Post-Fledging Range use of Great Tit Parus major Families in Relation to Chick Body Condition

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The timing of breeding and the chicks' fledging condition are major fitness-relevant traits in the Great Tit *Parus major*. Yet, the proximate mechanisms relating these traits to differential survival and recruitment are largely unknown. We analysed the range use of Great Tit family groups during the first 20 days after fledging, i.e. the period of post-fledging dependence, in relation to the juveniles' body condition. Radio-telemetry and colour marks were used to track 25 families with 107 chicks. The post-fledging home-ranges of families with fledglings of good condition (average body mass 19 g) were c. 3 times larger than of those with poorly nourished (average 15 g) young. The rate of movements exceeding 50 m per hour was also positively correlated to the chicks' mean fledging mass. We hypothesise that the fledglings' body condition resulted in large differences in flight performance, and consequently, spatial behaviour of the family groups. The slow movements and the close grouping of chicks of poor body condition likely increase their vulnerability to predation. In the late season, fledglings of poor condition had significantly lower food intake rates compared to those of good condition. We suggest that the relevance to survival and thus, fitness of the fledglings' physical condition, is via the behavioural and metabolic competence, which in turn may affect flight performance, range use, energy intake rate, and ability to escape predation.

Key words: reproduction, body condition, survival, range use, radio-telemetry, Great Tit, *Parus major*

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INTRODUCTION

The physical condition of bird fledglings is a main determinant of their subsequent survival and recruitment into the breeding population (overview in Magrath 1991, Verboven & Visser 1998, Naef-Daenzer *et al.* 2001a, Garant *et al.* 2004). However, the chain of proximate mechanisms that relate variation in condition to differential survival and eventually to fitness is largely unknown. Here, we use the Great Tit *Parus major* as an example organism to analyse the immediate consequences of juvenile body condition on their behavioural performance and potential links to the marked condition-related differentials in post-fledging survival (Naef-Daenzer *et al.* 2001a).

Since the energy flow to a brood of Great Tits is mainly limited by the abundance and size of prey (Keller 1993, Naef-Daenzer & Keller 1999, Naef-Daenzer *et al.* 2000), the parents have to

trade-off the number of chicks against chick quality (e.g. Smith *et al.* 1989, Perrins & McCleery 1989, Verboven & Visser 1998, Verhulst *et al.* 1995, Both *et al.* 1999, Naef-Daenzer & Keller 1999). The Great Tit is under strong selection synchronising the timing of breeding with the seasonal patterns in both prey availability and predation pressure. Optimally timed broods have the nestling period coincide with the 'caterpillar peak' (e.g. Perrins 1996, van Noordwijk *et al.* 1995, Naef-Daenzer *et al.* 2004), but are early enough to avoid the 'predation peak' on tit fledglings later in the season (Naef-Daenzer *et al.* 2001a). The relevance to fitness of these trade-offs is via differential survival in the period from fledging to recruitment (Dhondt 1979, Drent 1984, van Noordwijk *et al.* 1995, Verboven & Visser 1998, Naef-Daenzer *et al.* 2001a), however, the relevant ecological pathways remain unclear. Life history theory suggests three proximate mechanisms. The first hypothesis states that energetic limitations during the post-fledging period are the main determinant of differential survival. Energy constraints may indeed arise due to the seasonal decline of food resources (Martin 1987, Carey 1996), while the frequent moves increase the chicks' energy demands (Tatner & Bryant 1986, Nudds & Bryant 2000) just in this period. Declining food availability during summer and fundamental changes in food resources in autumn may further influence juvenile survival (van Balen 1980, Bejer & Rudemo 1985, Lehikoinen 1986). The second hypothesis suggests that good physical condition of fledglings is of prime importance to avoid predation, particularly during the very first days after leaving the nest (Drent 1984, Verhulst *et al.* 1997, Delestrade *et al.* 1996). Recent research revealed that predation during the first post-fledging weeks is indeed a major proximate cause of mortality of Great Tit fledglings (Naef-Daenzer *et al.* 2001a, Götmark 2002). This indicates that predator-prey interactions have a strong impact on the tits' reproductive system and quickly result in strong differential survival in relation to body condition and fledging date. The two hypotheses are not mutually exclusive. On the contrary, an interaction of the two mechanisms may even increase differentials in chick survival. A third hypothesis predicts that physical condition is a determinant of performance in intraspecific competition for resources and thus, of survival. Here, we analyse the range use of entire bird families in the period in which juveniles still depend on parental care. Thus, although intraspecific competition cannot be excluded at the level of individual behaviour (both parents and juveniles), the *competition hypothesis* is not evaluated in detail in this article.

