

Nadia Nour · David Currie · Erik Matthysen
Raoul Van Damme · André A. Dhondt

Effects of habitat fragmentation on provisioning rates, diet and breeding success in two species of tit (great tit and blue tit)

Received: 23 June 1997 / Accepted: 29 December 1997

Abstract The aim of this study was to examine the effects of forest fragmentation on the ability of parent birds to provide their young with an adequate food supply. To examine whether prey population densities of the great tit (*Parus major* L.) and the blue tit (*P. caeruleus* L.) vary between study areas in different forest size classes we compared provisioning rates and chick diet and related these parameters to breeding success. We filmed 217 nests over two breeding seasons and collected data on frass fall as a general estimate of caterpillar availability. Nests which were attended by none or one parent only during filming ($n = 46$) were excluded from the analyses. In both years and for both species feeding rates were highest in the smallest fragments and lowest in the large forest. There was also a suggestion that differences in feeding rates between areas vary between years. We found no consistent tendency for prey size to change with forest size, although both species brought slightly smaller prey items to the nest in the smallest forest fragments and feeding rates correlated negatively with prey size. Caterpillars were the main item fed to nestlings, in both species. We found no evidence to suggest that either frass fall or the proportion of caterpillars in the diet varied with forest size. There was also no correlation between mean frass fall and the total number of caterpillars brought to the nests, in either species. Breeding success, as measured by clutch size, brood size, fledging weight and fledging success, did

not differ between the small fragments and the large forest, in either species. There was also no relationship between provisioning rate (as concerns volume of prey fed to nestlings and the quality of chick diet) and breeding success parameters. In conclusion, this study does not suggest suboptimal foraging or breeding conditions in small fragments compared to a nearby large forest, for either species.

Key words *Parus* spp. · Forest size · Diet · Provisioning · Breeding success

Introduction

In many parts of the world, increased human activity has altered the original landscape, leaving a series of small, isolated patches of natural habitats, surrounded by a matrix of different vegetation and/or land use (i.e. habitat fragmentation). This can result in a reduction of the quality of the remnant patches, thus affecting populations of organisms inhabiting them (see reviews in Saunders et al. 1991; Opdam 1991). A number of studies have considered the effects of habitat fragmentation on bird populations, including changes in species composition and abundance, predation, food availability and genetic variation (Opdam et al. 1989; Møller 1989; Riddington and Gosler 1995; Robinson et al. 1995).

Food abundance and availability are important factors affecting the reproductive success of birds (Lack 1968). Population studies of tits (*Parus* spp.) carried out in different habitats have found smaller clutch sizes and a reduction in fledging success in evergreen woodland, gardens and hedgerows compared to mature deciduous woodland, which have been attributed to differences in diet and food availability (Gibb and Betts 1963; Van Balen 1973; Cowie and Hinsley 1987; Blondel et al. 1991; Riddington and Gosler 1995). Such differences might also result from effects of habitat fragmentation on prey populations. For instance, the density of winter moth (*Operophtera brumata*), one of the main prey items in the

N. Nour (✉) · D. Currie¹ · E. Matthysen R. Van Damme
A.A. Dhondt²
Laboratory of Animal Ecology, Department of Biology,
University of Antwerp (UIA),
Universiteitsplein 1, B-2610 Antwerp, Belgium
Fax: 32-3-820 22 77; e-mail: nour@uia.ua.ac.be

Present addresses:

¹ Laboratory of Ecological Zoology,
Department of Zoology, University of Turku,
Fin-20014 Turku, Finland

² Cornell Laboratory of Ornithology,
159 Sapsucker Woods Road, Ithaca, NY 14850, USA

diet of nestling tits in oak woodlands (Betts 1955; Van Balen 1973; Perrins 1979), has been shown to be adversely affected by habitat fragmentation (Van Dongen et al. 1994). If other prey species undergo similar decreases in abundance due to fragmentation, this will result in a reduction in food availability, possibly causing tits to suffer from food shortage. If, on the other hand, the spatial distribution of different prey species is not affected in the same way (e.g. some species may benefit from fragmentation), we expect a change in diet and possibly a change in food quality, with insectivorous birds switching to alternative/more common prey types.

