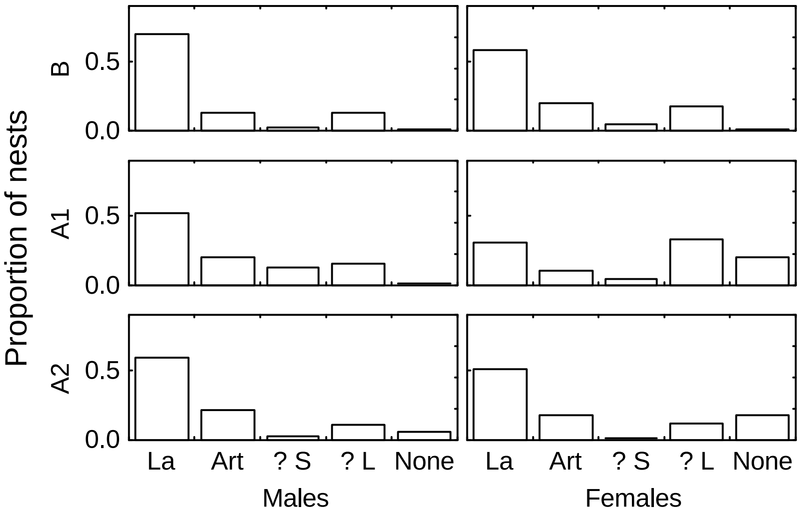


Figure 3. Composition of prey delivered to the nestlings at three visits by the parents (see white arrows in Fig. 1): (B) a visit where the parent gave the feeding call, (A1) a visit after an FC visit, and (A2) at the first visit after the one where the nestlings resumed begging. Each nest is represented by one feeding event for each type B, A1, A2, randomly chosen among those available (more intervals of one type were usually available in a videotaping session). Prey types: La, larvae; Art, adult arthropods; ? S, unidentified, smaller that bill width; ? L, unidentified, larger that bill width; None, no prey brought to the nest.

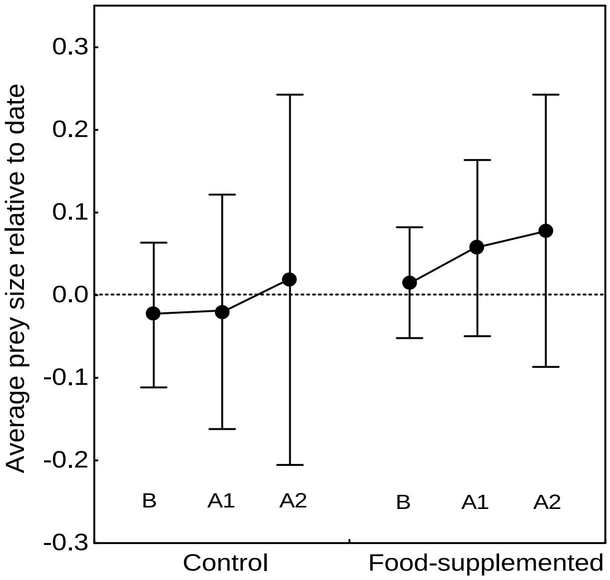


Figure 4. Average (± SD) prey size, at three feeding visits: (see white arrows in Fig. 1): (B) when the parent gave the feeding call, (A1) a visit after an FC visit, and (A2) at the first visit after the one where the nestlings resumed begging. Nests were included where visits of all three types were available. Prey size is expressed as deviation from the value expected at the date when filming was done.

Table 3. Paired comparison between values of size of larvae delivered by parent Blue Tits immediately before (B) , after (A1) performing feeding calls and after the first subsequent visit (A2) where parents did not give FCs (see Fig. 1). Prey size is expressed as deviation from the value expected at the date when filming was done.

BFI types considered			mean ± SD		number	*t*	*P*
(1)		(2)	(1)	(2)	of pairs		
B	-	A1	-0.041 ± 0.098	+0.005 ± 0.140	30	-1.959	0.06
A1	-	A2	+0.024 ± 0.126	+0.052 ± 0.189	21	-0.690	0.50
B	-	A2	+0.002 ± 0.087	0.033 ± 0.140	23	-0.87	0.39

$F_{1,19}$=1.67, P=0.21; the effect of treatment was significant when all measurements of larvae brought during a videotaping session were considered; F. Grieco & A. J. van Noordwijk, unpublished data). However, the lack of statistical evidence for the change in RPS along the sequence of visits could be due to the repeated measures design. In fact, only observation units (i.e., nests) were included where prey values were available for all three types of intervals (B, A1 and A2). For several sessions, one or more values in the sequence were missing because prey size could not be measured at the end of a certain visit (either size was not measurable or prey was not a larva). These sessions were not included in the analysis, reducing the sample size. I therefore compared RPS in sets of pairs, i.e. B vs. A1, A1 vs. A2, and B vs. A2. The results of the three comparisons are shown in Table 3. Parents returning after giving an FC brought a larva slightly larger than in the immediately preceding visit (B vs. A1, Table 3). The difference in RPS was significant in larvae brought by food-supplemented parents (Paired *t*-test on RPS at the end of B vs. A1: t_{16}= -2.214, P=0.04), not by controls (t_{12}= -1.066, P=0.31). The size of larvae taken at the end of interval A2 did not decrease relative to those brought at the end of A1 (Table 3), contrary to what would be expected from the shortened BFI at least for supplemented parents (t_{11}= -0.48, P=0.64). Nor was there a significant change in size of larvae in the following visits. For instance, the RPS of larvae brought at the end of intervals A1 and A2 was similar to that at the end of A4 and A5 (Paired *t*-test with RPS at the end of A1 and A2, and of A4 and A5 pooled respectively: t_{18}= -0.92, P=0.37). Therefore, I could not find evidence, for either supplemented or control nests, that prey size decreased when the parents resumed a high feeding frequency.

DISCUSSION

Short-Term Regulation of Provisioning Rate

Parent Blue Tits regulate their time spent away from the nest as response to changes in the interaction with the brood. A strong increase in the time to the next visit occurred after the parent gave a feeding call. The question is now whether it was the offspring behaviour (absence of begging) or the feeding call *per se* that induced changes in provisioning rates. Such question may be answered if there were cases when the parent did not give FCs after the chicks did not beg for food. Unfortunately this is not the case, however an increase of the time spent away was apparent even when FCs were not given. Sometimes the male entered the nest box with a food item when the female was brooding and delivered it to her without giving any FCs. In two nests, the female ate the prey in some of those instances. Curiously, the male stayed away for long time before the next visit (13 and 18 minutes, longer than the average BFI for those males, approx. 1 and 4.5 minutes respectively). These few cases do not allow to draw firm conclusions, however it seems (as it is reasonable to guess) that the parent is reacting to the behaviour of the brood or its partner, nor to its own behaviour.

The response to the absence of begging was much stronger in control than food-supplemented parents. This was due to the usually short feeding intervals for control parents, which reflected the higher provisioning rate in this group (Grieco 1999; F. Grieco & A. J. van Noordwijk, unpublished data). On the contrary, food-supplemented parents usually stayed away for longer time, and did not slow down their provisioning rate as much when the offspring stopped begging (Fig. 2). This may indicate that there was some upper limit for the time the parents could spend away from the nest. Leaving the brood for a longer time may be costly in terms of predation risk (e.g. Martindale 1982; Martin 1987; Soler & Soler 1996), or cooling of the nestlings (e.g. Betts 1955; Haftorn 1973). The fact that female Blue Tits significantly returned more often empty-billed when the chicks stopped begging may mean that this cost is reduced with the presence of the parent, even if it does not bring a food item (Houston & McNamara 1985).

When the parents returned to the nest (i.e. end of A1 in Fig. 1), they could either find the chicks well nourished and quiet, or otherwise again begging for food. In the latter case, the parents reduced the time spent in the next foraging trip. Therefore, the parents resumed a higher visiting rate as soon as the chicks started begging again. However, this response was clear only in food-supplemented nests. Control parents took a few more visits to resume the usual provisioning rate. A plausible reason for the slower response of control parents might be that returning to high feeding rates was limited by the performance of other, non-parental activities such as self-feeding. This is a reasonable assumption since food-supplemented parents had access to an extra-food source and consumed a great proportion of it, instead of giving it to the chicks. Those parents took on average 16 extra-food items per hour, but delivered only 15% of them (range 0 – 100%) to the offspring. The remaining proportion was assumed to be wholly consumed by the adults (they usually took an item away when leaving the nest). Observations at the nest made in 1998 support the view that the adults consumed the food taken away. If self-feeding implied an important time constraint, a reduced chick-feeding effort would cause birds to spend significant part of time looking for their own food. Control parents would need to spend more time self-feeding, and therefore would return to a high provisioning rate with some delay compared to parents enjoying an extra food resource.

The immediate changes in the between-feed intervals after FC visits lead us to the conclusion that the parents continually updated their estimate of offspring condition and adjusted their provisioning rate accordingly. Moreover, the magnitude and the duration of these short-term changes were affected by the state of the parent.

Provisioning Rate and Prey Choice

Female Blue Tits responded to the interruption of begging by visiting the nest with no meal at all. On the other hand, male parents kept on bringing a large proportion of caterpillars, while empty-billed visits were extremely rare. Thus, male and female parents differed in the strategy adopted to cope with the reduced need of the offspring.

Male Blue Tits maintain a constant proportion of food components between years, while females vary those components, for instance by bringing more non-caterpillar prey in bad years (Bañbura *et al*. 1994). Female Blue Tits, therefore, appear to be more flexible than males in the response to brood demand and food availability, both in short- and in long-term scales.

The reduced provisioning effort may have caused a change in prey choice in terms of size of items *within* a type. A slight, though not significant increase in the size of larvae was found between the visit when the parents gave a feeding call and the subsequent one. The parents appeared to bring large larvae that were underrepresented in the previous visit when they returned sooner to the nest. The increase in prey size was significant in food-supplemented, but not in control parents. If we assume that longer time away from the nest allows for accessing larger prey, the latter finding is contrary to what would be expected, because control parents increased much BFIs after giving a feeding call. However, the result may be interpreted in the light of the fact that control parents resumed high provisioning rates with more delay than supplemented parents after the chicks started begging again (see above). The fact that control parents did not bring larger larvae after an FC visit is in agreement with the possibility that these used a greater fraction of time for self-feeding than supplemented parents. Control parents would therefore have relatively less time to bring larger food items even though they stay long away from the nest.

The large size of larvae brought when the chicks resumed begging (prey at the end of A2 and subsequent intervals) is in contrast with the reduced time spent away from the nest, at least in food-supplemented pairs (compare Fig. 2 and Fig. 4). Apparently this is contrary to the hypothesis that more time could lead to access to large prey. A possible explanation for this is that parents may have returned to the preceding feeding site after catching a very profitable prey. Repeated visits to the same site are known for tits (Smith & Sweatman 1974; Naef-Daenzer & Keller 1999) and provide a considerable foraging gain to the birds. Thus the reward coming from the use of longer searching time (prey at the end of A1 in Fig. 4) might have been carried over to the next visit through repeated visits to the same feeding site.

There are essentially two ways a foraging bird may deliver larger food items to a central place if it stays away from the nest for longer: (1) the forager can travel further from the nest and, assuming that feeding sites further from the nest are exploited less (Andersson 1981; Naef-Daenzer 2000), it will be more likely to find larger prey, even if the foraging rule (i.e., minimum acceptable prey value, Lessells & Stephens 1983) does not change. A difference in prey size would be simply an artefact of the prey distribution in the environment. Alternatively, (2) a forager can use more time in searching for food, and reject a larger proportion of small or poor quality food items during each foraging bout. In other words, the forager will increase its selectivity. Hypothesis (1) assumes that the time away from the nest is a function of travel time, otherwise this mechanism could not explain the increase in the total time spent away. However, in a parallel study involving direct observations of Blue Tits while searching for food, the time between two feeds was strongly correlated with the time that the bird spent in the tree canopy within a foraging bout (r= +0.969, n=15 nests, P=0.0008). This indicates that the variation in BFIs was primarily explained by variation in search time. In contrast, there was no correlation between BFIs and the time employed in other activities than food searching, of which travel time was presumably the main component. From these findings one may conclude that the longer time spent away after an FC-visit was mainly due to the longer food-searching time. Consequently, the tendency for an increase in prey size following the reduction in provisioning rate could be explained by an increase in selectivity. The possible effect of differential allocation of searching time on food selectivity was also suggested by Hurtrez-Boussès *et al.* (1998) where female, but not male, Blue Tits in experimentally-deparasitized nests spent less time in nest sanitation, had longer foraging bouts and were more selective than control, parasitized nests. An increase in food selectivity of the parents is therefore the most likely explanation for the increase in prey size observed after cessation of the begging activity of the brood.

ACKNOWLEDGEMENTS

I thank the Board of the National Park 'The Hoge Veluwe' for permission to carry out fieldwork. Piet Drent provided the larvae for the experiment. Discussions with Rüdiger Cordts, Patsy Haccou, Kate Lessells, and comments by Sue Healy, Arie van Noordwijk, Tracey Parrish and two anonymous referees greatly improved the manuscript. This work was funded by the European Commission with a Marie Curie Fellowship (n. ERB FMBICT 971939).

Chapter 6

Effects of food availability on nestling growth and body asymmetry in the Blue Tit (*Parus caeruleus*)

Fabrizio Grieco

ABSTRACT

Growth patterns of nestling Blue Tits were studied in relation to food availability and hatching order. Two kinds of experiments were carried out in three years. In the first two years, food was offered to parents in their nestling-rearing phase. Nestlings in food-supplemented broods grew faster than control nestlings, but reached the same body mass, body condition index (i.e. residual of body mass on tarsus length) and tarsus length when close to fledging.

In the third year, the additional feeding experiment was carried out together with manipulation of hatching spread. In each nest, hatching of three eggs was experimentally delayed of about 3 days. Asymmetry of tarsi and wing feathers was also measured. Food-supplemented nestlings did not grow faster than controls, but their tarsi were more symmetrical than those of control nestlings. On the other hand, control nestlings tended to grow their wings faster than the food-supplemented ones. Last-hatched nestlings reached lower body mass and condition and suffered higher greater mortality than their first-hatched siblings, but they had tarsi and primary feathers of similar size. Food supplementation did not improve growth and survival prospects of last-hatched nestlings. The results suggest that higher food availability caused nestlings to devote more energy and/or nutrients in the control of developmental precision. In unmanipulated conditions, most of the resources are conveyed into the fast growth of traits with high fitness value for newly-fledged birds.

INTRODUCTION

In birds, postnatal growth rates vary not only among species, but also among populations of the same species (Ricklefs 1983; Gebhardt-Henrich & Richner 1998). Differences in growth rates can reflect genetic adaptations to different environmental conditions. While studies on poultry have shown that growth rates may be heritable (Singh *et al*. 1991), most studies of natural populations have failed to find significant genetic variation for growth parameters, except for asymptotic size (e.g. Gebhardt - Henrich & van Noordwijk 1994; Smith & Wettermark 1995). Most of the variation in growth curves has to be related to factors in the rearing environment, primarily food availability (Ricklefs 1983, Martin 1987). In many studies, the effect of food on growth has been tested through the indirect effects of brood size on the amount of food delivered per nestling. Experimental enlargement of broods has often shown that offspring growth and production decreases with increasing brood size, suggesting that food is limiting at greater than normal brood sizes (review in Martin 1987; for tits *Parus* spp. see e.g. Perrins 1965, Nur 1984b, Kunz & Ekman 2000). However, these studies do not address the question whether growth in normal conditions, and for normal-sized broods could be enhanced if more food were available to the parents. The existence of food limitation when energy demands are increased does not necessarily indicate that food was limiting at observed levels. This may be investigated more directly by providing the parents with extra food (e.g. Martin 1987, Simons & Martin 1990). A crucial test would be to combine food supplementation with manipulation of food requirements by the nestlings *within* a brood. By experimentally delaying the hatching of part of the clutch, it is possible to have nestlings of different age and size without the need of cross-fostering. Nestlings within broods compete for food (Godfray 1995b; Kacelnik *et al*. 1995), and small siblings suffer more starvation than large ones (Neub 1979, Magrath 1991; see Löhrl 1968 for behavioural mechanisms in tits). By comparing the growth of first-hatched chicks with that of last-hatched ones in different feeding regimes one should be able to see whether increased food availability reduces the competitive gap between siblings of different age and size. This would result in a reduction of the difference in growth rate between large and small siblings (van Noordwijk 1988, 1991).

Most studies of growth patterns in birds have focused on growth rate and final body mass of nestlings. However, little is known about the factors influencing the precision of development of bilateral traits such as tarsi and wing feathers. Fluctuating asymmetry (Ludwig 1932, van Valen 1962, Palmer & Strobeck 1986) is a measure of the ability of an organism to undergo identical development of bilateral characters on both sides of its body. Most studies on the effects of stress on fluctuating asymmetry are correlative, and, among the experimental ones, very few investigated the effect of food, primarily in insects (review in Bjorksten et. al. 2000). Among birds, manipulation of food availability affected asymmetry of feathers in adults (Nilsson 1994b, Swaddle & Witter 1994), but virtually no information is available on the effects of food quality or quantity on asymmetry during nestling growth.