A bird's physical condition has manifold effects on its physiological and behavioural performance, for example the metabolic capacity (Simon *et al.* 2004), the ability to escape a dangerous situation (the *predation hypothesis*, Veasey *et al.* 2000), or its social rank (Gosler & Carruthers 1999, Carrascal *et al.* 1998). The effects of a young bird's condition on its performance in spatial behaviour and in turn its access to resources (the *energy limitation hypothesis*) have hardly been investigated. Here we analyse effects of offspring condition on the home-range dimensions and movements of Great Tit family groups. First, we test whether the size of post-fledging home-ranges varies in relation to chick condition. If poor condition of the chicks impairs their flight performance, this will affect the range of action and thus, access to food resources. Second, we analyse the short-term movements within the home-ranges in relation to age and condition. Differences in body condition and thus, flight performance (Veasey *et al.* 2000, Simon *et al.* 2004), may strongly affect a bird's frequency and speed of movements for foraging and other daily routines.

METHODS

The study was conducted from 1995 to 1997 in the 'Blauen' region, a mixed deciduous/coniferous forest of the north-eastern Jura near Basel, Switzerland, at altitudes of 300–600 m above sea level. Over an area of c. 3 km^2, some 350 nest-boxes were placed along forest roads and footpaths. A detailed description of the methods, par-

ticularly the radio-tagging technique, is given in Naef-Daenzer *et al.* (2001a,b) and Naef-Daenzer (2007). Here, we give a brief summary. From nestling day (age) 15, broods were visited daily but only for quick visual inspections to prevent premature fledging. The age of nestlings was determined using standard tables of size and feather development derived from chicks of known age. Immediately before fledging, that is, on nestling day 17 to 20, juvenile tits were marked and weighted. All chicks of a brood were individually colour-marked and 3–4 juveniles per brood were instrumented with a radio-tag. This allowed transmitter failures and losses to be discerned from mortality because surviving birds with 'dead' or lost radios could be recorded visually as long as at least one transmitter per family was working (Naef-Daenzer *et al.* 2001b).

To assess post-fledging survival (Naef-Daenzer 2001a), 178 Great Tit fledglings were radio-tagged using an improved version of the miniature transmitter presented in Naef-Daenzer (1993). The tags were mounted with a Rappole-type harness made from 0.5 mm cotton cord (Rappole & Tipton 1990). Including the harness, the total mass of these tags was 470–480 mg, which is 2.4–3.3% of a Great Tit's fledging mass. The aerial consisted of 7 cm of 0.15 mm multithread steel of green colour. Individuals of less than 14 g were colour-marked but not equipped with transmitters. Transmitters and attachments were first tested on captive juvenile tits. We observed no differences in behaviour or manoeuvrability between tagged and untagged birds. A control group of 88 Great Tit fledglings were individually colour-marked or left unmarked (max. 1 per brood). As with radio-tagged birds, waterproof pencils (Edding 500) were used to apply one or two bands of colour on the ventral feathers. The recombination of two out of four colours (black, blue, red, none) allowed each bird of a family to be marked individually, but patterns occurred repeatedly among families. Except for very short periods, the families were well separated from each other, thus repeat patterns did not confound the identification of individuals. A quantitative analysis of possible adverse effects of radio-tagging on survival and short-term movements is given in Naef-Daenzer *et al.* (2001b).