If arthropod prey organisms are reduced in quantity or quality in habitat fragments, habitat fragmentation might result in breeding birds experiencing a cost in terms of reduced reproductive success. This paper examines the effect of forest fragmentation on chick feeding rates and diet in the great and blue tits. We investigate whether there are differences between areas in fledgling weight and breeding success, and whether these can be attributed to differences in provisioning rates and chick diet. We also collected data on frass fall as a general estimate of caterpillar availability.

Methods

Study areas

The study was carried out in one study plot inside a large forested area of c. 200 ha, and in 12 patches of mature woodland, varying in size from 0.8 to 25 ha. All study areas are situated near Antwerp, N. Belgium and contain established nestbox populations (Table 1). Forest fragments were grouped into four size classes: (1) *large*: a 12.5-ha area with nestboxes in a 200-ha forest site (area PB: plot B from Dhondt et al. 1990); (2) *medium-sized*: 17 ha with nestboxes in

a 25-ha fragment of forest and parkland (area CX: plot C from Dhondt et al. (1990); (3) *small*: three fragments between 6 and 11 ha, fully covered with nestboxes; (4) *very small*: eight fragments between 0.4 and 3 ha, fully covered with nestboxes. These forest fragments are dispersed in a mainly agricultural landscape and are separated from one another by meadows, fields and residential areas. Most forest fragments are separated from one another by at least 200 m of open area. Two-thirds of nestboxes had 32-mm entrance diameters and were mainly occupied by great tits, one-third had 26-mm entrance diameters and were only occupied by blue tits.

Vegetation in all study plots is dominated by common oak *Quercus robur* (70–90%), interspersed with individual trees of other species (5–20%), such as beech *Fagus sylvatica*, birch *Betula* spp., larch *Larix decidua* and sycamore *Acer pseudoplatanus* (for further details, see Nour et al. 1997). In area CX beech is relatively more abundant than at the other sites, and vegetation is more diverse.

Nest monitoring

From late March, and throughout the breeding season, nestboxes were checked weekly, the contents noted and first-egg date (FED), clutch size, hatching date, brood size and fledging success (number of fledglings per egg, *f/e*) determined. All broods were weighed at the age of 15 days as a unit, from which mean chick weight on day 15 (brood weight / brood size) was calculated. Mean chick weight was used as a measure of weight at fledging (Perrins 1979).

Feeding rates

Parent birds were trapped at the nest when the chicks were 8 (occasionally 7) days old, and individually colour-ringed. A cage/perch, which allowed access to the nesthole in one direction only, and which prevented the parent birds from flying straight into the nest hole (Currie et al. 1996) was mounted the following day. Parental feeding was filmed 1 day later still, to obtain information on provisioning rate and diet during the peak in chick feeding (Perrins 1979). For filming video cameras (8 mm and VHS), were placed on a tripod about one metre from the nest. Feeding rate calculations started from the first feed (for more details see Currie et al. 1996)

Table 1 Study areas, area classes, forest size, number of nestboxes and number of nests filmed per area. Note that in area 1 (PB) the actual study area was 12.5 ha in size

Area			Nest boxes available		Nests filmed ^a			
Code	Class	Size (ha)	Great tit	Blue tit	Great tit 1994	Great tit 1995	Blue tit 1994	Blue tit 1995
PB	1	ca 200	118	59	8	13	6	7
CX	2	17	100	50	6	9	3	9
ZZ	3	11.1	64	32	7	7	5	3
KB	3	10.0	60	30	6	2	8	6
LO	3	6.2	38	20	3	5	5	3
Total					16	14	18	12
ZN	4	1.5	12	6	2	2	2	2
HN	4	2.8	15	8	2	1	4	3
KL	4	1.6	10	5	1	3	1	3
VS	4	1.3	8	4	2	2	2	3
LW	4	1.0	6	4	1	2	1	2
HM	4	0.8	4	2	1	1	1	0
LS	4	0.5	5	3	0	1	1	1
ZW	4	0.4	4	2	0	1	1	1
Total					9	13	13	15
Overall Total					39	49	40	43

^aExcluding nests attended by 0 or 1 parents during filming

using one hour of recordings after the initial feed. Only first broods were filmed.