In this paper, I have examined the effects of food supplementation on the growth of the Blue Tit *Parus caeruleus*. The reproductive success of this species is dependent on the abundance of insect food, primarily caterpillars, which markedly vary during the breeding season (e.g. Gibb & Betts 1963, Nur 1984b, Perrins 1991, Dias & Blondel 1996). If parents are constrained in the amount of energy and/or nutrients that they can deliver to the offspring, food supplementation is predicted to result in faster growth rate and/or greater body size at fledging. In addition, an increase in food availability is predicted to decrease asymmetry of bilateral characters (Nilsson 1994b). However, the way resources are directed to the growth of different traits may not be the same in different environments. In some traits with high fitness value for young birds, growth may be protected against periods of food shortage more than in others by means of active mechanisms of resource allocation (Nilsson & Svensson 1996a, Kunz 1999). I thus looked at whether greater food availability led to growth patterns that could reflect use of more resource in usually non or less protected traits. (e.g. tarsi vs. flight feathers). For instance, if protection of growth and control of precision was greater in flight feathers than tarsi, we would expect a greater effect of the experiment on the latter (e.g. longer or more symmetrical tarsi). The effect of food addition on growth patterns has been analysed *between* nests (effect of treatment) as well as *within* nests (interaction between treatment and hatching hierarchy). Greater availability of food should reduce the competitive gap between nestlings of different age.

METHODS

The study was carried out in the National Park 'De Hoge Veluwe', central Netherlands, in a mixed-deciduous forest patches provided with nest boxes. The patches were habitats on poor sandy soil dominated by Scots pine *Pinus silvestris*, European oak *Quercus robur*, Birch *Betula pendula*, with some occurrence of American oak *Quercus borealis* and Beech *Fagus sylvatica* (van Balen 1973). The study area contains 400 nest boxes. Supplementary feeding experiments were carried out in the years 1997 to 1999. In addition, hatching spread was manipulated in 1999 for all boxes involved in the feeding experiment.

Supplemental feeding experiment

Mealworms (*Tenebrio molitor*, family *Tenebrionidae*) and larvae of waxmoth (*Galleria mellonella*, family *Pyralidae*) were offered from the date of hatching of the first egg (day 0) to the date of fledging of the young. At early chick ages (day 0 to 6), food consisted of a mixture of the two species, while afterwards it was composed of mealworms only. The amount of food daily offered was calculated as one half of the estimates of food consumption of nestling Blue Tits (Gibb & Betts 1963). The daily food amount increased approximately linearly from day 0 to day 10, then levelled off around 20 g/day for a 12-chicks brood. Adjustments in quantity were made for smaller and bigger broods. The larvae were placed in small trays (5.5×3.5×4.5 cm) inside the nest boxes to prevent other birds than the focal adults to consume them. Feeding trays were replenished each day according to the scheduled amount. Half of the boxes were food-supplemented (FS), while the other half were not and served as a control. Food-supplemented and control boxes were chosen randomly within pairs in order to have the same range of hatching dates. Effort was made to assign different treatment levels to boxes in similar habitats. In 1998 and 1999, I videotaped the adults feeding the young at the nest (more details in Grieco 1999), so that the rate of extra-food consumption could be assessed.

Hatching order manipulation

Nests were checked every morning in order to mark each egg individually. At the start of incubation (i.e., the day the female was found brooding the eggs or the nest cup was found open and warm), three eggs (number 3, 4 and 5 in the sequence) were removed and placed in a small glass tube 3.5 cm high, × ∅ 2.8 cm, together with some moss to prevent them from rolling. The tube and the eggs were then placed in a corner of the box, and covered by nest material. Removed eggs were turned once a day to prevent egg content to deposit on one side. Two days after the removal, eggs were returned to the nest cup. This was done in the late afternoon, i.e. around 1800. Given that the female was assumed to have started the incubation the evening before she was found in the nest, the total time the female had not warmed the three delayed eggs was approximately three days.

Nests were checked daily for hatching. The manipulation created a difference in hatching date between non-delayed nestlings (henceforth called First-hatched nestlings, FHNs) and delayed nestlings (Last-hatched nestlings, LHNs). The delay, expressed as the number of days between hatching date of the first eggs of the delayed and non-delayed groups was 3.6±0.8 (SD) days (n=19). Control and food-supplemented broods did not differ in this time lag (t_{17}= -1.28, P=0.22). Nor did they differ in the mean number of eggs hatched out of the three delayed (average 2.0±1.0, t_{20}= -1.54, P=0.14).

Measurements

In 1997 and 1998, nestlings were weighed with a pesola spring balance to the nearest 0.1 g at 6, 10 and 14 days after hatching of the first egg, and their left tarsus was measured (to the nearest 0.05 mm) only at day 14.

In 1999, nestlings were weighed at the same ages as in the previous years, while left and right tarsi and eighth primaries (P8; to the nearest 0.5 mm) were measured at day 10 and 14. Last-hatched nestlings were measured at 6, 10, and 14 days after hatching of the first delayed egg. The portion of the shaft (SH) where the barbs distended out at that age was also measured. A feather development index (FD) was calculated as the ratio SH / P8.

For tarsi, primaries and their FD index, asymmetry was defined as the unsigned difference between the right and the left side (|R-L|). This index included measurement error since I did not take multiple measurements. For all paired variables, signed difference (R-L) was distributed normally (Shapiro-Wilk test, all $P>0.10$), its mean did not depart significantly from zero (one-sample t test, all $P>0.50$), and was not correlated with trait size within nestling age (correlation, all $P>0.10$). Therefore, no size correction of asymmetry index was applied.

In all years, nestlings were ringed six days after hatching of the first egg. In 1999, LHNs were ringed six days after hatching of the first delayed egg in the brood.

Statistical Analysis

Because of the hatching order manipulation in 1999, the analysis was done separately for the years 1997-1998 and 1999. All variables were analysed with repeated-measures analysis of variance (RMANOVA) in Statistica 5.5 (Statsoft 1999), where nestling age (in days after hatching) was the repeated-measures factor. An index of body condition was calculated for each nestling as the residual from the regression of log body mass on log tarsus length. This was done since body size corrected for linear size has been considered as a good predictor of lipid reserve (Johnson *et al*. 1985; Blem 1990; Merilä & Svensson 1997). Nests were the unit of observations, and mean brood measures were entered in the analysis. Effect of hatching order (HO) was tested by introducing the factor HO, with levels 0 for FHNs, and 1 for LHNs. Thus, nests with both nestling types were represented by two data points. Because in several nests LHNs died before the scheduled date of measurement or none of the three delayed eggs hatched, those nests were represented by one data point relative to HO=0. These were the majority of nests at day 14 (12 of 20). To further test for effect of hatching order, paired *t*-tests were performed between growth variables of LHNs and FHNs within broods. If the effect of HO was not significant, the effect of food supplementation was assessed by considering one data point per brood, i.e. by averaging the trait measurements of all the nestlings of each brood.

Body mass, tarsus and primary length and feather development index were normally distributed, while unsigned asymmetry indexes were usually not. In this case, they were log transformed (Y'= log(Y+0.5)), while body condition index was cubic-square transformed.

For all analyses, hatching date was expressed as departure from the median of the population in that year. Mean parental tarsus was used to estimate parental skeletal size. This and brood size, standardized hatching date and their squares were considered as covariates and were entered in the models together with the interactions with factors. Non significant variables and interactions were removed from the models.

RESULTS

Food consumption

From direct observations and videotaping at the nest, I observed parent Blue Tits eating the provisioned larvae or delivering them to the young at each supplemented nest. Food consumption was total (i.e. 100% of the mass daily offered) in 468 (67.7%) of the 691 nest feeding days. The parents totally ignored the larvae in just 21 (3%) of the nest feeding days. During videotaping in 1998 and 1999, the adults took on average 16 items per hour (range 0 - 49). Extra-food consumption rate increased with age of nestlings (Spearman rank correlation: r_s=+0.45, n=39 videotaping sessions, P<0.005,), but not with brood size (P>0.1). However, the adults delivered to their young only 15% (range 0-100%) of food items taken from the tray. This proportion increased with nestling age (r_s=+0.41, n=37, P<0.02), but again not with brood size (P>0.10).

Food supplementation and growth: 1997-1998

Figure 1 shows the growth of nestlings in the two experimental groups in 1997 and 1998. Repeated-measures ANOVA on body mass showed a significant interaction between treatment and day of measurement ($F_{2,78}$= 4.24, P=0.018). Separate analyses for each of the three chick ages showed a significant effect of food-supplementation at age 10, not at age 6 and 14 (ANOVA, Table 1). Thus nestlings in FS broods accelerated growth but did not reach greater weight. At all ages considered, nestling

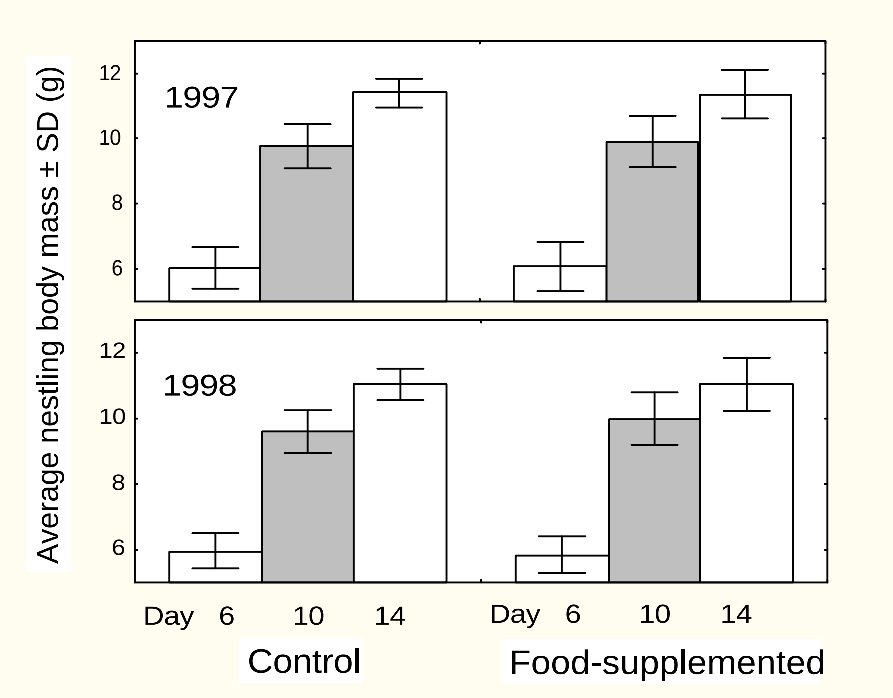


Figure 1. Body mass (average ± SD of each brood) of Blue Tit nestlings in food-supplemented and control nests in 1997 and 1998. The three adjacent columns indicate body mass at day 6, 10, and 14 after hatching, respectively. Hatched bars indicate the age at which the effect of food addition was significant, controlled for hatching date square.

Table 1. Analysis of body mass of Blue Tit nestlings at different ages in 1997 and 1998. Results refer to models with only significant variables left in. HD: standardized hatching date; HD^2: standardized hatching date square; TR: treatment. *n*, number of nests.

Chick Age (days)	Source	SS	d.f.	MS	*F*	*P*	Direction
6 (*n*=47)	HD^2	1.73	1	1.73	4.77	0.034	peak at middle dates
	Error	16.70	46	0.36			
10 (*n*=46)	TR	1.85	1	1.85	4.38	0.042	food-suppl. > control
	HD^2	4.04	1	4.04	9.57	0.003	peak at middle dates
	Error	18.15	43	0.42			
14 (*n*=46)	Year	1.86	1	1.859	6.59	0.014	1997 > 1998
	HD	1.39	1	1.39	4.94	0.032	early > late
	HD^2	2.00	1	2.00	7.09	0.011	peak at middle dates
	Error	11.85	42	0.28			

body mass was significantly related to standardized hatching date square (Table 1). The negative coefficients of the quadratic term indicated that body mass peaked in the middle of the breeding season, in both years and for both control and supplemented broods. The effect of squared date was greater at day 10 than at the other ages. In addition, a negative linear component of hatching date (Table 1) was significant at day 14, indicating that fledglings in late-hatched broods were lighter than in early-hatched ones. Food-supplementation did not change this relationship.

Nestlings in FS broods had tarsi of similar length as controls (ANCOVA, $F_{1,41}$= 1.42, P=0.24, controlled for year, brood size and mean parental tarsus), and were in similar body condition as controls (ANCOVA, $F_{1,41}$ = 0.53, P=0.47, controlled for year, standardized hatching date and its square). Compared to 1997, nestlings in 1998 were lighter, but had longer tarsi than those of 1998 ($F_{1,42}$= 10.74, P=0.002, controlled for brood size and mean parental tarsus; Figure 2). As a result, body condition index was much higher in 1997 than 1998 ($F_{1,42}$= 14.79, P=0.0005). However, the interaction treatment × year was not significant, indicating that food provision did not improve body condition even in the poorer year 1998.

Summarising, food-supplementation only affected nestling growth rate. Body mass and tarsus length close to fledging were more influenced by year and timing within the season.

Food supplementation, hatching order and growth: 1999

Body mass and condition

Contrary to what was found in 1997 and 1998, food supplementation did not increase nestling growth rate in 1999. In a repeated measures ANOVA model, with treatment and hatching order as factors, treatment and its interaction with nestling age (6, 10 and 14 days) were not significant. Instead, the interaction between HO and measurement day was highly significant ($F_{2,48}$= 5.43, P=0.008). This indicated that a difference in body mass between FHNs and LHNs emerged at certain ages (Figure 3). To investigate this difference further, I considered only those nests with both FHNs and LHNs. Within-brood comparisons showed that six-days old LHNs were as heavy as FHNs at day 6, but they tended to be lighter at later ages (Table 2). Moreover, LHNs were in poorer condition than FHNs, particularly in the middle of the growth period

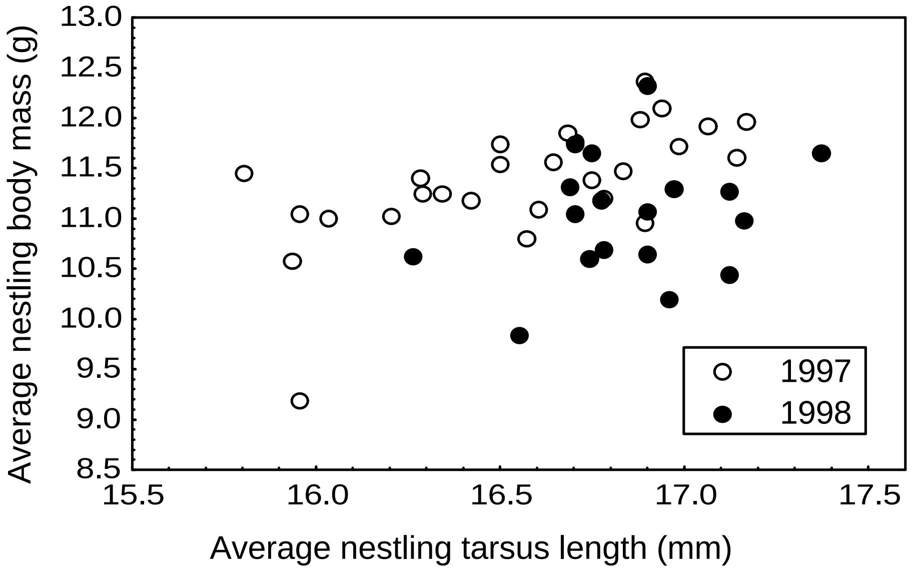


Figure 2. Body mass of Blue Tit nestlings in relation to mean tarsus length, in two study years. Each dot represents one brood. Body mass was greater in 1997 than in 1998, even within the same range of tarsus length. See also the results for body condition index.

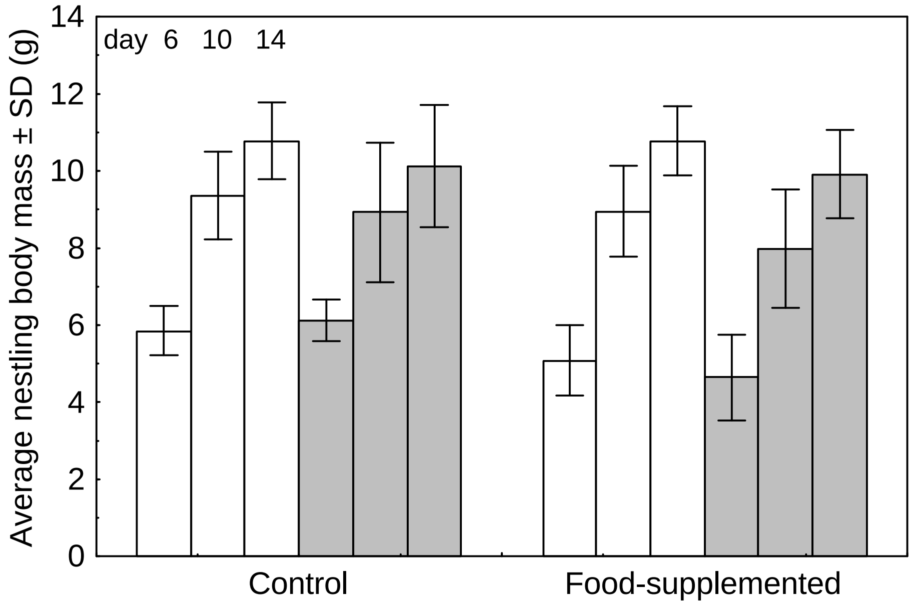


Figure 3. Mean body mass of first-hatched nestlings (FHNs, open bars) and last-hatched nestlings (LHNs, hatched bars), in control and food-supplemented Blue T it nests, at three ages (6, 10, 14 days after hatching, respectively). Age of each nestling was counted from the date on which the first egg of its group (FHNs or LHNs) hatched.