Our estimate of the expected fledging day was imprecise. While some broods had already fledged when the field team arrived for tagging (<10%) others remained in the nest for up to two days. Hence, on a qualitative level, there is no evidence that the late handling of the chicks caused them to fledge prematurely.

Data collection

Data on range use and behaviour were collected for a sub-sample of 25 families with 107 chicks. After locating the family groups by 'homing-in' (Kenward 2001), all birds were identified visually. Observation sessions lasted for 1 hour per family. To assess short-term movements and to collect data on behaviour and resource selection, additional observations were carried out on families selected at random. The total observation time per family was therefore 2 to 6 hours per day depending on the number of families that were tracked simultaneously. Locations were recorded at 6-min intervals on topographic maps and digitised using a planimeter. In each of the intervals, group size and behaviour of adults and chicks were recorded according to the following scheme: the minutes one and two were used to determine the location of the family party, to record the number and identity of birds present and to estimate the maximum distance between the most distant birds in the party (four categories: <5 m, 5–10 m, 10–50 m, >50 m). We also recorded the approximate height of the group (four categories: on ground, <5 m, 5–10 m, >10 m). The minutes three and four were used for recording the behaviour of a focus-animal (Altmann 1974) selected randomly among the juvenile birds present, and during the minutes five and six of the observation cycle, a similar focus-record was made for one of the adults.

Analysis

We used a fixed kernel procedure to estimate the size of family home-ranges ($h = 50$ m, grid cell size 10x10 m; Worton 1989, 1995). Calculations were performed with the software GRID (Naef-

Daenzer 1993, Wood *et al.* 2000), using the 30% and 90% contours of the density distribution as home-range and core-area estimates, respectively. To analyse home-range dimensions in relation to brood condition, the effect of sample size (i.e. the observation time per family) must be taken into account. To test for an effect of fledging mass on home-range size, we therefore used multiple regression models including the location sample size as a correction factor.

Animals typically move non-randomly, thus consecutive locations are serially correlated. This does not impose problems with kernel home-range estimates. However, if locations are collected too infrequently or over too short observation periods parts of the home-range will be missed, which cannot be corrected for in any analysis. De Solla *et al.* (1999) have shown that eliminating serial correlation may substantially reduce the accuracy of home-range estimates. In home-range estimates, the single location is not used as an independent replicate, but is the basis to calculate one estimate of the animals' home-range. Therefore the correct degrees of freedom representing the units of the analysis (the family groups) is used.

To test the frequency of movements in relation to fledgling condition, we used a binary variable where 0 refers to distances of ≤ 50 m (i.e. the family staying at the same site, criterion according to field tests of location/mapping error), and 1 for distances exceeding 50 m (i.e. the family moved to a new location).

To test effects of season, age, and condition of fledglings on the average food intake we used the observation intervals (n = 653) in which focus samples of juveniles were achieved. The total food intake was estimated as the sum of food items delivered by both parents and the items collected by the juveniles themselves. Estimating the mass of items was impossible. Due to the small sample size, the families were assigned to rough categories in relation to season ('early': fledging date < median fledging date of the year; otherwise 'late'), age (<10 d / ≥ 10 d from fledging) and physical condition ('poor': fledging mass < mean fledging mass of the year, otherwise 'good').

RESULTS

Home-range area

The average area of post-fledging home-ranges was 8.3 ha ± 3.2 SD (range 3.2–13.7 ha, 90% contour, n = 18 families with >100 locations). These ranges were considerably larger than the area used during the nestling period (4.7 ± 2.1 ha, Widmer & Naef-Daenzer, unpubl. data). The area of the minimum convex polygon including the largest home-range covered up to 77.2 ha, which illustrates that the birds had made considerable excursions out of the core ranges. Neighboured ranges overlapped largely, and we did not observe any agonistic interactions amongst family groups (Fig. 1).