A total of 217 nests were filmed over two breeding seasons. No feeds were observed at 6 nests, and only one parent was observed at 40 nests. In 13 of these cases only one parent had been caught prior to filming. We only analysed data from nests where both partners were known to be alive and contributed to chick provisioning (i.e. observed during filming). These were 88 great tit nests and 83 blue tit nests (see Table 1).

Total feeding rates are calculated as the total number of prey items delivered to the chicks per hour (sometimes more than one item per visit; cf. Gibb and Betts 1963; Van Balen 1973; Cowie and Hinsley 1987), and feeding rate per chick as total feeding rate divided by brood size.

Effects of time and date

Parental feeding was filmed between 0700 and 1500 hours EST. Overall total feeding rates did not change with the hour of filming (Spearman rank correlation; great tit, $r_s = 0.16$, $P = 0.2$; blue tit, $r_s = -0.14$, $P = 0.1$). This variable was therefore not considered further. Nests were filmed between 6 May and 3 June 1994, and between 5 May and 29 May 1995. Since first FEDs differ between areas and years (Perrins 1979; Dhondt et al. 1984), we recalculated FED of focal nests as the difference from the mean FED of all nests in the respective area. Filming dates were then expressed in these relative units.

Diet

Prey items brought to the nests were assigned to one of the following groups: Lepidoptera (larvae, pupae and imagines), Diptera, Coleoptera, spiders and "unknown". In 1995 we further distinguished between caterpillars of the three major Lepidoptera families: Geometridae, Noctuidae and Tortricidae, which are said to make up the main food source of tits (Betts 1955; Van Balen 1973; Royama 1970; Minot 1981; see also Cramp and Perrins 1993). Larvae that belonged to other Lepidoptera families were grouped into a separate fourth category; a final category contained all unknown larvae. Winter moths (*Operophtera brumata*, Geometridae) were counted separately. Identification of the caterpillars was facilitated by comparing the video images to photographs of specimens collected in the field, from chicks using neck collars or taken from parents trapped in the nestbox.

Prey size

In 1994, prey lengths were estimated using a scale bar on the perch and were grouped into five size categories. In 1995, actual prey lengths and widths were measured and a volume index was calculated for each prey item using the formulas $(\pi/4) \times L \times w^2$ for Lepidoptera (larvae, pupae and imagines), Diptera and Coleoptera (cylindrical bodies) and $(\pi/6) \times L \times w^2$ for spiders (ellipsoidal bodies), where L = prey length and w = prey width (Blondel et al. 1991).

Mean prey volume delivered per hour (total volume/total number of feeds) and prey volume per chick per hour (total volume/brood size) were also calculated. Due to problems with image resolution from one of the cameras used, volumes were calculated only for 48 great and for 42 blue tit nests.

Food availability

In 1995, frass fall under oak trees was measured in the 24 h prior to filming, to obtain an estimate of caterpillar abundance (Henrich-Gebhardt 1990). Frass was collected by placing a wooden board (25 × 25 cm) covered with a sheet of clear sticky backed plastic