Table 2. Within-brood comparison of body size, asymmetry indexes and survival rate in first-hatched chicks (FHNs) and last-hatched chicks (LHNs) in Blue Tit broods in 1999.

Trait	FHNs	LHNs	*n*	paired *t*	*P*
Body mass (g)					
Day 6	5.66 ± 0.44	5.31 ± 1.15	11	t_{10}= 1.11	0.29
Day 10	9.51 ± 0.48	8.45 ± 1.65	10	t_9= 2.24	0.051
Day 14	11.04 ± 0.30	10.05 ± 1.34	8	t_7= 2.25	0.059
Tarsus length (mm)					
Day 10	14.95 ± 0.63	14.83 ± 0.81	10	t_9= 0.49	0.64
Day 14	16.48 ± 0.19	16.22 ± 0.51	8	t_7= 1.29	0.24
Tarsus asymmetry (mm)					
Day 10	0.18 ± 0.08	0.17 ± 0.13	10	t_9= 0.32	0.76
Day 14	0.13 ± 0.11	0.24 ± 0.26	8	t_7= -1.72	0.13
Primary length (mm)					
Day 10	13.46 ±2.11	13.23 ± 2.93	10	t_9= 0.27	0.79
Day 14	24.71 ± 1.98	25.12 ± 2.79	8	t_7= -0.43	0.68
Primary asymmetry (mm)					
Day 10	0.29 ± 0.11	0.59 ± 0.73	10	t_9= -1.34	0.21
Day 14	1.82 ± 0.78	1.92 ± 1.17	8	t_7= -0.23	0.83
Feather development *					
Day 10	0.06 ± 0.04	0.08 ± 0.07	10	t_9= -1.07	0.31
Day 14	0.45 ± 0.07	0.48 ± 0.07	7	t_7= -1.13	0.30
Feather dev. asymmetry					
Day 10	0.02 ± 0.004	0.03 ± 0.03	9	t_8= -0.20	0.84
Day 14	0.04 ± 0.02	0.05 ± 0.05	8	t_7= 0.54	0.61
Body condition #					
Day 10	0.05 ± 0.04	-0.07 ± 0.13	10	t_9= 3.44	0.007
Day 14	0.03 ± 0.03	-0.06 ± 0.13	8	t_7= 2.29	0.056
Survival	0.79 ± 0.34	0.21 ± 0.40	17	t_{16}= 5.11	0.0001

* proportion of shaft where barbs are growing; # residual from regression of log body mass on log tarsus length. Asymmetries: |R-L| for all traits.

(day 10, Table 2). This does not mean that the LHNs could catch up their siblings. Given that only runts in good condition could survive up to later ages, the gap between FHNs and LHN was reduced at day 14. The large variation in condition index of LHNs (Figure 4) was due to four broods where LHNs were of similar condition as their siblings, while LHNs in other four broods were in much worse condition. The 'good condition' LHNs were in broods with higher survival rate of LHNs (0.88±0.25, n=4) than in those broods with 'poor condition' LHNs (all 0.0, n=4; t-test, t_6 = -7.0, P=0.0004). The two groups of broods with LHNs did not differ in brood size and number of FHNs at any growth phase (t-tests, all P>0.20). Thus, there were large differences among nests (i.e. among parents or territories) both in the ability to raise runts at all, and in the ability to bring them to fledging in good condition. Yet, food supplementation did not ameliorate nestling body condition (RMANOVA, effect of treatment, $F_{1,24}$= 0.01, P=0.92), even in LHNs (Figure 4; RMANOVA, $F_{1,6}$= 0.11, P=0.75) .

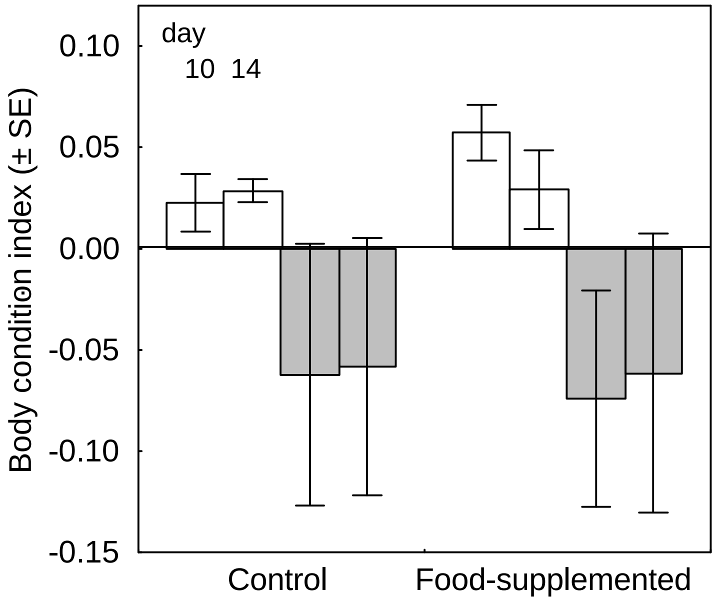


Figure 4. Index of body condition, calculated as the residual from the regression of log body mass on log tarsus length, of nestlings of different hatching order (FHN, open bars, and LHNs, hatched bars), and for control and food-supplemented nests, at 10 and 14 days, respectively. Age of each nestling was counted from the date on which the first egg of its group (FHNs or LHNs) hatched.

Tarsi

Food supplementation did not result in nestlings having greater skeletal size close to fledging in 1999, as well as in the two previous years. FS nestlings had tarsi as long as control nestlings (RMANOVA, effect of treatment, $F_{1,24}$= 2.01, P=0.17). Also, tarsus length did not differ between last-hatched nestlings and their siblings at the same age (Table 2). Thus, it appears that environmental differences within and among nests did not influence skeletal growth. However, FS nestlings were less asymmetrical than controls (RMANOVA, effect of treatment, $F_{1,24}$= 7.56, P=0.011). This effect was clear in both FHNs and LHN, as illustrated in Figure 5. The analysis was repeated on two data sets: the first, with only nests without LHNs (n=12), the other with both FHNs and LHNs (n=8). In the first group, food-supplementation decreased tarsus asymmetry significantly (RMANOVA, $F_{1,10}$= 8.34, P=0.016), while in the second the effect was similar, but not significant, presumably because of the small sample ($F_{1,6}$= 2.84, P=0.14). Thus, there is evidence that tarsus asymmetry decreased with good food conditions, independent of hatching order.

Primary feathers

Primary feathers of FS nestlings did not grow faster and were not longer at 14 days than those of controls. Rather, there was a slight tendency of control nestlings to have longer P8 at both ages of 10 and 14 days (Table 3; RMANOVA, $F_{1,18}$= 3.71, P=0.07; interaction TR×age n.s.; one value per nest included as HO was not significant). Within broods, last-hatched nestlings developed feathers of similar length as first-hatched chicks (Table 2). Similar results were found for the development index of P8. Feathers of control nestlings had barbs growing along a slightly greater portion of the shaft than FS nestlings (Table 3; RMANOVA, effect of treatment, $F_{1,18}$= 3.20, P=0.09). However, the two groups did not differ in the degree of asymmetry of P8 length and of feather development index (RMANOVA, effect of treatment, both $P>0.50$). Within broods, asymmetry of feathers was the same in siblings of different hatching order (Table 2). Therefore, it may be concluded that feather development was little influenced by experimental manipulations, both within and among nests.

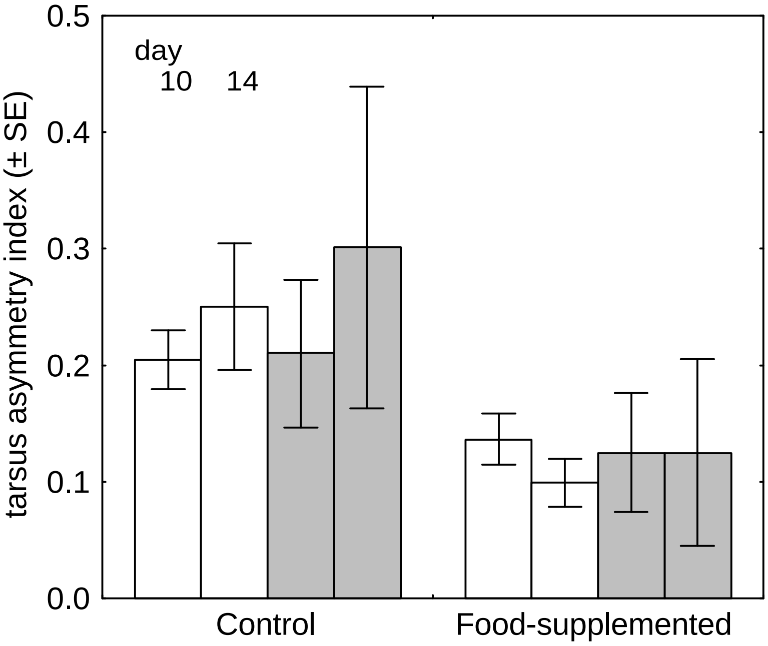


Figure 5. Index of tarsus asymmetry, calculated as absolute value of the difference R-L, of nestlings of different hatching order (FHN, open bars, and LHN, hatched bars), and for control and food-supplemented nests, at 10 and 14 days, respectively. Age of each nestling was counted from the date on which the first egg of its group (FHNs or LHNs) hatched.

Table 3. Length of eight primary feather (P8, in mm), feather development index (FD) and their unsigned asymmetry index in control and food-supplemented Blue Tit nestlings, 1999. Numbers in brackets indicate number of nests.

Trait	Day 10		Day 14	
	Control	Food-suppl.	Control	Food-suppl.
P8 Mean length	14.18±1.86 (10)	12.74±1.68 (10)	25.77±1.72 (10)	24.38±1.70 (10)
P8 asymmetry	0.33±0.15 (10)	0.27±0.09 (10)	1.44±0.72 (10)	1.28±0.84 (10)
Mean FD	0.09±0.03 (10)	0.05±0.03 (10)	0.46±0.06 (10)	0.42±0.08 (10)
FD asymmetry	0.03±0.01 (10)	0.03±0.01 (9)	0.04±0.02 (10)	0.04±0.02 (10)

FD is the proportion of the shaft with barbs distended out.

DISCUSSION

Food availability and growth in the Blue Tit

In two years out of three, nestling Blue Tits in food-supplemented broods grew faster, but did not reach greater body mass and condition than control nestlings, indicating that they enjoyed a higher food intake. This could be the result of two processes: on the one hand, food-supplemented parents delivered part of the extra food to their offspring, and increased this delivery as the nestling grew older. This also suggests that the total amount of energy that the parents must deliver to the brood is usually more constrained in this phase of growth. However, the feeding experiment may also have positively influenced nestling growth in another, more indirect way. By delivering extra-food to the nestlings and by consuming the rest, the parents presumably saved time that would otherwise be used in the search for natural food. This may have led parents to use more time to select larger (Grieco 1999) and/or better prey (i.e. green caterpillars; Grieco & van Noordwijk, unpubl. data).

In 1999, food supplementation did not affect nestling growth rate. The hatching order manipulation carried out in that year may have obscured the effect of the feeding experiment. The presence of small, last-hatched nestlings may have reduced competition for food among first-hatched nestlings, and therefore caused the latter to grow at slightly faster rates. The improvement of the feeding conditions for FHNs may have been sufficient to obscure any positive effect of food-supplementation.

Previous experimental work on birds has shown higher growth rates and/ or asymptotic weight following food addition (Simons & Martin 1990, Crossner 1977, Richner 1992, Garcia *et al*. 1993). In my study, Blue Tit nestlings grew faster but were not heavier at fledging when food was offered to their parents. This indicates that fledging body mass was not limited by food availability in those years (see also Verhulst (1994) for a similar experiment in the same area). Between-year differences in the effects of additional food on nestling growth have been interpreted as consequence of annual variation in food limitation (Simons & Martin 1990). In rich-food years, fledglings would probably not benefit from a further increase in body mass. A heavier body is not advantageous as it impairs flight performance and increases predation risk (Adriaensen *et al*. 1998). This has been considered a possible reason why very heavy tit fledglings survive less (Tinbergen & Boerlijst 1990; Lindén *et al*. 1992). Yet, nestling Blue Tits did not benefit from food provision even when food limitation was more likely to occur. In two years out of three, nestlings in early and late broods were lighter than those in intermediate ones (effect of hatching date square in Table 1; in the third year, the small range of hatching dates made it difficult to detect seasonal effects on growth). This may reflect the lower food availability for broods that are too early or too late relative to the period of maximum caterpillar abundance (e.g. Perrins 1991; Dias & Blondel 1996). If food was the main factor limiting nestling growth early and late in the season, we would expect a greater effect of food addition at early and late than at intermediate dates, i.e. an interaction between treatment and hatching date square. This was not the case in any of the growth phases considered. Perhaps the lighter nestlings in early and late broods reflected the intrinsic quality of the brood or of the parents that could not be positively affected by the consumption of additional food. For instance, last-hatched nestlings may have fledged in worse condition due to the increased infestation of *Protocalliphora* late in the season, as it occurred in 1999. The provision of food may have not fully compensated for such negative seasonal effects.

Food availability, body symmetry and its consequences

Although natural food abundance positively influences tarsus length in the Blue Tit (Kunz 1999), experimental addition of food did not have an effect on tarsus length. However, food-supplemented nestlings had more symmetrical tarsi than controls, both when 10 and 14 days old. There is little experimental work on the effect of food availability on symmetry of body traits in birds (review in Bjorksten *et al*. 2000). A study by Swaddle & Witter (1994) found that nutritional stress of adult European starlings *Sturnus vulgaris* resulted in increased feather asymmetry during development. Nilsson (1994b) demonstrated in the nuthatch *Sitta europaea* that induced tail feathers grown during winter were more symmetrical in those individuals that could have access to extra food. The results of my study indicate that, also in birds as nestlings, the degree of body asymmetry is affected by the rate of energy intake. During growth, some unknown machinery requires energy to maintain developmental precision. Especially during the phase of rapid growth, stress may reduce the energy available to this mechanism, thereby increasing FA. This explains why asymmetry increases in periods when growth rate of the trait is the highest (Teather 1996).

Contrary to tarsus, I found no evidence that food addition reduced asymmetry of primary feathers. This finding is similar to that by Björklund (1996), where Blue Tit nestlings attended by only the female (and that presumably were under greater food stress, see e.g. Sasvári 1986) had similar feather asymmetry than those in broods with two parents. Why is wing asymmetry not influenced by food stress during early development? To answer this question, let us first consider the growth of primaries. Food-supplemented nestlings did not grow their wing feathers faster than control nestlings. Surprisingly, the latter tended to have longer primaries both at 10 and 14 days. A similar, non-significant trend was found in another Blue Tit study (Kunz 1999), where nestlings growing far from the caterpillar peak date had longer wings than those growing near it. Other studies showed faster growth of wings, not tarsus or body size, in poor rearing conditions (Zach 1982, Smith & Wettermark 1995, Nilsson & Svensson 1996a). This suggests that Blue Tits adaptively accelerate the growth of wings when breeding conditions are poor. Well-developed wings are necessary for nestling tits to leave the nest, follow the parents and escape from predators more easily. Tits are especially vulnerable to predation during the first days out of the nest (Perrins & Geer 1980), when primary feathers are not yet fully grown. Also, symmetrical wings are crucial in flight performance (Swaddle *et al*. 1996, Swaddle 1997), thus we may expect wing asymmetry to be protected as well as wing growth. If control of feather symmetry imposes energy demands (Nilsson 1994b), more resources may be adaptively directed to control precision of high fitness value traits at the expense of traits of lower survival value for newly-fledged birds, such as tarsus symmetry. This might explain why primary feather asymmetry was unaffected by food provision.

There is at least another possible reason why food-supplemented nestlings had more symmetrical tarsi but not wings, apart from the possible effect of greater measurement error due to lower accuracy of wing measurements. The timing of growth differs between tarsi and flight feathers. If food stress is the highest around day 10 when body growth is the most rapid, that may have consequences on asymmetry of tarsi, which are still growing in that phase, not of primary feathers since these have just started to grow at that age. Food stress would therefore have a detectable effect only on the developmental precision of tarsi rather than primary feathers.