We found a strong positive effect of the chicks' average fledging mass on the size of the post-fledging home-ranges of tit families (R^2_{adj} = 0.35, $F_{2,23}$ = 8.18, P < 0.002; multiple regression model in Table 1, Fig. 2). We excluded one exceptionally large split home-range (Family 242-1995, shown in Fig. 1). The result suggests that the home-range of a family with 19-g chicks was about twice the size of that of a family with 15-g fledglings. The non-linear increase of the home-range area with sample size is biologically irrelevant but indicates that samples of less than 100 locations resulted in a considerable underestimation of the effective home-range.

A similar, weaker relationship also existed for the core-area in the home-range, i.e. the area integrating the 30% of the location distribution with highest use density (R^2_{adj} = 0.22 $F_{2,23}$ = 4.98, P < 0.02). This suggests that families with well-conditioned chicks used significantly larger areas for both the daily routines (the core-areas) and for exploring the habitat (the total home-range) than those with chicks of low condition. We conclude from this that fledgling condition had a marked effect on the range covered during the period of post-fledging dependence.

Short-term movements of family parties

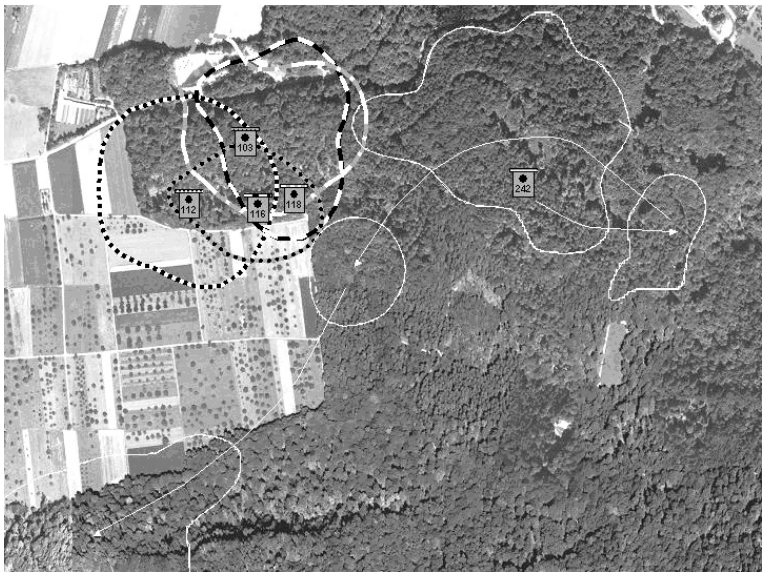The body condition of fledglings affected the frequency and speed at which the family groups

Figure 1. Ortho-photo of a part of the study area with the post-fledging home-ranges of four Great Tit families observed in 1996. The approximate location of nest boxes and the 90% location kernel density contours are shown. Technical details of the kernel procedure are given in the methods section. The examples illustrate the large mutual overlaps between the home-ranges. Also shown is the exceptionally large and split home range of family 242 (1995) which was excluded from statistical analyses of home-range dimensions (©SWISSIMAGE; reproduced with permission of swisstopo, BA081376).

Table 1. Multiple regression results for the home-range area used by Great Tit families in relation to the average fledging mass of the brood. The location sample size was included into the model to correct for differences in total observation time. One family with exceptionally large split home-range was excluded from the analysis, but is shown in Fig. 2 (white dot). Dependent variable: Area covering 90% of locations (ha). $n = 24$ family groups, $R^2_{adj} = 0.35$, $F_{2,23} = 8.18$, $P < 0.002$.

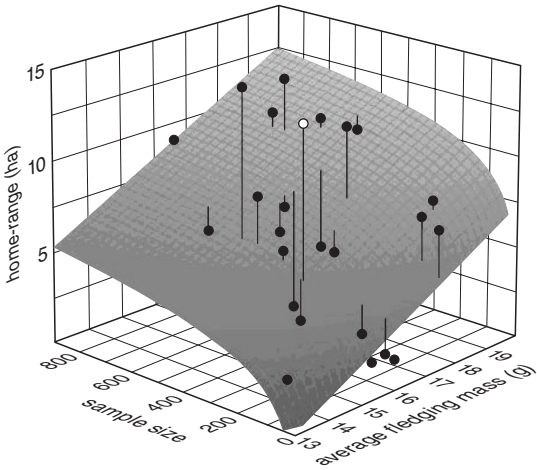| Factor	$B \pm SE$	t_{21}	P
Constant	-19.22 ± 8.09	-2.38	0.03
Ln(number of locations)	1.652 ± 0.56	2.93	0.008
Avg. fledging mass, g	1.024 ± 0.49	2.09	0.05