under three large oak trees nearest to the focal nestbox. When the sheets were collected, a paper sheet with 2 × 2 cm grid was attached to the sticky side of the plastic. Sheets were not analysed if it had been raining during the period of sampling. Frass fall was thus measured for 82 out of the 113 nests filmed in 1995. At 6 of these nests only two sheets of frass fall were collected and at 2 only one sheet. Frass fall was counted on ten randomly selected (2 × 2 cm) squares on the grid, the sum of which was used as a measure of frass fall for each sheet. Counts from ten squares were assumed to give a reliable estimate of total frass fall on the board as they correlated well with counts from a larger 5 × 5 square quadrant ($r = 0.88$, $n = 9$, $P < 0.02$). The stage of oak leaf development was recorded for the trees from which frass was collected. Leaf development was categorised as (1) early trees with fully open leaves; (2) intermediate stage with half of the leaves open; (3) late trees with few leaves open.

Statistical analyses

As most of our data were not normally distributed, we used log transformations (feeding rates, prey length and volume, frass fall and fledging weights), arcsine transforms for percentage data (e.g. percentage of caterpillars) and square root transforms for clutch size and brood size (Sokal and Rohlf 1996).

All tests and comparisons on these transformed data were performed with two, three or four-way analyses of variance (ANOVA) or/and co-variance (ANCOVA) using PROC GLM of the SAS statistical package (SAS 1994). These allowed us to simultaneously examine the main effects and two- or three-way interactions between area, species, year and date effects on a variable under investigation. We first tested the full model without the four-way interaction term, and then gradually simplified the model by removing the least significant, highest order interaction one by one. If an interaction was statistically significant we performed separate analyses (e.g. per species) as appropriate. Using GLIM (Crawley 1993) we performed logistic regressions on fledging success, because no transformation can normalise the very skewed distribution of fledging success.

Only significant interactions or/and effects are given in detail.

Results

Total feeding rate

To compare total feeding rates in relation to standardised date of filming (SDF), we used an analysis of covariance, where area, species and year were classes and SDF a covariate. None of the three- or two-way interactions, nor effects of date or year were significant (all $P > 0.1$). Blue tits brought more food to the nest than great tits ($F_{1,166} = 71.62$, $P = 0.0001$) with a mean feeding rate per hour (all areas, both years) of 56 ± 19 for blue tits and 34 ± 18 for great tits.

Feeding rates differed between area classes (area effect, $F_{3,166} = 6.97$, $P = 0.0002$) but there was no indication that feeding rates were less in the smaller fragments (Table 2). On the contrary, feeding rates were highest in the smaller fragments and lowest in the large forest (PB).

Food availability (1995 data only)

The mean number of frass pellets per 40 cm² varied between 13 in area 2 and 52 in area 3 (Table 2). We

Table 2 Mean (\pm SD) total feeding rates (per h), frass fall (per 40 cm²; 1995 data only) and percentage of caterpillars brought to the nest per area class. Means that have the same superscripts do

not differ significantly (least square means test per area on the two years combined). Sample sizes in Table 1

Area classes	Total feeding rate		Frass fall	Percentage of caterpillars	
	Great tit	Blue tit		Great tit	Blue tit
1 (c. 200 ha)	27.1 \pm 08.8	39.1 \pm 09.7 ^a	37.7 \pm 15.6 ^b	84	76 ^a
2 (17 ha)	31.8 \pm 15.2	60.5 \pm 15.7 ^b	13.0 \pm 8.8 ^c	76	85 ^b
3 (10 ha)	34.8 \pm 19.9	55.1 \pm 13.0 ^b	52.1 \pm 40.7 ^a	86	80 ^a
4 (\leq 3 ha)	41.7 \pm 18.6	64.4 \pm 24.0 ^c	31.1 \pm 38.4 ^b	85	83 ^b

performed a two-way ANOVA to test whether frass fall differed between areas, taking into account the stage of oak leaf development (stage). Neither the area \times stage interaction nor the stage effect itself were significant (area \times stage, $F_{7,228} = 0.9$, $P = 0.4$; stage, $F_{2,230} = 0.83$, $P = 0.4$). However, frass fall differed significantly between areas ($F_{3,230} = 27$, $P = 0.0001$). A least square means test ($P < 0.05$) resulted in three groups: class 2 had the lowest amount of frass, classes 1 and 4 were intermediate, and class 3 had the highest amount of frass (see also Table 2). When we included the effect of date (SDF) in an ANCOVA with the same area classes we found that date effects differed significantly between areas (area \times SDF; $F_{1,75} = 5.96$, $P = 0.02$). Separate analyses showed that frass fall decreased with date in areas 3 and 4, where initial frass fall density was very high, but not in the other areas (Fig. 1).