Symmetric body traits have been causally related to greater fitness (e.g. Møller 1994, Brown & Brown 1998; reviews in Møller & Thornhill 1998, Møller 1999). It is possible that tarsus asymmetry progressively diminished after the last measurement at day 14, so that the effect of food addition on asymmetry disappeared at fledging. However, tarsi generally grow until 14-15 days after hatching in tits (O'Connor 1977; van Noordwijk *et al*. 1988; Kunz 1999), thus compensatory growth by means of an extended growth period is constrained. As a result, factors influencing tarsus asymmetry in early development may have long lasting effects, even in other traits (Møller 1990). However, it is not known what consequences asymmetrical tarsi may have on the survival probability and mating success of the individual.

Food availability, hatching order and growth

Experimentally assigned runts survived less than their siblings, indicating that death was primarily caused by sibling competition and not by low overall food availability. Food supplementation did not reduce this competitive gap, thus the hatching spread seems to have been too large for the parents to handle. However, Kunz (1999) found no effect of natural food abundance on the difference in size between runts and their siblings, even though the difference in hatching dates between the two was smaller than in this study (2 days vs. 3.6). Thus, food availability is likely to produce little effect on within-brood differences in growth patterns. In this study, LHNs in some broods could reach the 14-day stage, but suffered lower growth rate, and were in poorer condition than their siblings. This within-brood difference in body mass and condition was not due to sibling competition being stronger than in other broods, since LHNs in poor condition were in broods of similar size as the LHNs in good condition. It is more likely that the parents differed in the ability of raising runts, independent of the feeding conditions experienced. The view that the feeding conditions did not affect within-brood variation in growth relative to hatching order is also supported by the fact that the parents did not feed LHNs more frequently when food-supplemented (F. Grieco, unpubl. data). Therefore, the parents did not modify their provisioning rules in presence of more available food.

Contrary to body mass and condition, growth of wings was not reduced in LHNs (see Kunz (1999) for a similar result). This suggests that compensatory mechanisms may allow last-hatched chicks to grow wings rapidly even in poor feeding conditions. Last-hatched nestlings that are still in the nest suffer the cost of reduced feeding rate when the parents feed nestlings that have already left. Therefore, LHNs are forced to fledge at a younger age than FHNs to avoid the risk of being fed less (Nilsson 1990) and eventually die. This may impose a pressure on LHNs to keep up in maturity with older siblings and to avoid a prolonged developmental time.

ACKNOWLEDGEMENTS

I thank the board of the National Park ‘De Hoge Veluwe’ for permission to carry out this research. Piet Drent provided the larvae for the feeding experiment. Comments by Niels Cadée and Arie J. van Noordwijk improved the presentation. This study was part of a PhD project partly funded by the University of Pavia and by the European Commission with a Marie Curie Research Fellowship (n° ERB FMBICT 971939).

Chapter 7

Blue Tits learn when best to breed

Fabrizio Grieco, Arie J. van Noordwijk & Marcel E. Visser

ABSTRACT

Timing of reproduction has large fitness consequences in many bird species (Nilsson 1999). While it is generally accepted that the start of reproduction depends on environmental cues, we show that in Blue Tits learning is also involved. Blue Tits' laying date is affected by the synchrony of their brood with the peak of nestling food availability in the previous year. We show for the first time that this is causally linked to the experienced synchrony: Blue Tits that received additional food in the nestling period altered their laying date in the next year as if they had been better synchronised. Thus learning apparently plays a role in determining the timing of reproduction and, therefore, enables the birds to cope, at least in part, with the advancement of the period of maximum food availability due to recent large scale climatic changes.

INTRODUCTION

In birds, laying date is adapted to the time of maximum abundance of food needed later for the nestlings (Lack 1954, 1955). Since reproduction starts much earlier than the time of maximum food requirement of the offspring, we expect birds to start reproduction in response to cues, available at the time of egg laying, which predict the moment of maximum food abundance (Wingfield *et al*. 1992, van Noordwijk & Müller 1994). A number of cues have been suggested that would allow birds to adaptively adjust their timing of breeding, including temperature, food abundance at the time of egg production, and phenology of the vegetation (Wingfield *et al*. 1992; Lambrechts *et al*. 1996; Visser & Lambrechts 1999; Hau *et al*. 2000). However, all these studies emphasise the importance of current environmental factors in determining phenotypic plasticity of laying date. A recent study on Great Tits (Nager & van Noordwijk 1995) suggested that laying dates were also affected by the birds' past breeding experience. Females laid later than expected in the following year when they had reared their young too early relative to the caterpillar peak in the previous season. Conversely, females laid earlier than expected when they had raised their young after the caterpillar peak date in the previous year. Direct causal evidence for an effect of past feeding conditions on laying date comes from an experiment in which we supplemented parent Blue Tits with insect larvae throughout the nestling period.

METHODS

Routine field work

The study was carried out in the National Park 'De Hoge Veluwe, central Netherlands. The area consists of plots of mixed forest dominated by Oak (*Quercus robur*) and Scots Pine (*Pinus sylvestris*) (van Balen 1973) and contains 400 nest boxes. Nest boxes were checked daily from the end of March until early May during the breeding seasons of 1997 to 2000, so that the exact day on which the first egg was laid was known. Laying date is expressed as April date, e.g. 1=April 1st, 35=May 5th.

In 1998 and 1999, adult Blue Tits were caught and weighted when the young were 7 and 14 days old.

Caterpillar peak date

Caterpillar abundance was measured from 1997 to 1999 by collecting caterpillar frass in two cheese cloth nets (van Balen 1973) placed under trees at 7 standard localities scattered over the study area. Collection started around the first of May and continued until early June, depending on when the amount of frass became negligible). Nets were emptied every three or four days, except when they were wet because of rain. Frass was dried for 24 hours at 70 °C, separated from debris and weighed to the nearest 0.1 mg. Caterpillar biomass was estimated using the formula of Tinbergen & Dietz (1994) and temperature from the KNMI in De Bilt. The values for the two nets under each tree were first averaged, and then the per tree values are averaged per date (i.e. middate between the dates on which the nets were emptied).The annual caterpillar peak date was defined as the date (expressed as April date) on which the highest caterpillar biomass was recorded.

Pre-laying additional feeding.

Female birds are subjected to energetic and protein constraints during egg formation (Perrins 1970; Houston 1998), so they may be unable to advance laying date even if environmental cues signal that advanced laying would be advantageous. To reduce potential resource constraints, all Blue Tit nests were provided with domestic fly (*Musca domestica*) pupae from the onset of nestbuilding until laying of the first egg from 1997 to 2000. Each day we offered 25 fly pupae in small feeding trays inside the nest boxes. Food supplementation started on average 8.7 days (range 5 –19) before the onset of laying. The duration of pre-laying food provisioning in number of days and the amount of food consumed did not differ between nests that also received food later in the nestling phase and those which did not (*t*-tests, both $P>0.50$).

Post-hatching additional feeding.

Mealworms (*Tenebrio molitor*) and larvae of the waxmoth (*Galleria mellonella*) were placed in small trays inside the nest box from the day of hatching of the first egg to the day of fledging of the young in the breeding seasons 1997 to 1999. Feeding trays were placed near the entrance hole, so that only the adults could take the food. In the first six days after hatching food consisted of a mixture of the two species, while afterwards it was composed of mealworms only. We provided one half of the estimated daily food consumption of nestlings (Gibb & Betts 1963). This amount increased approximately linearly from 1.0 g/day on day 0 to 20 g/day on day 10 after hatching and then levelled off at 20 g/day for a 12-chick brood. Proportional adjustments in quantity were made for smaller and bigger broods. Remaining food was replaced each day with the scheduled amount. Half of the nests were food-supplemented, while the other half served as a control. Treatments were chosen within pairs of nests with similar hatching dates. An effort was made to assign different treatment levels to nests in similar habitats.

Data treatment.

For each female that laid in two successive years we calculated (1) the difference in laying date between the two years (laying $\text{date}_{\text{year 2}}$ - laying $\text{date}_{\text{year 1}}$) and (2) the between-year difference in common environment, expressed as the mean laying date of the other females laying in nest boxes within a radius of 200 m from the focal nestbox of the female (mean laying $\text{date}_{\text{year 2}}$ – mean laying $\text{date}_{\text{year 1}}$). We calculated the regression of between-year difference in laying date on the difference in common environment ($R^2= 0.56$, $n=15$), so that its residuals were the non-environmental changes in laying date of individual females from one year to the next (Nager & van Noordwijk 1995). The degree of synchronisation between tits' breeding and the caterpillars was defined as the difference in days between day 10 of the tits' nestling period (approximately the midpoint of the nestling period) and the caterpillar peak date. Throughout the text, food-supplemented females refer to females receiving food in the nestling phase.

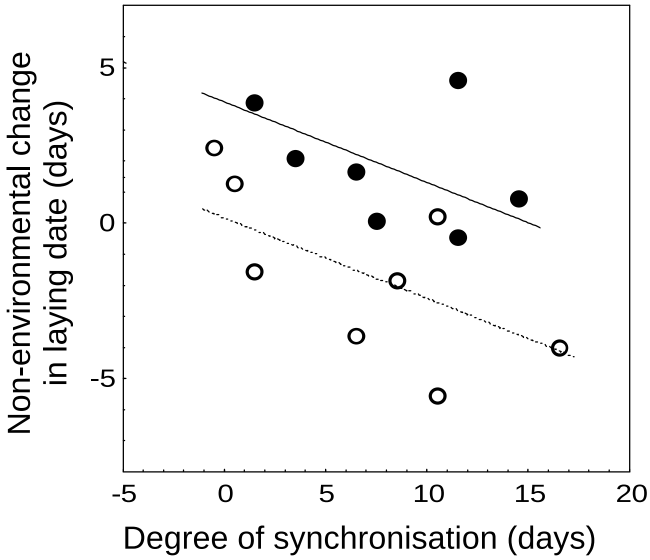


Figure 1. Effect of food supplementation on change in laying date of individual females from year 1 to year 2 (see Methods) controlled for the change in the mean laying date of the other females locally breeding against the synchronisation between their brood and peak caterpillars abundance in year 1 from 1997 to 1999. Open dots and broken line: control females. closed dots and solid line: food-supplemented females.

RESULTS

Among the females that bred in the following year, those that were food-supplemented laid at the same time or slightly later than in the previous year, corrected for changes in the environment, while females that were not food-supplemented tended to advance laying date the next year (Figure 1; effect of treatment, $F_{1,12}$= 12.38, P=0.004 after controlling for degree of synchronisation in the year of experiment). This shift was in the opposite direction from that expected if the supplemented food had acted by improving the nutritional status of the females. Food-supplemented females lost less weight during brood rearing than the control females (change in body mass of females between day 7 and day 14 after hatching: control –0.20±0.27 (n=22); food-supplemented +0.11±0.46 (n=14); t-test on log-transformed mass changes: t_{34}= -2.32, P=0.027). Weight loss in the parent may represent the cost of raising the brood (Martin 1987). Therefore, food supplemented females may have been in better condition the next year (although both control and supplemented

Table 1. Degree of synchronisation between Blue Tits' breeding season and caterpillars, in the year of the feeding experiment and in the following year.

year	Control (*n*)	Food-suppl. (*n*)	Effect of treatment
year of experiment	6.75 ± 5.92 (8)	8.07 ± 4.69 (7)	t_{13}= -0.474
following year	4.00 ± 3.21 (6)	11.36 ± 3.93 (7)	t_{11}= -3.650 **
change (paired t)	t_5 = 0.63	t_6= -2.63 *	

Synchronisation is expressed as the difference in days between day 10 of the tits' nestling stage and the annual caterpillar peak date. Paired t-tests are performed on individuals that had nestlings in both years (*n*=6 controls, 7 food-supplemented). Two of eight control females abandoned the nest before hatching the following year. *, P<0.05; **, P<0.005.

females received extra-food in the laying period, see Methods), and would therefore be expected to lay, if anything, earlier than other females in the population (Pettifor 1993; Nilsson & Svensson 1996b). This would lead food-supplemented females to advance laying more than controls while the opposite was the case. Another possibility could be that food-supplemented females may have worked harder if their young survived better than controls, therefore food-supplemented females may have been in poorer condition the next year. However, the number of young fledged did not differ between nests of the two groups (mean ± SD, control: 7.5 ± 3.3 (*n*=38); food-supplemented: 6.6±3.6 (*n*=31); $F_{1,64}$= 1.96 after controlling for effect of year and hatching date). Moreover, food supplemented females worked even less than controls as indicated by their lower feeding frequencies (Grieco 1999).

If Blue Tits used food abundance in the nestling phase as a cue to improve their timing in the following year, that is if they learn when it is best to breed, we expect food-supplemented females to be less synchronised in their next reproductive attempt, particularly in recent years when the peak date of caterpillar peak abundance has advanced (Visser *et al.* 1998). In the experimental year, the degree of synchronisation did not differ between food-supplemented and control females, but the following year food-supplemented females were a week later than controls relative to the caterpillar peak that year (Table 1 and Figure 2). This between-treatment difference in synchronisation could be the result of either of two

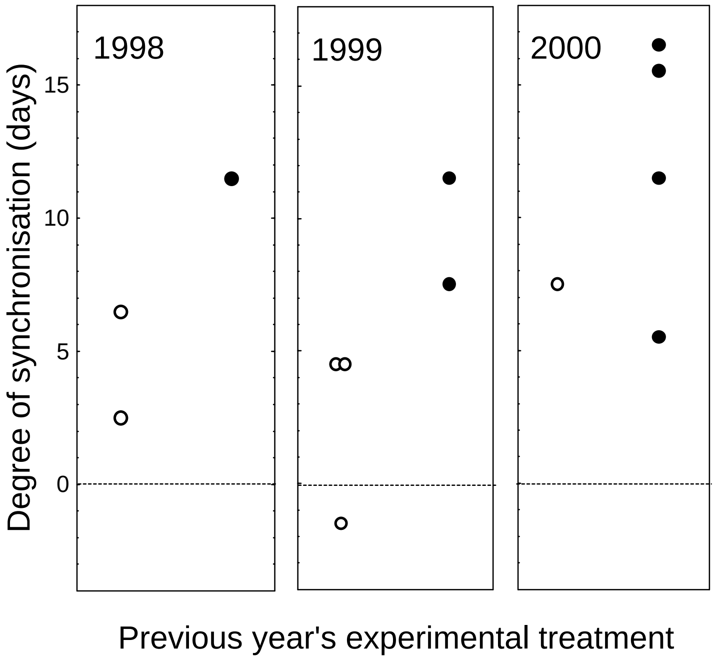


Figure 2. Effect of food supplementation on the degree of synchronisation between tits' breeding time and caterpillar peak date in the year following the experiment against the treatment in the experimental year. Open dots: control females. Closed dots: food-supplemented females. The broken line indicates full syncronisation (i.e., nestlings being 10 days old when caterpillars are at the maximum density)

phenomena: (a) control females improving the synchronisation relative to the previous year while food-supplemented maintaining substantially the same time gap; or (b) control females maintaining the same degree of synchronisation while food-supplemented females doing worse the next year. There is evidence that this latter was the case. Food-supplemented females increased their asynchrony with the caterpillars from one year to the next, while control females did not change it significantly (Table 1). Thus, the use of an extra food resource led to a mistiming of breeding the next year. This strongly suggests that natural food variation experienced by the female is involved in the fine-tuning of reproduction in tits.

Over the last two decades, spring phenology has advanced due to large scale climate change. Many bird species have advanced their date of laying over this period (McCleery & Perrins 1998; Forchhammer *et al*. 1998; Crick & Sparks 1999), but there are concerns about the ability of birds to respond optimally to environmental changes (Visser *et al*. 1998). Our findings suggest that learning the optimal time for rearing young, may contribute to the birds' ability to cope with rapid environmental changes.

ACKNOWLEDGEMENTS

We thank the Board of the National Park "De Hoge Veluwe" for permission to carry out this research in their park. Thanks to L. Holleman and P. J. Drent for providing the fly pupae and the larvae for the experiments. J. Harvey and K. Lessells provided useful comments. This project was partly funded by the University of Pavia and the European Commission with a Marie Curie Research Fellowship to F. G.