Figure 2. Multiple regression model for the area of post-fledging home-ranges in relation to location sample size and average fledging mass of the brood. Based on observations of 24 families (black dots). One outlier was excluded from the statistical analysis (white dot). Regression results are given in Table 1.

Table 2. Logistic regression results for the probability that a family moved over more than 50 m within one hour in relation to the average fledging mass of the chicks. –2 Log Likelihood = 1669.58, χ^2_2 = 53.68, P < 0.0001.

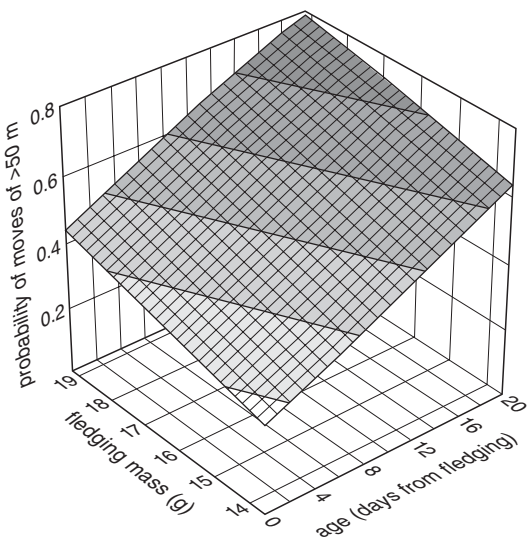| Factor	$B \pm SE$	Wald χ^2	df	P
Constant	–2.80 ± 0.76	13.65	1	<0.0001
Avg. fledging mass, g	0.13 ± 0.045	8.60	1	0.003
Days from fledging	0.078 ± 0.013	36.71	1	<0.0001

Figure 3. Multiple logistic regression results for the probability of moves of more than 50 m per hour in relation to age (days from fledging) and average fledging mass of the brood. Statistical results are given in Table 2.

moved within their home-ranges. A logistic regression model showed a strong positive effect of both age and average chick fledging mass on the rate of movements (Table 2, Fig. 3).

Families that had lost all their chicks during post-fledging dependence had moved significantly less intensely compared to those of which at least one chick reached independence (ANOVA, chick survival (two categories: all chicks lost / ≥ 1 chicks survived): $F_{1,236}$ = 4.69, P = 0.03, controlling for age (four categories): $F_{3,236}$ = 0.89, P = 0.44). On average, the families losing their entire brood had moved at a pace of 73 m h^{-1} compared to 126 m h^{-1}

in families with surviving chicks. This result indicates a potential effect of short-term movements on chick survival, however, our data do not allow a relationship between spatial behaviour and mortality incidents to be established.

Prey availability and food intake of juveniles

After the peak around mid-May, the average biomass of prey quickly declined such that most post-fledging tit families experienced relatively low food abundance (Fig. 4). Since tree species that still offered abundant food such as oak *Quercus* sp. or wild cherry *Prunus* sp. made up for less than 5% of the canopy, rich food resources were rather rare and widely dispersed. We found a significant effect of season and fledgling condition on the average food intake rate of tit juveniles (ANOVA results given in Table 3). In the late season, intake rates were generally lower than in the early season ($F_{1,646}$ = 13.88; P < 0.001). Furthermore, the sig-

Table 3. Effects of season, age and body condition on the average food intake rate of Great Tit fledglings. ANOVA, dependent variable: total intake rate in items per hour. n = 653 time intervals with visual observations of juveniles. Effect sizes are shown in Fig. 5