Diet

Prey composition

Caterpillars (Lepidoptera larvae) were the main item fed to the nestlings in both great and blue tits (83% and 82% of all prey items, respectively) with little difference between area classes (between 76% and 85% for all species/area combinations). Geometridae were the commonest family (c. 50% of prey items) followed by Noctuidae and Tortricidae. Surprisingly, winter moth caterpillars made up a low proportion of the diet (between 2% and 18% per species/area combination; overall mean = 11.8%).

To compare proportions of caterpillars in the diet in relation to area and date, an ANCOVA was performed

Fig. 1 Mean frass fall per nest in relation to standardized date of filming for the four study areas

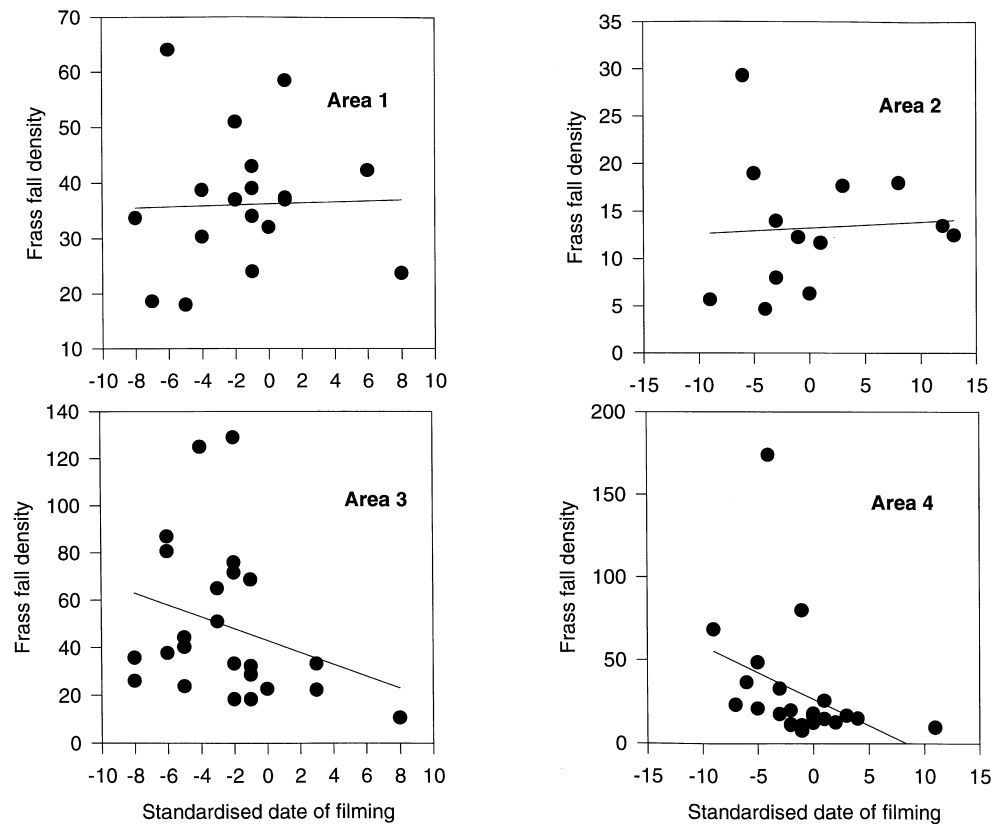
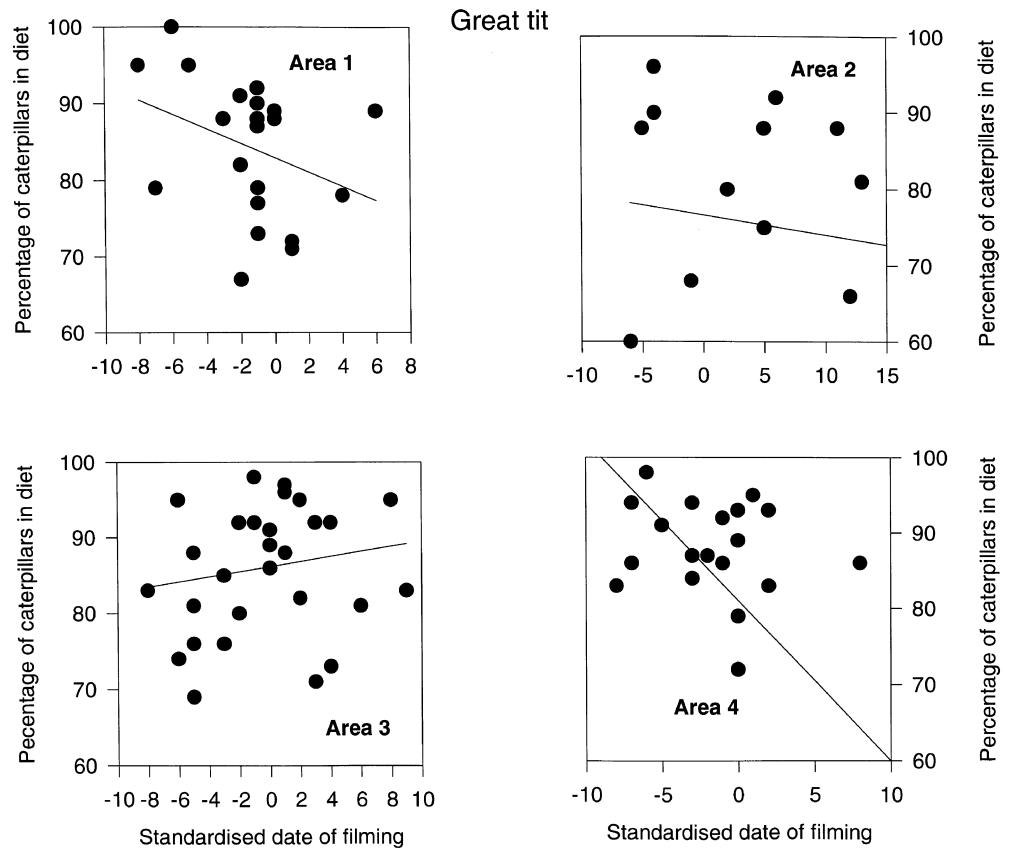


Fig. 2 Percentage of the caterpillars in great tit's diet in relation to standardized date of filming for the four study areas



where areas, species and years were considered as classes and SDF as a covariate.

The effects of date differed between area classes and species in a complex way ($SDF \times area \times sp$; $F_{3,149} = 4.30$, $P = 0.006$). The year effect was non-significant ($P > 0.1$). Separate analyses for both species showed that in great tits the percentage of caterpillars decreased with date in areas 1 and 4, but not in the other areas ($SDF \times area$: $F_{3,80} = 4.35$, $P = 0.007$; Fig. 2, see also Table 2). In blue tits, the proportion of caterpillars decreased with date in all areas in the same way ($SDF \times area$: $P > 0.4$; SDF : $F_{1,78} = 8.44$, $P = 0.005$) and fewer caterpillars were brought in areas 1 and 3 ($F_{3,78} = 3.96$, $P = 0.01$). (Table 2, Fig. 3). Surprisingly, there was no correlation between mean frass fall and the total number of caterpillars brought to the nests, in either species (Spearman rank correlation; great tit, $n = 34$, $r_s = -0.18$, $P > 0.1$; blue tit, $n = 30$, $r_s = -0.3$, $P < 0.1$).