Chapter 8

General Discussion

During its lifetime an organism makes numerous behavioural decisions. Decision rules describe which of the alternative options should be taken as a function of (1) the environment and (2) the state of the individual. With regard to reproduction, several successive decisions have to be made. The first is, of course, whether to reproduce or not. To be able to reproduce an animal has to adapt physiologically and behaviourally. If reproduction is decided upon, the subsequent decision is when to start the reproductive attempt. Figure 1 illustrates the possible factors involved in this decision. Certainly, the state of the individual does determine some variation in the start of reproduction. For instance, older birds often start laying eggs earlier than young birds (Perrins & McCleery 1985; Dhondt 1989; Perdeck & Cavé 1992). The individual also responds to a series of factors in the environment. This study is about the role of these external factors, particularly the availability of food. On the one hand, the individual utilises food to gather the energy and the nutrients that are needed to produce the eggs. We can then see food as *resource* for egg formation (Figure 1). If food is scarce in the environment, the animal can find it hard to gather energy and nutrients to start reproducing at a certain time of the year, even if that would be advantageous for the offspring. The existence of energetic constraints has been invoked to explain why birds do not lay early in the season even if early breeding results in benefits for the offspring in terms of higher survival (Perrins 1970). Laying date can sometimes be experimentally advanced by providing the birds with supplementary food (Martin 1987; Arcese & Smith 1988; Boutin 1990; Nager *et al*. 1997). Also, providing extra food can result in birds laying larger eggs. In this study, birds that consumed part of the food offered laid eggs independent of temperature, while birds that ignored the food laid smaller eggs in colder days (*Chapter 2*). The fact that egg volume is dependent on the temperature and can increase with food abundance is usually interpreted as supporting the hypothesis that birds are energy-limited early in the season.

However, supplemental food not only provides additional energy and nutrients but might also act as a cue signalling that the period of maximum food abundance is near. More generally, food levels in nature could be seen as *information* that predicts the optimal period for the raising the offspring. In tits, this is thought to be the period of maximum abundance of caterpillars, the main food for the nestlings (Perrins 1991,

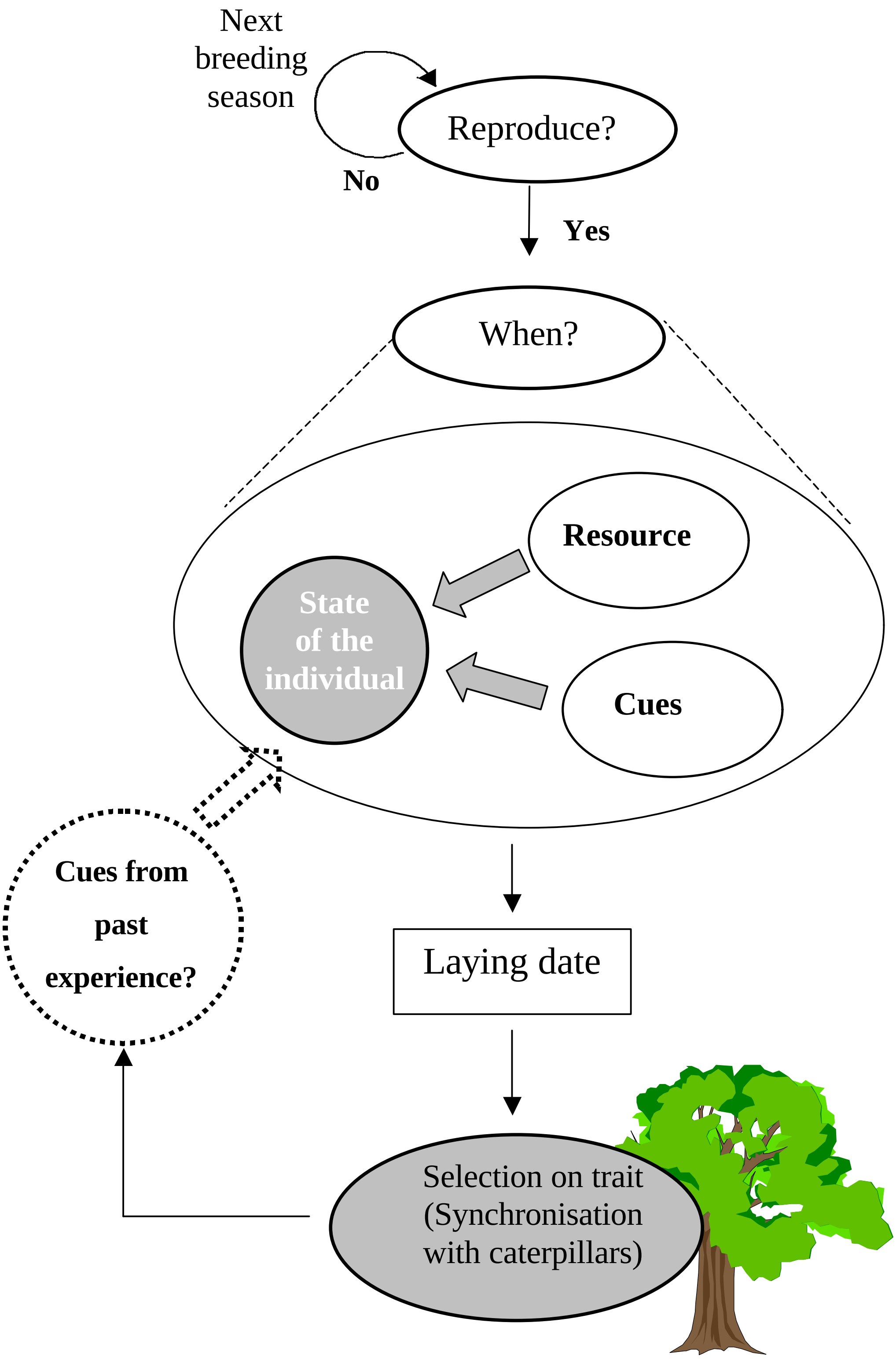


Figure 1. Reproductive decisions and possible role of food levels in the breeding phase in fine-tuning of timing of egg laying.

van Noordwijk & Müller 1994, Nager & van Noordwijk 1995). It is now established that birds use cues from the environments to time their breeding season (Visser & Lambrechts 1999; see below). One of these cues may be the appearance of specific food in the environment early in spring (Ligon 1978; Perrins 1991; Nilsson 1994; Hau *et al*. 2000).

How to cope with a seasonal environment

The temperate zone is characterised by strong fluctuations in the availability of food for organisms at the higher trophic levels, such as insectivorous birds. As it is crucial for animals to match the energy and nutrient requirements of their offspring with the availability of food, only a short period of the year is suitable for reproduction (Murton & Westwood 1977). The time within a year at which food availability peaks varies between areas and years (Perrins 1979; Nager & van Noordwijk 1995), and as a consequence the timing of reproduction will vary (Perrins 1979; van Noordwijk *et al*. 1995). As reproduction is initiated much earlier than the time of maximum food abundance, animals are expected to start reproduction in response to cues, available at the time of reproductive decision making, which predict the moment of maximum food abundance (Wingfield *et al*. 1992). However, this prediction cannot be perfect, because the environment at which the phenotype (i.e., laying date) is formed and the environment at which that phenotype is selected (nestling phase) are not tightly linked (van Noordwijk & Müller 1994). In other words, a warm period early in spring might lead birds to lay the eggs, but subsequently the weather may turn unfavourable so that the caterpillars will develop later than expected, with negative consequences on the breeding output of the birds that laid early (van Noordwijk *et al*. 1995). Birds can adjust their timing after the start of egg laying to a limited extent, for instance by varying the number of egg laid or the start of incubation (Nilsson 1994). But their potential of speeding up or slowing down is much smaller than that of the prey species.

Previous studies of laying date have concentrated on the causal factors present in the environment at the time of egg laying (Visser & Lambrechts 1999). This assumes that the birds can only rely on signals at the time laying date is expressed. However, a study on Great Tit showed that experienced females changed their laying date relative to other, neighbouring females in a way that these changes correlated with the environment at which the previous laying date was selected on (Nager & van Noordwijk 1995). The authors suggested that, since there were consistent differences in the caterpillar's timing among localities, tits could use previous breeding experience to improve their timing in relation to local caterpillar populations.

Food as information for fine-tuning laying the next year

In this thesis I have presented experimental evidence that the Blue Tit relies on information on peak food abundance gathered in a previous breeding event to time egg laying in the current reproductive attempt. Nager & van Noordwijk (1995) had shown that the non-environmental changes in laying date of individual Great Tit females from one year to the other were associated with the degree of synchronisation of the Tits' nestling phase and the caterpillar peak date. However, this was a correlative study. Direct evidence came from our experimental approach. If birds use food levels in the nestling phase as a source of information to re-calibrate their next reproductive attempt, food supplementation should cause birds to change, on average, their laying date to a lesser extent. An additional prediction would be that birds provided with food would mistime reproduction the next year, because they would use the additional food as indicator of the optimal time for raising the brood.

Food supplemented females laid later the next year, while most control females advanced laying date (Figure 2; see details in *Chapter 7*). Notice that the effect of the experimental manipulation is opposite to that expected if food acted as an energy source. Food-supplemented pairs worked less hard to raise their nestlings, as shown by the lower feeding frequency (*Chapters 3-5*). Moreover, females provided with food lost less weight during the breeding period than control females. Thus, it is reasonable to assume that food-supplemented females were more likely to be in a better than in a worse condition at the start of the next reproductive attempts. Female birds in better condition lay earlier than those in poorer condition (Drent & Daan

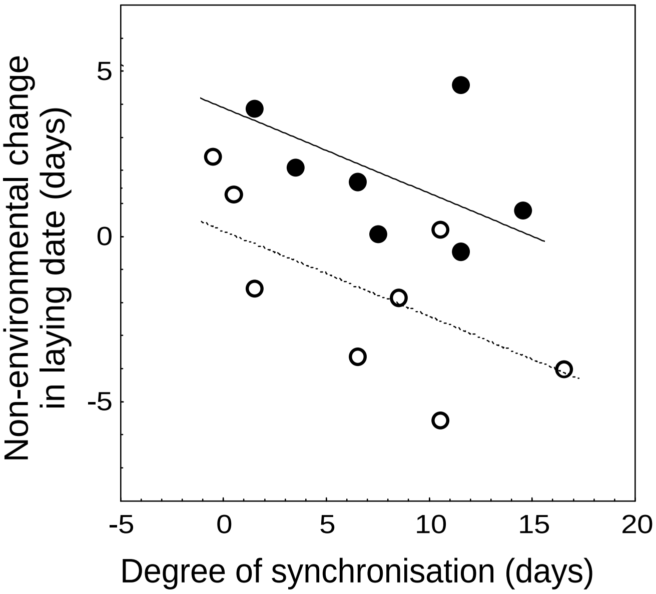


Figure 2. Effect of food supplementation on non-environmental change in laying date of individual females in the Hoge Veluwe. The non-environmental change in laying date is the residual of between-year difference in laying date from its regression on the between-year change in mean laying date of the other females laying in the same local area (see *Chapter 7*). The degree of synchronisation between tits and caterpillars is the difference between the midpoint of the tits' nestling stage and the annual caterpillar peak date. Open dots and broken line: control females. Closed dots and solid line: food-supplemented females. The interaction between treatment and synchronisation was not significant ($F_{1,11}$= 0.67, P=0.43).

1980; Price *et al.* 1988). Thus, we would expect food-supplemented birds to lay if anything earlier than control females. The results, however, show that food-supplemented females delayed laying date compared to control females. Food supplementation may decrease the female's condition next year in some indirect ways. For instance, it is likely that food supplementation increases the probability of producing a second clutch (see Verboven 1998 for the Great Tit). On its turn, producing a second clutch negatively affects survival and possibly also condition in the next year (Tinbergen & Daan 1990, Tinbergen & Dietz 1994). This was not the case in our Blue Tit population, where incidence of second broods is very low. Alternatively, food-supplemented females may have worked harder if their nestlings survived better, i.e. if they had more offspring to feed. However, there is no evidence that food-supplemented broods were larger at fledging, and furthermore, food-

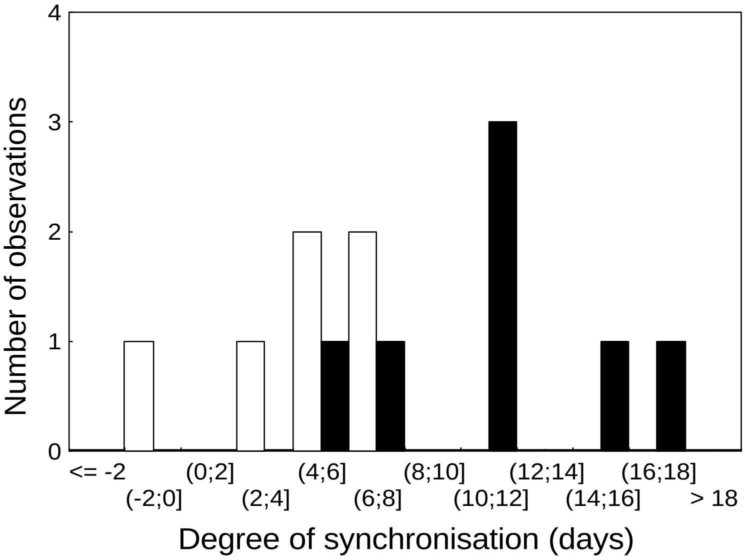


Figure 3. Frequency distribution of the degree of synchronisation between Blue Tits' breeding and caterpillars in the two experimental treatments. The degree of synchronisation between tits and caterpillars is the difference between the midpoint of the tits' nestling stage and the annual caterpillar peak date. Open bars: control females. Filled bars: food-supplemented females.

supplemented females worked less hard as indicated by the feeding rate data (Grieco 1999).

In these last few years the caterpillar peak was earlier than the breeding period of most birds. Therefore, control birds might have responded more strongly to the natural food variation in one year. These results are in line with the view that food levels experienced by the parent in the breeding period play a role in timing of reproduction the next year, independent of energetic and nutritional aspects. In line with the second prediction, females that were food-supplemented in one year were tricked in mistimed reproduction the next year. The time gap between the mid date of the nestling period and the caterpillar peak date increased from the year of the experiment to the next, and those females performed worse than controls (Figure 3). However, given the small samples involved in this study we do not know whether food-supplemented females suffered additional fitness costs in terms of reduced survival of the brood and/or lower recruitment rate of the young raised at the 'wrong' time. Numbers are simply too small to detect differences in survival and recruitment rates.

It is only possible to speculate about the mechanisms involved in the fine-tuning of the onset of reproduction. We can imagine that the female may ‘measure’ the time at which she raises the brood relative to the development of caterpillars. Given that food-supplemented females hardly change laying date, the causal route may presumably be via the work rate of the female while feeding the young. On the other hand, in natural conditions the female is responding to early or late breeding by shifting laying date accordingly (Nager & van Noordwijk 1995). Thus, the female seems to ‘know’ whether she is too late or too early relative to the caterpillar peak during the nestling phase in a particular year. This would imply that the female is somehow able to measure the phase of development of the caterpillars while feeding the young.

Implications for climate change

In the past decades the phonology of the vegetation has advanced due to higher spring temperatures (Myneni *et al*. 1997). It has been shown that many bird species in Britain have advanced their date of egg laying over the last 25 years (Crick *et al*. 1997), and that such trend can partly be accounted for by changes in climate (Crick & Sparks 1999). Similar patterns were confirmed by long-term studies of few bird populations (Winkel & Hudde 1997; McCleery & Perrins 1998). However, no advancement of laying date was found for a Great Tit population in the same area in which this research was carried out, despite the advancement of the caterpillar peak date (the Pied Flycatcher however did advance in laying date; Both & Visser, in press). As a result, Great Tits are progressively later and later than the caterpillars (Visser *et al*. 1998). This has raised concerns that the increased spring temperature could disrupt the synchronisation of tits’ breeding with the period of peak abundance of their nestlings’ food. There may be selection on the reaction norm relating temperature, environmental cues used for timing of breeding and laying date, however the birds may not respond quickly enough to rapid environmental changes (Visser *et* *al*. 1998). The study described in Chapter 7 suggests that learning the optimal time for rearing the young may contribute to the birds' ability to cope with rapid environmental changes.

Food availability and parental effort

This study addressed a few questions about the behaviour of a parent bird in the presence of additional food. First, do parents make use of the extra food and, if yes, how much of it is allocated to the young and how much is consumed by the parent itself. We observed that, in any of the study years, the parents picked most of the food items offered but fed only a small proportion of them to the young. From a point of view of cost-benefit analysis, feeding the young with the mealworms is extremely advantageous since finding natural prey takes a long time and much energy. Flying back and forth from the nest to the foraging sites is commonly recognised as very costly, however costs of food search have been underestimated. First, food search constitutes the largest proportion of time spent by parents while feeding the young (Smith & Sweatman 1974; Naef-Daenzer & Keller 1999; this study, *Chapters 3 & 4*). Second, the foraging mode of tits, with rapid hops and hovers along branches, impose a high cost per time unit (Tinbergen & Dietz 1994). The small amount of extra-food fed to the nestlings could be due to the quality of food being sub-optimal for nestlings. Although mealworms are rich in proteins (Redford & Dorea 1984), their cuticle may have been too hard for the nestlings, especially at young age.

Videotaping and direct observations at the nest indicated that the parents used most of the additional food. This probably changed the state of the parents, which were less limited in energy intake (as suggested by the absence of a loss in weight in female parents during brood rearing) and presumably needed to spend less time self-feeding in the trees. Extensive videotaping allowed to address interesting questions about the consequences of the availability of extra-time on provisioning strategies. In particular, I studied the rate at which the parents visited the nest and the size of larvae delivered to the brood.