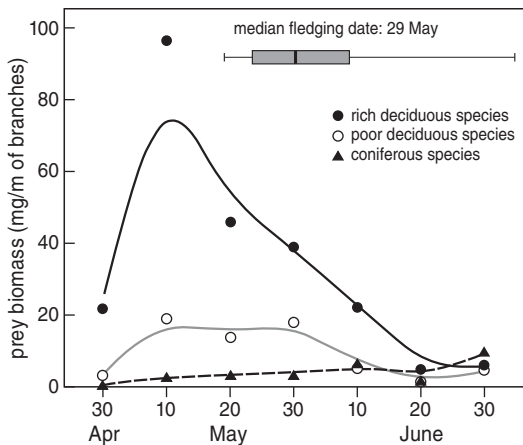| Effect	$F_{1,646}$	P
Intercept	121.50	<0.0001
Season (early/late)	13.88	<0.001
Age class (<10 d / ≥ 10 d)	0.37	0.54
Condition (good/poor)	1.23	0.26
Season x Age class	0.10	0.75
Season x Condition	4.76	0.03
Age class x Condition	3.13	0.077

Figure 4. The seasonal development of prey biomass (caterpillars and spiders) in the Blauen area for three categories of tree species in 1995–1997. Closed dots: food-rich deciduous tree species (oak *Quercus* sp., maple *Acer* sp., cherry *Prunus* sp.). Open dots: poor deciduous species (Beech *Fagus silvatica*, Ash *Fraxinus excelsior*, Hornbeam *Carpinus betulus*). Triangles: coniferous species (*Pinus* sp., *Abies alba*). Lines were fitted by least squares smoothing. The boxplot in the upper part gives the frequency distribution of fledglings produced in the three years. Most broods fledged when food availability was declining but still relatively high. From c. 20 June food availability was equally low in all tree species.
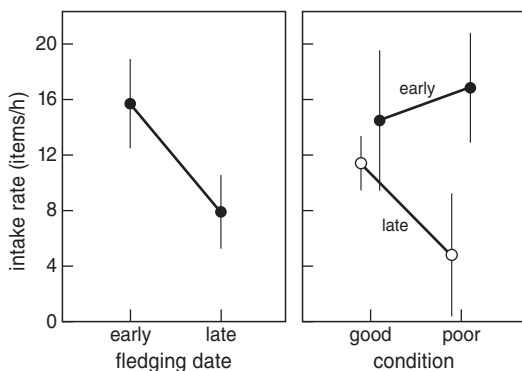

Figure 5. Variation of the total food intake of juvenile Great Tits in relation to season and body condition. Full ANOVA results are given in Table 3. Graphs show corrected means and SEs for all other variables in the analysis.

nificant interaction of season x fledging mass indicates that the drop in intake rates was higher for juveniles of poor physical condition compared to well-conditioned conspecifics ($F_{1,646} = 4.76$; $P = 0.03$, Fig. 5).

DISCUSSION

The relationships of the post-fledging range use of Great Tit families with the fledging condition of the juveniles indicate how a phenotypic trait (physical condition) is related to behavioural performance (movements and range use). Families with poorly nourished chicks moved at a much lower rate than those with chicks of high average fledging mass, and they did so within a much smaller area of forest. This was particularly pronounced in the first five days after leaving the nest, which is also the period of maximum mortality (Naef-Daenzer *et al.* 2001a). The results suggest that poor physical condition results in poor behavioural performance and in turn poor survival prospects. Proximately, reduced body condition likely restrains the juveniles' mobility and use of space, because of their deficient flight performance and the predominantly short distances of moves. This may have serious consequences in at least two aspects, foraging ecology and predator impact. First, families that moved rarely may have been handicapped in exploiting food resources (the *energy limitation* hypothesis). The observed seasonal decline in food intake rates in fledglings of poor physical condition suggests that weak animals face increasing energetic deficiencies when food resources decline. We conclude that poorly conditioned fledglings are handicapped in gaining food, however, we were unable to estimate the daily energy intake on the basis of our restricted sample.