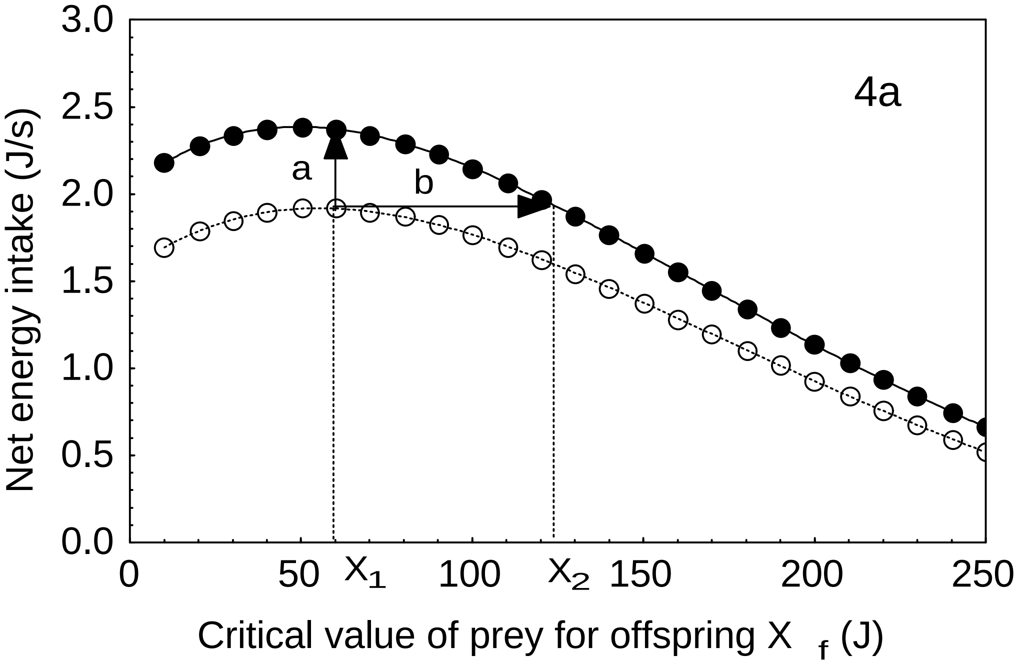
What the parent does when more time is available for food searching

Recent studies involving extensive radio tracking of parent Great and Blue Tits provide a causal explanation for why it is crucial for tits to match the breeding phase with the period of maximum caterpillar abundance. Naef-Daenzer & Keller (1999) found that the average time spent searching by the parents in the tree canopy was negatively correlated with the caterpillar density (expressed in number of larvae per meter of tree branch). The tits took 2-3 minutes to find a prey when feeding the young at the caterpillar peak date, while they took up to 5 minutes before and after the peak date. This suggests that finding a single item requires a considerable time, and this time must be taken into account among the constraints on the flow of energy and nutrients operating in this system. From central place foraging theory (Stephens & Krebs 1986) we know that the time the parent invests in prey search is also depending on the value (e.g. size) of the prey item. For instance, the more selective the forager, the greater will be the number of items that the forager rejects during the foraging bout before it encounters the right one. Therefore, the more selective the forager, the longer it has to search for prey keeping all conditions constant (i.e., encounter rate, average size of prey, etc.). This leads us to wonder whether the parent changes its criteria for prey choice (i.e. its minimum acceptable prey value; Lessells & Stephens 1983), when the time available for foraging changes. However, classical central place foraging models do not predict any change in prey choice depending on the state of the parent or the brood. For instance, if the parent has more time available to forage it will simply take more feeds pre time unit while prey selectivity won't change. This is because the parent is assumed to deliver energy at the maximum rate attainable at those conditions (prey availability and size, encounter rate etc.). Yet, many field studies have so far shown that the diet choice criteria by the parent are much more complex, and selectivity may change over a very short time scale (e.g. Lifjeld 1988, *Chapter 5*).

In *Chapters 3 and 4* of this thesis, I addressed two questions: first, whether the parents change their rate of natural food provisioning when they have access to an extra food resource, and second, whether any change in the visit rate was associated with a change in the size of prey delivered to the brood.

With regard to the first question, the parents may use the food in three ways: (a) they may consume it, saving time that would be used in self-feeding; (b), they may use it to feed the young, thereby saving time that would be employed to search for nestling food; or (c) both. In each case, the parents are expected to have more time to perform non-parental and parental activities, including feeding. There are thus two main options to the parent, which also depend on the proportion of food that is given to the chicks relative to the proportion that is consumed. On the one hand, the parent can use the extra-time to provide more prey items, i.e., it will deliver more natural feeds per time unit. This is likely to occur when finding a natural prey item is very time-consuming, for instance in habitat with low prey density. Markman *et al*. (1998) supplemented parent Orange-tufted Sunbirds *Nectarinia osea* with sugar nectar. This food type could not be given to the nestlings, which are usually fed arthropods. The parents responded by delivering more feeds per nestling. The authors conclude that the high food quality allowed parents to invest more time and/or energy in the young. This may be seen as an example where the parents used the extra-time to increase visit rate and consequently, energy delivery to the brood.

Another possible response of the parent is to use the extra time to increase the average search time per prey item. This could result in parents increasing prey selectivity. What we would then observe is, on average, a longer time gap between deliveries, and larger size of prey (or, alternatively, prey of better nutritional type) being brought to the nest. Chapters 3 and 4 showed that parent Blue Tits reduced the rate of delivery of natural prey, and made longer foraging excursions when they had an extra-food supply. However, the parents delivered on average larger larvae to the nest. The key question is now to identify the conditions at which the parent chooses to respond by delivering large prey at a reduced rate, rather than increasing food delivery rate (Markman *et al*. 1998). In a simplified model of central place foraging, it is assumed that the parent has to eat a certain amount of food to fulfil some energetic need (*Chapter 3*). With the consumption of extra food, the parent is freed from the need to spend some time searching for its own food. This model shows that, by keeping the same selectivity (critical prey value, X_f; Figure 4a) as in unmanipulated



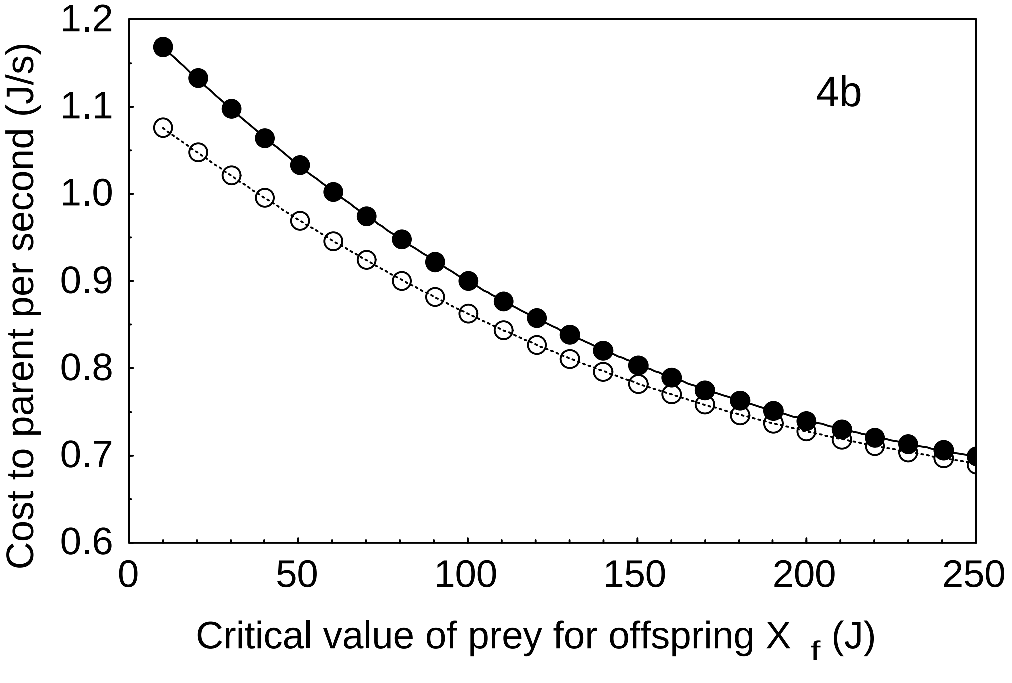


Figure 4. (a) Net rate energy intake of the brood in relation to degree of prey selectivity of the parent (minimum acceptable value of prey for offspring), when the parents have different energetic requirements. (b) Cost per time unit of the foraging excursion in relation to the degree of prey selectivity. Open dots: the parents forage to cover full costs of travelling and foraging; filled dots: the parents need to cover 10% of those costs.

conditions, the parent can deliver a greater amount of food at the same time (this model assumes that the parent acts to maximise the net rate of energy intake, that is the energy gathered minus the cost of foraging, per time unit). This is indicated by the arrow (a) in Fig. 4a. However, the net energy intake could be greater than that needed by a brood. In such a situation, at some stage the parent should stop provisioning. In other words, we expect to observe food-supplemented parents to alternate phases of high feeding rates – and no change in selectivity – with periods of no feeding at all. This is clearly in contrast to the field data. The parents with extra-food supply feed the nestlings less frequently, and deliver on average larger food items. This corresponds to the parents working in the right part of the curve, as shown by the arrow (b) in Fig. 4a. By increasing selectivity, the parents deliver a similar amount of food per time unit. Control parents cannot do that, because part of the time employed in a foraging excursion is devoted in time self-feeding, so that a similar net energy intake is achieved at lower selectivity. Moreover, food-supplemented parents can find a higher selectivity advantageous because of the lower costs incurred per time unit. The curve in Figure 4b shows the cost per second that the parent pays while foraging with a certain critical prey value for the offspring, X_f (*Chapter 3*). Obviously, the cost of foraging decreases with the time spent in the feeding site, because the proportion due to the flight cost (which is greater than search time cost) progressively becomes smaller. However, for a bird that has to find less food for itself, as in the case of food-supplemented parents, the cost of searching is relatively higher than for a bird that has to find more food. This is because, keeping X_f equal, the food-supplemented parent spends relatively shorter time searching for its own food plus the food item for the offspring, thus the flight cost will be proportionally higher (black-dotted line in Fig. 4b). A decrease in the cost per time unit is possible if the food-supplemented parent increases its time spent searching, that is, if it searches for large prey items to bring to the nest. By increasing selectivity, the bird can still deliver a comparable amount of food as in the unmanipulated situation, but at a lower cost per time unit.

The model presented in Chapter 3 can explain the changes in provisioning rate and prey size observed when Blue Tits have access to another food resource. Notice that this model does not take into account the possibility that the additional food is used by the parents to feed the young. In this model, food supplementation only

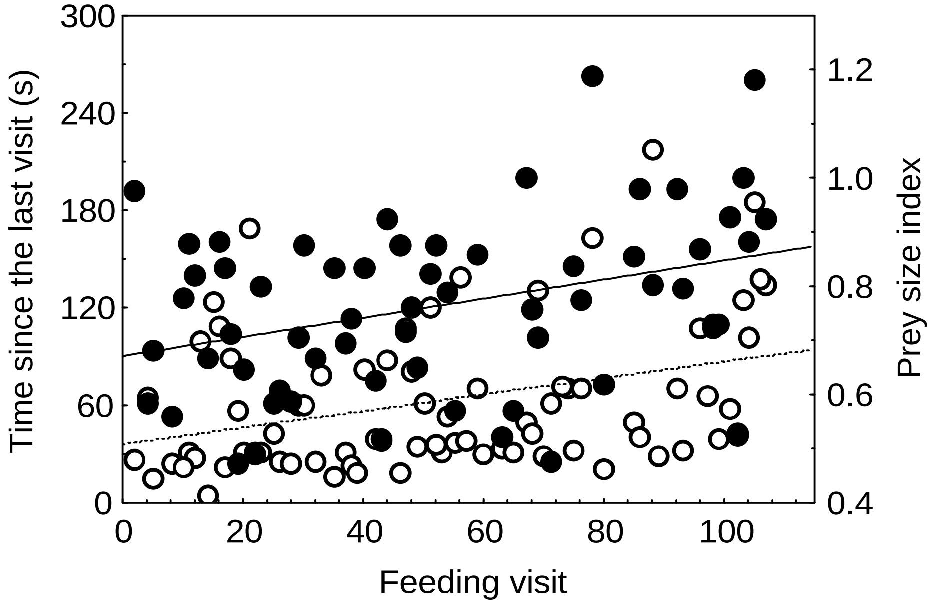


Figure 5. Changes in time since the last visit (circles) and size of the larva brought to the nest (dots) in a sequence of visits during a 1.5-hour videotaping session. Prey size is expressed as the width of the larva's head capsule relative to the bird's beak width. Positive trends like this are not the rule across videotaping sessions. In some sessions, time since the last visit and prey size decrease with time from the start of filming, while in others there is no clear trend in any direction.

modifies the amount of food that has to be eaten by the parent before searching for nestling food. If the parents feed the young the larvae offered, the state of the brood will change as well as the parents' state. Provided that the parents regulate their feeding effort according to the brood's hunger level (e.g. Bengtsson & Rydén 1983, Price and Ydenberg 1995, Leonard and Horn 1996; *Chapter 5*), they would probably deliver smaller amounts of natural food. Thus, they would be expected to slow down further their visit rate. In this way, the effect of the experiment on the prey selectivity would be even greater than if the parents had to take the same amount of natural food as control parents had. In fact, the delivery of part of the extra-food to the chicks would correspond to a further shift to the right along the black-dotted curve in Fig. 4a, so that the parents would deliver natural food at a lower rate. The effect of the brood's state could also explain changes in provisioning rate and prey size that occur *within* nests, *within* videotaping sessions (Figure 5). As we have seen in Chapter 4, changes in prey size are more likely to be due to variation in search time, not to the use of feeding sites at different distances. If we assume that the state of the parent does not change within an hour, we may hypothesise that the parent is responding to the brood's state by making foraging excursions of different duration. Abrupt changes in visit rate and prey size have clearly been associated with changes in the begging behaviour of the brood (*Chapter 5*). Thus, a more comprehensive model should incorporate changes in the state of the brood as determinants of the time available for foraging, and therefore selectivity.

Fitness consequences of variation in food availability

Seasonal environments are characterised by temporal fluctuations in food availability and food is one of the important factors affecting reproductive success (Lack 1968, Martin 1987). The amount of food available during the nestling period has been shown to influence various fitness components such as nestling growth (Gebhardt-Henrich & Richner 1998), survival (Simons & Martin 1990) and local fledgling recruitment (Verhulst 1994). Little is known on the effects of food stress on the precision of development, measured by fluctuating asymmetry. This is a fitness component that has often been neglected, given the known effects of symmetry in individual performance (e.g. flight, Swaddle 1997). My study has shown that food supplementation reduced asymmetry of tarsi in nestling Blue Tits, suggesting that the degree of body asymmetry is affected by the rate of energy intake (*Chapter 6*). To my knowledge, this is the first study that shows such an effect in birds in early stages of life as a consequence of an experimental manipulation.

We found no evidence that wing asymmetry was reduced with food addition. This is agreement with the view that flight feathers are more protected against food shortage by active mechanisms of allocation of resources (i.e. energy and nutrients) than others because of their high survival value in newly-fledged young (Kunz 1999). In unmanipulated situations, and in habitats where food conditions are generally good, most of the resource is used in the protection of growth and asymmetry of such traits (this is also shown by the high growth rate of flight feathers in control birds). Thus, food supplementation is more likely to produce an effect on those traits that *usually* are not protected. Another explanation could be due to the fact that tarsi and wings grow in different time windows. If the effect of food stress on asymmetry is clear only when the growth rate is the highest, e.g. at 10 days after hatching, when tarsi are still growing but wings have just started to develop. Thus, any effect of food stress could be detected only in traits that grow around that age.

Conclusions: binding together food limitation at different times of the breeding cycle

We have seen in Chapter 1 that the average reproductive strategy of a species should reflect evolutionary selection pressures, and it should result in food limitation for both parents and offspring. However, responses should vary around these average strategies with variation in food in ecological time. This variation in food can be expressed at least in part by the resources of the female at the onset of reproduction (Figure 1 in Chapter 1). These resources are crucial to the reproductive strategy because they must last through the entire reproductive cycle (egg laying to independence of young). Any decrease in reserves at the initial phase of the reproductive event must be met either by decreased investment in current offspring (i.e., reduced proportion of PE , Chapter 1) or increased dependence on exogenous resources during breeding, which takes time and energy away from caring for the brood. This problem can be seen in the female bird when producing eggs. The laying female is expected to reduce its initial effort (i.e., less resources to be put into eggs) if producing large eggs has to be done at the expense of higher cost in later phases of breeding (e.g., lower provisioning effort). This is particularly the case when, above some size threshold, reduction in egg size may have negligible impact on nestling survival (Martin 1987)

In the laying period, food availability does influence egg quality and number, as shown by various studies involving food supplementation. This study shows that food limitation on egg quality is likely to occur, although only in part of the environmental conditions that the female bird experiences during laying. The use of extra-food positively influenced egg volume, but only at average temperatures up to 8-10 °C (Figure 4 in Chapter 2). At higher temperature, egg size did not depend on whether or not the extra-food was consumed by the female. The question now arises in which proportion of the laying period egg formation is limited in the female Blue Tit. This obviously depends strongly on the frequency of cold days in the laying period. In years such as 1997, when temperature was low and did not show abrupt changes during the laying days, food probably limited egg size in up to 50% of the days. On the other hand, in relatively warm years such as 1998 and 1999 this proportion dropped to about 20% (Figure 1 in Chapter 2). This indicates that, for a significant proportion of the environmental values a bird experiences during laying, we could detect effects of food limitation.

In contrast to what was seen for egg production, there were no clear effects of food limitation on growth and final body condition of nestlings. However, food limitation does act in this crucial phase. The increase of extra-food consumption with nestling age perhaps reflects important constraints on food gathering in the parents. Food limitation has subtle effects, as shown by the reduced asymmetry of tarsi of nestlings when more food is available. The absence of effects of food limitation on most growth traits suggests that active mechanisms of resource allocation protect growth of such traits, not of others. On the other hand, it is quite clear that food limitation is at least in part overcome by increased feeding effort of the parents. An increase in brood demand (e.g. with large broods, or older broods) is met by an increase in provisioning feeding rate. This is not without cost to the parents. A recent study has shown that daily energetic expenditure of parent Blue Tits feeding the young when food is scarce can reach values around 6-7 times the basal metabolic rate that can only be sustained at the cost of lower survival (Thomas *et al*. in press). The authors also showed a clear negative relationship between daily energetic expenditure and synchronisation with the local caterpillar population. Therefore, the greater the time mismatch between resource supply and demand, the higher the cost the parent have to pay to raise the brood.

However, the results of this thesis show that the Blue Tits in the Hoge Veluwe feed the young at a rate near the maximum attainable in a wide range of feeding conditions. This is in line with the general idea in life-history theory that the parent should avoid decreases in reserves at the beginning of the reproductive attempt (due to greater investment in egg production) that can negatively affect parental investment in later phases of breeding. All data lead to the conclusion that Blue Tits work near the maximum rate under average conditions and cannot fully compensate shortages of food in below average conditions.

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Summary

This dissertation deals with the direct and indirect effects of food availability in different phases of breeding in a small insectivorous bird, the Blue Tit (*Parus caeruleus*). Previous studies have emphasised the dual nature of food influencing reproductive decisions in birds. On the one hand, food constitutes energy and nutritional resource for the individual. This thesis has focused on the effects of food as a resource in two highly demanding phases: (1) the period of egg laying and (2) the period of brood rearing. On the other hand, food in the laying phase could also function as a cue predicting the best time for rearing the brood. This means that the female bird could react to the appearance of specific food (e.g. insect larvae) in the environment that signals that the optimal time for having the offspring is near. A recent study on Great Tits suggested that food may act as information over a longer time scale. According to this hypothesis, female birds of seasonally breeding species might react to the environmental conditions experienced in a past breeding attempt to fine-tune the timing of the next breeding attempt. In the case of tits *Parus* spp., which feed the offspring mainly with caterpillars (larvae of *Lepidoptera*), the female would react to the poor synchronisation between the nestling period (peak food demand) and period of maximum caterpillar abundance (peak food supply) by delaying or advancing laying date the next year in order to improve their synchronisation. This intriguing hypothesis was tested with a series of additional feeding experiments carried out in 1997 to 1999 in which extra-food was offered to the parents throughout the nestling period. It was expected that food-supplemented females would, on average, change laying date the next year to a lesser extent than unfed, control females.

In order to investigate the between-year changes in laying date independent of energetic limitations on egg formation, we supplemented Blue Tit pairs with food also in the phase of nestbuilding, so that the female could rely on an additional resource and lay the eggs in response to the potential predictive signals from the environment. This provided the opportunity to analyse patterns of egg size as a function of daily temperature and food availability (*Chapter 2*). Egg size varied with temperature only in one year, when food was not given during egg laying (food was offered until laying of the first egg). However, this could also be due to the fact that spring temperature in that year was on average lower than in the other two years. Other data, however, suggest that the change in the relationship between temperature and egg size was due to different food availabilities. For nests where food was not accepted by the birds, egg size decreased in days of cold weather. On the contrary, females that consumed food laid eggs for which the size was not dependent on temperature.

They laid large eggs even in cold days. The data suggest that food limitation on egg size may occur in 20 to 50% of the days in the laying season, depending on the proportion of days when the average temperature drops below 8-10 °C. Temperature also influenced the probability that the female interrupted laying for one or more days (i.e., produced laying gaps). In short periods of cold weather Blue Tits significantly produced more laying gaps than in other periods. However, food consumption appeared not to influence the 'decision' to interrupt laying, indicating that laying gaps may occur as a process that does not operate only through energy resource of the female. It is possible that the female reacts to abrupt changes in temperature that occur a few days earlier than the day of laying the egg concerned. If the temperature has been higher than some threshold in the critical 'switch' period, the female will lay anyhow even if the temperature drops just before the actual day of laying.

Food supplementation in the nestling period provided the opportunity to investigate how parental provisioning strategies change in the presence of extra-food. In particular, we wanted to see (1) how the parents used extra-food (that is, how much of extra-food was allocated to the young and how much would be consumed by the parents); (2) how provisioning rates changed with food supplementation, and whether the effect of treatment differed across brood sizes and nestling ages; and (3) whether the parents changed their criteria of choice of natural prey when more time was available for searching for nestling food. These questions could be addressed with the extensive use of videorecording at the nest.

Chapter 3 describes the effects of the food addition on (a) the provisioning rate of natural prey and (b) the average size of larvae brought to the nest (most of them being caterpillars). Food-supplemented parents brought fewer natural feeds per time unit but fed the chicks larger larvae than control parents. In control nests, prey size was smaller if the parents had to feed larger broods. However, supplemented parents delivered large prey even when feeding large broods, suggesting that prey choice was more constrained when brood demand was greater. A model that takes into account the effects of parental energy requirement on minimum acceptable value of prey for the offspring can explain the changes in size of delivered prey observed in this study. When the parent gets extra-food, it can save time that otherwise would be spent in self-feeding. This way, more time will be allocated to food search, and selectivity can increase as long as it results in a net rate of energy intake of the brood comparable to that in unmanipulated conditions. *Chapter 4* and *5* describe how a lower feeding frequency, that is a longer average time between feeds may allow the parents to be more selective and bring larger prey to the brood. Chapter 4 analyses within-nest, within-video session variation in between-feed time and prey size. In unmanipulated conditions, prey size tends to increase with the time spent away from the nest. Direct observations of parents foraging in the tree canopy strongly suggest that this variation can be explained by the time allocated to food search, not to travel time. The longer the time spent searching, the larger the larvae taken to the nest. This shows that any increase in meal size could only be traded-off against reduced visit rate. Chapter 5 shows that changes in those two variables are tightly linked and occur over a very short time scale. These changes are also related to the state of the brood: if the nestlings stop food-begging, the parents leave the nest for a longer foraging excursion and bring on average larger prey. This suggests that the parents continually monitor the state (hunger level) of the brood and consequently change their selectivity according to the time available.

Food provisioning did not result in increased final weight of the young, although food-supplemented nestlings grew faster than controls. This suggests that, for this population, food limitation in the environment could easily be overcome by increased feeding effort by the parents (*Chapter 6*). However, food-supplementation appeared to improve the control of developmental precision. Nestlings in food-supplemented broods had more symmetrical tarsi than those in control broods, while asymmetry of their wings was unaffected. This indicates that developmental stability requires energy, and that during early development most of the resource is allocated in the protection of growth of traits important for fledgling survival, such as wing length and symmetry.

Chapter 7 addresses the most intriguing question of this study. Female Blue Tits experiencing additional food during the nestling period laid relatively later the next year than unfed females, controlled for between-year changes in the environment. As a result, those females mis-timed reproduction and raised the brood far from the caterpillar peak the next year. This suggests that food levels experienced during breeding are involved in fine-tuning the timing of breeding the next year. The expression of an individual’s phenotype (i.e., laying date) depends not only on the current environment but also on past environmental conditions.

This thesis has shown that food limitations occur both during the phase of egg formation and laying and in the phase of brood rearing. In the first case, the female has to collect enough resources to produce large eggs in cold weather, when the cost of maintenance is high and/or food availability is reduced. In a significant proportion of the days, the female cannot produce eggs of the maximum size. In the second case, the parent has to deliver a certain amount of energy and nutrients per nestling despite periods of low food availability (e.g. before or after the caterpillar peak date) and increased total demands (e.g. large broods). Flexibility in provisioning rate and prey choice allow parents to cope with increased brood demand. The results are in line with the view that Blue Tits work near the maximum rate in a wide range of conditions.

Samenvatting

Dit proefschrift gaat over de directe én indirecte effecten van voedselbeschikbaarheid op het reproductie-besluit tijdens verschillende broedfases van een kleine insectenetende vogel, de Pimpelmees (*Parus caeruleus*). Vorige studies hebben benadrukt dat de invloed van voedsel op het reproductiebesluit bij vogels tweeledig is. Enerzijds voorziet voedsel in de energie- en nutriëntenbehoefte van het individu. Dit onderzoek heeft zich gericht op de effecten van voedsel als bron in twee fases waarin de vogel veel voedsel nodig heeft: (1) de eilegperiode en (2) de periode waarin de jongen worden grootgebracht. Anderzijds kan het voedselaanbod tijdens de eilegperiode ook een indicatie zijn van de beste tijd om de jongen groot te brengen. Dit houdt in dat het vrouwtje zou kunnen reageren op het verschijnen van specifiek voedsel (vnl. insectenlarven) dat aangeeft dat de beste tijd om nakomelingen te hebben is aangebroken.

Een recente studie van de Koolmees (Parus major) suggereert dat voedsel zou kunnen dienen als informatiebron op de langere termijn. Volgens deze hypothese zouden de vrouwtjes kunnen reageren op ervaringen tijdens eerdere broedsels om het volgende broedsel te fine-tunen. In het geval van de mezensoorten, die hun jongen voornamelijk met rupsen (Lepidoptera larven) voeren, zou het vrouwtje reageren op de zwakke afstemming van de nestperiode (hoge vraag naar voedsel) en de periode van de maximale beschikbaarheid aan rupsen (hoog aanbod van voedsel) door het vertragen of vervroegen van de legdatum in het volgende jaar om deze afstemming te verbeteren. Deze hypothese is in de periode 1997-1999 getest met een serie voedselexperimenten waarin tijdens de nestperiode extra voedsel aan de ouders werd aangeboden. De verwachting was dat de vrouwtjes die extra voedsel kregen, gemiddeld genomen, hun legdatum in het volgende jaar minder zouden variëren dan een controlegroep van niet bijgevoerde vrouwtjes. Om op basis van informatie over de eieren de jaarlijkse variatie in legdatum, onafhankelijk van energetische beperkingen, te onderzoeken hebben we aan paartjes Pimpelmezen ook voedsel aangeboden in de nestbouwfase. Op deze manier kon het vrouwtje gebruik maken van extra voedsel en kon ze de eieren leggen in antwoord op de potentieel voorspellende signalen vanuit het milieu.

Dit bood de kans om de eigrootte als functie van de dagelijkse temperatuur en voedselbeschikbaarheid te analyseren (*Hoofdstuk 2*). De eigrootte varieerde met de temperatuur in slechts 1 jaar toen er tijdens het leggen van de eieren geen voedsel werd gegeven (het voedsel was aangeboden tot het leggen van het eerste ei). Dit zou echter ook veroorzaakt kunnen zijn door het feit dat de voorjaarstemperatuur in dat jaar gemiddeld lager was dan in de andere twee jaren. Andere gegevens suggereren dat de verandering in de relatie tussen temperatuur en eigrootte afhangt van de mate van de beschikbaarheid van voedsel. In nesten waar het extra voedsel niet door de vogels werd geaccepteerd werden in dagen met koud weer kleinere eieren gelegd. Vrouwtjes die het voedsel wel accepteerden legden eieren waarvan de grootte geen relatie vertoonde met de temperatuur; ook tijdens koude dagen legden zij grote eieren. De gegevens suggereren dat voedselbeperking in 20 tot 50% van de dagen in het legseizoen voor kan komen, afhankelijk van het aandeel van de dagen waarin de gemiddelde temperatuur beneden de 8 – 10 °C zakt. De temperatuur beï nvloedt ook de kans dat het vrouwtje de eilegperiode voor een paar dagen onderbreekt. In korte periodes van koud weer onderbraken Pimpelmezen significant vaker hun eileg dan in andere periodes. Het bleek echter dat voedselconsumptie het besluit tot het onderbreken van de eileg niet beï nvloedde. Dit duidt erop dat de onderbrekingen niet alleen afhangen van de energiebronnen van het vrouwtje. Het is mogelijk dat de vrouwtjes reageren op plotselinge temperatuursveranderingen die zich een paar dagen voor het begin van de eilegperiode voordoen. Wanneer de temperatuur boven een bepaalde drempel-waarde is geweest tijdens de kritische ‘switch’ periode zal het vrouwtje, ondanks een temperatuursdaling vlak voor de dag van de aanvang van de eileg, toch haar eieren leggen.

Verder gaf het toedienen van extra voedsel tijdens de nestperiode de kans om te onderzoeken hoe de ouders hun strategie van voedselaanvoer zouden veranderen. We wilden in het bijzonder zien (1) hoe de ouders het extra voedsel gebruiken (hoeveel van het extra voedsel aan de jongen werd gegeven en hoeveel de ouders zelf gebruikten); (2) hoe verandert de voedselgift aan de jongen met het toevoegen van extra voedsel? En wat is het effect hierop van het aantal jongen en hun leeftijd? En (3) of de ouders hun keuzecriteria t.a.v. natuurlijke prooien veranderden wanneer ze meer tijd hadden om voedsel te zoeken. Deze vragen konden worden beantwoord m.b.v. een videocamera in het nest.

Hoofdstuk 3 beschrijft de effecten van extra voedsel op (a) het aandeel natuurlijke prooien en (b) de grootte van de insekten die naar het nest worden gebracht (voornamelijk rupsen). Ouders die extra voedsel kregen toegediend brachten minder natuurlijke prooien per tijdseenheid, maar deze waren wel groter dan de prooien die de controlegroep aanvoerde. In de controlenesten was de prooigrootte bij grotere broedsels kleiner dan bij kleinere broedsels. De ouders die voedsel kregen toegediend leverden echter altijd grote prooien, ook bij grote broedsels. Dit suggereert dat bij een grotere vraag vanuit het nest de prooikeuze beperkt is. Een model dat rekening houdt met de energetische effecten voor de ouders om een minimaal acceptabele prooi voor de jongen te vangen kan de veranderingen in prooigrootte verklaren. Wanneer de ouders extra voedsel krijgen kunnen ze tijd besparen dat anders zou zijn besteed aan het zoeken naar voedsel voor zichzelf. Zo zal meer tijd worden besteed aan het zoeken naar voedsel en kan er kieskeuriger worden gefoerageerd. Dit resulteert in een hoger energetische aanvoer dan in vergelijkbare, ongemanipuleerde omstandigheden.

Hoofdstuk 4 en *5* beschrijven hoe een lagere voerfrequentie (langere tijd tussen twee voerbeurten), het de ouders mogelijk maakt om selectiever te zijn en grotere prooien naar het nest te brengen. Hoofdstuk 4 geeft aan de hand van de nestvideo een analyse van de variatie tussen voerfrequentie en prooigrootte. Onder natuurlijke omstandigheden is de prooigrootte groter naarmate er meer tijd buiten het nest wordt besteed. Observaties van ouders die in de boomkruin foerageerden suggereren dat deze variatie kan worden verklaard door de tijd die wordt besteed aan het zoeken en niet aan de reistijd tussen het nest en de foerageerplaats. Hoe meer tijd er wordt besteed aan zoeken, hoe groter de larven die naar het nest worden gebracht. Dit laat zien dat elke toename van de prooigrootte alleen maar het gevolg kan zijn van een lagere voerfrequentie.

Hoofdstuk 5 laat zien dat veranderingen in deze twee variabelen sterk zijn gelinked en slechts een zeer korte tijdschaal beslaan. Deze veranderingen zijn ook gerelateerd aan de toestand van de jongen; als ze stoppen met het bedelen, verlaten de ouders het nest voor een langere tijd en brengen grotere prooien aan. Dit veronderstelt dat de ouders continu de toestand van de jongen (de mate van honger) monitoren en hun selectiviteit aanpassen aan de beschikbare tijd. Het toedienen van extra voedsel resulteerde niet in zwaardere jongen, hoewel ze wel sneller groeiden. Dit suggereert dat, voor deze populatie, een beperkt voedselaanbod gemakkelijk kan worden overbrugd door een verhoogde inzet van de ouders (*Hoofdstuk 6*). Verder bleek dat het toevoegen van extra voedsel de lichamelijke ontwikkeling verbeterde. De tarsi van de jongen waarvan de ouders extra voedsel kregen toegediend, waren meer symmetrisch dan die van de jongen van de controlegroep. De asymmetrie van hun vleugels werd niet beï nvloed. Dit geeft aan dat de ontwikkelingsstabiliteit energie behoeft en dat tijdens de vroege ontwikkeling het grootste aandeel van de energiebronnen wordt aangewend voor de bescherming van de groei van die lichaamsdelen die belangrijk zijn voor het vliegen, zoals vleugellengte en symmetrie.