Second, the results are in agreement with experimental evidence that physical condition is a prime factor determining a birds' power for escape (Veasey *et al.* 2000). Probably, young tits of poor body condition had a seriously reduced ability to avoid predation and to escape dangerous situa-

tions. Also, we hypothesise that the low rate of short-distance movements of poorly conditioned chicks made them more likely to be discovered by potential predators because they remained begging on the same spot for considerable time. In fact, some individuals were so weak and unvigilant that they could have been captured by hand. Occasional observations in the field made clear that physical strength indeed enables a tit to escape an attack of, for example, a woodpecker *Dendrocopos* sp. or a Jay *Garrulus glandarius*. These are unable to kill a tit fledgling instantly, and once we observed a (strong) tit fledgling struggling off the grasp of an ambushing Great Spotted Woodpecker *D. major*. Furthermore, observations of Great Tit and Coal Tit *P. ater* pairs that had lost all chicks within 1–2 days from fledging suggest that predators are apt to return to the place of a first capture although such an effect could not be demonstrated statistically (Naef-Daenzer *et al.* 2001a).

The tracking results provide further evidence that the period of post-fledging dependence is a very important phase in the reproductive system of the Great Tit. It appears that much of the relevance to survival and thus, fitness, of many of the parents' reproductive decisions is via differential behavioural performance during the very early post-fledging period (Drent 1984, Naef-Daenzer *et al.* 2001a). Our results support both the *energy constraint* and the *predation* hypotheses, although they do not proof either of them. This first investigation indicates a chain of relationships that link the physical condition to the short-term survival prospects, and thus, fitness. Further experimental research is required to quantify, for example, the impact of restricted home-range use on the food intake rate of the juvenile birds and thus, their further development during the post-fledging period.

There was no evidence that the parents of poorly conditioned broods behaved less well than those of broods with high fledging mass. By contrast, the frequency of feedings per fledgling and unit time was higher in broods with low fledging mass, which suggests that the parents of these broods made attempts to compensate their deficiency in condition (Naef-Daenzer, unpubl. data).

So far, the mechanisms that determine how frequently and where a family party moves to are unclear. The data do not provide information on the movements of individual chicks and thus the analysis cannot account for any within-family effects of fledgling condition and behaviour.

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SAMENVATTING

Bij Koolmezen *Parus major* zijn de timing van broeden en de conditie van de jongen bij het uitvliegen kenmerken met belangrijke consequenties voor de fitness van de vogels. Er is echter weinig bekend over de manier waarop deze kenmerken overleving en vestiging in de broedpopulatie beïnvloeden. In het onderhavige onderzoek wordt het gebiedsgebruik beschreven van mezenfamilies gedurende de eerste 20 dagen na het uitvliegen van de jongen (de periode waarin jongen onafhankelijk worden van hun ouders) in relatie tot de conditie (gewicht) van de jongen bij het uitvliegen. Met behulp van radiotelemetrie en het aflezen van gekleurringde mezen werden 25 families met 107 jongen gevolgd. Families met jongen in goede conditie (gemiddeld gewicht 19 g) gebruikten een ongeveer drie keer zo'n groot gebied als families met jongen in slechtere conditie (gemiddeld 15 g). De conditie bij het uitvliegen was positief gecorreleerd met de verplaatsingssnelheid, tenminste voor families die meer dan 50 m per uur aflegden. Wij veronderstellen dat de conditie bij het uitvliegen van invloed is op de vliegprestatie en daarmee op het gebiedsgebruik van de familiegroepen. De lage verplaatsingssnelheid en dichte clustering van jongen in slechte conditie resulteren waarschijnlijk in een groter predatierisico. Jongen in slechte condities hadden een relatief lage voedselopnamesnelheid, vooral laat in het seizoen. Wij veronderstellen dat de effecten van de conditie bij het uitvliegen op de overleving (en dus fitness) tot stand komen door effecten van conditie op gedrag en fysiologie, die vervolgens vliegprestatie, gebiedsgebruik, energieopname, en predatierisico beïnvloeden.   (NJD)