Hoofdstuk 7 behandelt de meest intrigerende vraag van deze studie. Vrouwelijke Pimpelmezen die extra voedsel kregen toegediend tijdens de periode waarin ze nestjongen hadden legden het volgende jaar hun eieren later dan de niet bijgevoerde vrouwtjes (gewogen voor jaarlijkse variaties in het milieu). Deze vrouwtjes timeden hun broedtijd verkeerd en brachten in het daaropvolgende jaar hun broedsel ver buiten de rupsenpiek groot. Dit suggereert dat voedselniveaus die tijdens de broedtijd worden ervaren worden betrokken bij de fine-tuning van de broedtijd voor het volgende jaar.

De expressie van een individueel fenotype (de legdatum) hangt niet alleen af van het huidige milieu maar ook van de vroegere milieucondities. Dit proefschrift heeft bewezen dat voedselbeperkingen zowel tijdens de eilegfase als tijdens de voertijd voorkomen. In het eerste geval moet het vrouwtje genoeg voedsel verzamelen om grote eieren tijdens koud weer te leggen; een flink deel van de dagen kan het vrouwtje geen eieren van maximale grootte leggen. Ook dienen de ouders in tijden van een lage beschikbaarheid aan voedsel (voor of na de rupsenpiek) en een vergrote vraag (bij grote broedsels) een bepaalde hoeveelheid energie en nutriënten per jong aan te leveren. Flexibiliteit in de aanvoercapaciteit en prooikeuze geven de ouders de mogelijkheid om te reageren op een verhoogde vraag van het broedsel. De resultaten stemmen overeen met het idee dat de Pimpelmezen in een brede range van milieucondities dichtbij het optimum zitten.

Vertaald door Ir. Albert de Hoon

Riassunto

Questa tesi tratta degli effetti diretti e indiretti della disponibilita' di cibo in diverse fasi della riproduzione di un piccolo uccello insettivoro, la Cinciarella (*Parus caeruleus*). Studi condotti in precedenza hanno sottolineato la natura ambivalente del cibo come importante fattore nelle decisioni riproduttive negli uccelli. Da una parte, il cibo costituisce la risorsa di energia e nutrienti per l'individuo. Questa tesi ha esaminato gli effetti del cibo come risorsa in due periodi altamente dispendiosi: (1) il periodo di deposizione delle uova e (2) il periodo di allevamento della nidiata. Dall'altro canto, il cibo nella fase di deposizione potrebbe anche funzionare come informazione che segnali l'approssimarsi del periodo migliore per allevare la prole. In altre parole, la femmina potrebbe rispondere alla comparsa di cibo specifico (per esempio larve di insetti) nell'ambiente perche' questo segnala l'incremento della densita' delle prede per la nidiata. Uno studio recente sulle Cinciallegre ha proposto l'idea che il cibo possa fungere da veicolo di informazione su scale temporali piu' lunghe. Secondo questa ipotesi, le femmine di specie che nidificano in ambienti stagionali potrebbero rispondere alle condizioni ambientali vissute in passate stagioni riproduttive per regolare finemente il periodo di riproduzione l'anno successivo. Nel caso delle cince *Parus* spp., che nutrono la nidiata soprattutto con bruchi (larve di Lepidotteri), la femmina risponderebbe alla scarsa sincronia tra il periodo di allevamento dei pulcini (picco di domanda di cibo) e il periodo di massima abbondanza di bruchi (picco di cibo) anticipando o ritardando la data di deposizione l'anno prossimo in modo da migliorare tale sinchronia. Questa interessante ipotesi e' stata verificata con una serie di experimenti di aggiunta di cibo effettuati dal 1997 al 2000 nei quali e' stato offerto del cibo (vermi della farina *Tenebrio molitor* e larve di falena *Galleria mellonella*) ad adulti di Cinciarella durante l'allevamento dei pulcini. Ci si attendeva che le femmine con il cibo avrebbero cambiato la data di deposizione l'anno prossimo in minor misura delle femmine senza cibo (controlli).

Per studiare i cambiamenti di data di deposizione tra gli anni indipendenti da limitazioni energetiche della formazione delle uova, il cibo e' stato offerto anche nella fase precedente la deposizione, cosi' che la femmina poteva 'decidere' quando deporre le uova in risposta a potenziali segnali predittivi dall'ambiente, senza limitazioni di risorsa. Cio' ha creato l'opportunita' di analizzare la variazione della dimensione delle uova in funzione della temperatura e del consumo di cibo (Capitolo 2). Il volume dell'uovo variava con la temperatura solo in un anno, quando il cibo non era stato dato durante la deposizione (il cibo fu offerto fino alla deposizione del primo uovo). Tuttavia, questo poteva essere dovuto al fatto che la temperatura in primavera di quell'anno era in media piu' bassa che negli altri due anni.

Altri dati, comunque, mostrano che il cambiamento della relazione tra temperatura e volume dell'uovo era duvuto a diverse disponibilita' di cibo. Nei nidi in cui il cibo non fu accettato dagli uccelli, la dimensione dell'uovo diminuiva nei giorni freddi. Al contrario, le femmine che consumarono il cibo offerto deposero uova il cui volume era indipendente dalla temperatura. Queste femmine deposero uova grandi anche in giorni freddi. I dati suggeriscono che la limitazione di cibo ha effetti sulla dimensione delle uova nel 20 fino al 50% dei giorni della stagione di deposizione, a seconda della proporzione di giorni con una temperatura media sotto gli 8-10 °C. La temperatura influenzava anche la probabilita' che la femmina interrompeva la deposizione per uno o piu' giorni. In brevi periodi di freddo le Cinciarelle hanno interrotto la deposizione piu' spesso che in altri periodi. Comunque, il consumo di cibo aggiunto non influenzava la decisione se o no interrompere la deposizione. Questo indica che le interruzioni si verificano come processo che non agisce soltanto attraverso le risorse di energia della femmina.

L'offerta di cibo nel periodo dell' allevamento dei pulcini ha dato l'opportunita' di stabilire come le strategie parentali di approvvigionamento variano in presenza di cibo addizionale. In particolare, si e' voluto sapere (1) come i genitori avrebbero usato il cibo offerto loro (cioe', quanto cibo veniva distribuito ai pulcini e quanto veniva consumato dai genitori stessi); (2) come la frequenza di imbeccata sarebbe cambiata successivamente l'aggiunta di cibo, e se l'effetto del trattamento sarebbe stato diverso in nidiate di diverse dimensioni ed eta'; e (3) se i genitori avrebbero mutato i criteri di scelta delle prede naturali nel caso avessero avuto piu' disponibilita' di tempo per cercare il cibo dei pulcini. A queste domande si e' potuto rispondere utilizzando estesamente il metodo di videoregistrazione al nido. Il *Capitolo 3* descrive gli effetti della aggiunta di cibo sulla (a) frequenza di imbeccata naturale e (b) dimensione media delle larve portate al nido (in grande maggioranza larve di lepidotteri). Gli adulti con cibo addizionale portarono meno prede naturali per unita' di tempo, ma portarono larve piu' grandi di quelle raccolte dagli adulti controllo. Nei nidi senza cibo addizionale, la dimensione delle larve portate al nido era piu' piccola se la nidiata era composta da un maggior numero di pulcini. Gli adulti con cibo portarono larve grandi anche quando dovevano nutrire grosse nidiate, indicando che la scelta della preda in condizioni normali (controlli) era piu' limitata quando la domanda energetica della nidiata era maggiore. Un modello che tiene conto degli effetti della domanda energetica del genitore sul minimo valore accettabile della preda puo' spiegare i cambiamenti della dimensione della preda osservati in questo studio. Quando il genitore consuma il cibo addizionale, puo' risparmiare tempo altrimenti impiegato a nutrirsi. In questo modo, piu' tempo puo' essere usato per cercare la preda per la nidiata, e la selettivita' (cioe, la dimensione media delle prede) puo' aumentare purche’ risulti in un tasso netto di apporto di energia alla covata comparabile con quello in condizioni non manipolate. I *Capitoli 4* e *5* descrivono come una diminuita frequenza di imbeccata naturale, cioe’ un tempo medio piu’ lungo tra due imbeccate, puo’ permettere agli adulti di di essere piu’ selettivie portare prede piu’ grosse alla nidiata. Il Capitolo 4 analizza la variazione dell’intervallo di tempo tra imbeccate e della dimensione della preda a livello dei singoli nidi, e della singloa sessione video. In condizioni non manipolate, la dimensione delle larve tende ad incrementare col tempo speso lontano dal nido. Osservazioni dei genitori impegnati nel foraggiamento suggeriscono che questa varazione puo’ essere spiegata dal tempo dedicato alla ricerca della preda, non dal tempo di spostamento dal nido al sito di foraggiamento. Maggiore e’ il tempo impiegato a cercare, piu’ grande era la larva portata al nido. Un incremento della dimensione della preda poteva solo essere fatta a scapito della frequenza di imbeccata. Il Capitolo 5 mostra che i cambiamenti in queste due variabili avvenivano ad una scala temporale molto ridotta. Inoltre, tali variazioni erano legate allo stato della nidiata: se i pulcini cessavano di sollecitare i genitori a nutrirli, questi ultimi lasciavano il nido per piu’ lunghi intervalli e successivamente portavano larve piu’ grandi. Questo indica che i genitori raccolgono informazioni sullo stato (livello di fame) della nidiata in modo continuo, e cambiano selettivita’ in accordo col tempo disponibile.

L’aggiunta di cibo non ha determinato un aumento del peso dei pulcini all’involo sebbene questi crebbero piu’ velocemente dei pulcini controllo. Questo indica che, per questa popolazione, la limitazione di cibo nell’ambiente puo’ essere facilmente compensata dal maggiore sforzo di approvvigionamento dei genitori (Capitolo 6). Comunque, i pulcini in nidi con cibo avevano tarsi piu’ simmetrici di quelli nelle nidiate controllo, mentre l’asimmetria delle ali non cambio’ con l’aggiunta di cibo. Questo indica che il controllo della stabilita’ e della precisione dello sviluppo richiede energia, e che la maggior parte delle risorse nello sviluppo precoce sono dedicate alla protezione della crescita di tratti importanti per la sopravvivenza dei giovani dopo l’involo, come la lunghezza e la simmetria delle ali.

Il *Capitolo 7* ci riporta alla domanda piu’ interessante di questo studio. le femmine di Cinciarella che poterono accedere al cibo addizionale nel periodo dell’allevamento dei pulcini l’anno successivo deposero le uova piu’ tardi delle femmine senza il cibo, anche dopo aver tenuto conto delle differenze ambientali tra gli anni. In tale anno, la riproduzione di tali femmine fu meno sincronizzata con il picco naturale di cibo. Questo indica che i livelli di cibo nel periodo di allevamento dei pulcini contribuiscono alla regolazione fine dell’inizio della riproduzione l’anno successivo. L’espressione del fenotipo dell’individuo (data di deposizione) dipende non solo dall’ambiente in quel momento, ma anche dalle passate condizioni ambientali.

Questa tesi ha mostrato che le limitazioni di cibo si verificano sia nella fase diformazione e deposizione delle uova che nella fase i allevamento della nidiata. Nel primo caso, la femmina dave assumere sufficienti risorse per produrre grosse uova in giorni freddi, quando il costo energetico di mantenimento e' alto e/o la disponibilita' di cibo e' ridotta. In una significativa proporzione di giorni, la femmina non puo' produrre uova della massima dimensione. Nel secondo caso, il genitore deve portare al nido energia e nutrienti a dispetto di periodi di scarsa disponibilita' di cibo (per es. prima o dopo il periodo di picco delle larve in natura) e maggiore richiesta della nidiata (per es. in nidiate piu' grandi). Flessibilita' nella frequenza di imbeccata e scelta della preda permettono agli adulti di affrontare maggiori necessita' alimentari della nidiata. I risultati sono in linea con l'ipotesi secondo cui le Cinciarelle lavorano con uno sforzo prossimo al massimo in un ampio spettro di condizioni.

Acknowledgements

I express my gratitude to Arie van Noordwijk for allowing me to conduct a PhD under his supervision at the Netherlands Institute of Ecology, Centre for Terrestrial Ecology. The superb facilities of this Institute were a determinant resource in this project. Also, I wish to thank Arie for giving me the opportunity to come to the NIOO in 1995 to carry out post-graduate projects on Great Tits and Cormorants. Many thanks to Rüdiger Cordts, Charlotte Deerenberg, Kate Lessells and Marcel Visser for discussions, help with statistical problems and suggestions on both this and the Cormorant work. Piet Drent gave essential advice on how to perform feeding experiments in the field. Rüdiger also helped me with the preparation of the layout of the thesis. Thanks to Kate for her interest in the role of the Journal Club in our workgroup. Jan Visser helped me many times extracting data from the long-term data bank, while Ietje Struiving provided a number of copies of papers not available in the institute library.

Financial support was provided by the University of Pavia and by the European Commission (Marie Curie Research Fellowship n° ERBFMBICT 971939). The NIOO also partially funded the printing of this thesis.

Although he was not involved in the Blue Tit work, I am deeply grateful to Adriaan Kortlandt who wanted to tell me as much as possible about real ethology, the behaviour of cormorants and humans, and how to study it properly. Although I have seen him very rarely, I have the impression that what I learned from him largely exceeds what I learned from textbooks. I promise him that I will always try to look at the smallest detail of what is around us.

During my stay at Heteren I met people of great humanity, in particular Rinse Wassenaar and Leonard Holleman among them. I am indebted to Mw. M. C. Root who helped me a lot and showed sincere hospitality when I arrived in 1995.

And now, to the ‘Alliance’.

In alphabetic order: ‘Bird Killer’ Iris Charalambides, ‘Brazilian Touch’ Francisco de Souza and Joana Salles, ‘The Viking’ Arve Doksater, ‘Lily Willy’ Will Goodall-Copestake, ‘The Small’ Silvia Perez, ‘Polish Resistance’ Beata Sznajder, ‘Dave the Scot’ David Thomson, ‘Wild Dancer’ Monika Zavodna, plus the two Aussies Tracey

Parrish and ‘Sleepy Dave’ David Fullagar. Thanks for the countless cheeky e-mails, dinners, pit parties, birthday parties, Easter lunches, Christmas dinners, happy Fridays, gratis patat and expensive pizzas (by the way thank God Sa Lolla exists), nights out in Nijmegen, movies, wild dancing nights and everything that allowed us to live a *quasi*-normal life. Not to mention all the endless conversations about life with research and research without life. I will never forget you. I hope you all will have an honourable life and career. Keep avoiding agendas, and see you all in Italy for a gangster wedding. I cannot forget to mention my flat mates Gwendolyn Koldenhof, Aliou Saidou, Robert Jan van Zandaam, and ‘The Greek Hero’ Sergios Karatzos. In addition, Douwe Buma, Jelmer Elzinga, Christel Mols and Marije Verduijn at the NIOO and others who left earlier the Institute, Kate Oddie and Michele Incagli among them. I express deep appreciation to Jelmer for his outstanding dance performances at the ‘Het Gat’. Special acknowledgments to ‘Lazziale’ Claudio Carere for his virtuoso guitar performance at my 30th birthday and to my friend ‘Bravo man’ Albert de Hoon who made a Dutch summary of this dissertation. Albert, thanks for showing me how great Kriek beer is. I hope you did not learn how to behave like a Rimini man.

My parents and my family always supported me. My generation has been given unconditioned love and protection in the face of real adversity. Given the unprecedented challenges of the near future, I am not sure that the next generation will be that lucky. Finally, I wish to mention Elena who brought sunshine to me with hundreds of letters and phone calls.

Curriculum Vitae

Fabrizio Grieco was born in Pavia (Italy) on July, 14th, 1969. He obtained in 1988 his Secondary School Diploma at the National Technical Institute (area computer science) of Pavia. In 1992 he graduated in biology with honours at the University of Pavia, with a dissertation on the breeding biology and colony structure in tree-nesting Great Cormorants. From the end of 1995 to 1996 he worked on the timing of reproduction in the Great Tit at the Netherlands Institute of Ecology, Heteren. At the same time he started an ongoing research project in collaboration with Dr. Adriaan Kortlandt for the study of the processes of formation and maintenance of the pair bond in the Cormorant in the zoo colony of Amsterdam. In 1997 he started his PhD project at the Netherlands Institute of Ecology on the breeding ecology of the Blue Tit.

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