Prey size

We analysed differences in mean prey volume (1995 data only) in relation to area and SDF using an ANCOVA. None of the three or two-way interactions nor the date effect were significant (all $P > 0.1$). Great tits provided larger prey than blue tits ($F_{1,85} = 57.2$, $P = 0.0001$) (Table 3). Mean prey volume differed between areas

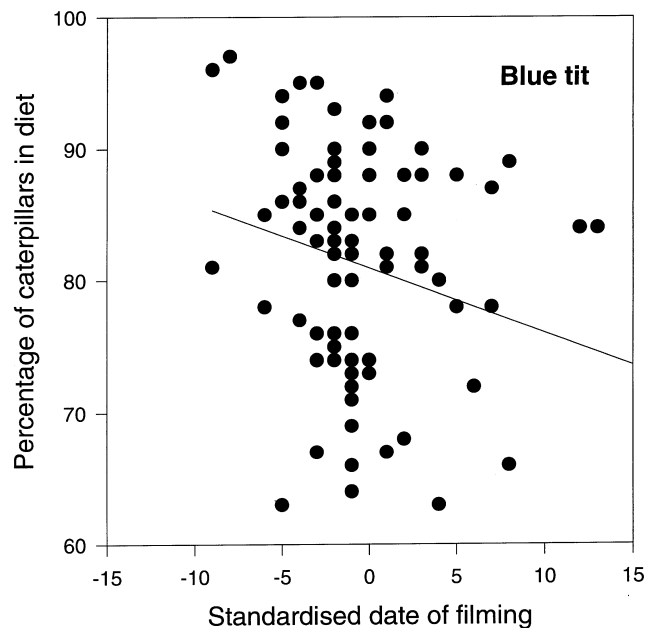


Fig. 3 Percentage of the caterpillars in blue tit's diet in relation to standardized date of filming for the four study areas combined

($F_{3,85} = 5.8$, $P = 0.001$), but there was no consistent trend over the fragmentation classes. The smallest prey were provided in the smallest fragments (area 4) and the medium-sized fragment (area 2) (least square means test,

see also Table 3). We tested whether there was a relationship between mean prey volume and total feeding rate (TFR) in an analysis using area and species as additional factors. This confirmed the effects of area and species as above, and pointed out that mean prey volume was inversely correlated with TFR ($F_{1,84} = 21.8$, $P = 0.0001$) suggesting that provisioning parents altered their feeding frequencies inversely to the volume of food brought (all interactions were non-significant at $P > 0.1$).

The total prey volume received per chick was higher in great tits ($F_{1,88} = 4.1$, $P = 0.04$) but did not differ between areas (area effect and area \times species interaction both $P > 0.1$) (Table 3).

Table 3 Mean (\pm SD) prey volume (mm^3) and mean volume received per chick per area class for great and blue tit. Means that have the same superscripts do not differ significantly (least square means test on the two species combined). Sample sizes in Table 1 (1995 data only)

Area classes	Mean prey volume		Volume per chick	
	Great tit	Blue tit	Great tit	Blue tit
1 (c. 200 ha)	214 \pm 62	130 \pm 20 ^a	664 \pm 243	536 \pm 73
2 (17 ha)	163 \pm 76	103 \pm 16 ^b	606 \pm 269	544 \pm 218
3 (10 ha)	212 \pm 71	125 \pm 27 ^a	644 \pm 218	507 \pm 92
4 (\leq 3 ha)	163 \pm 38	100 \pm 24 ^b	727 \pm 170	612 \pm 220

Table 4 Mean (\pm SD) **a** clutch size, **b** fledging weight, **c** brood size and **d** fledging success for great and blue tits per area class and per year. Means that have the same superscripts do not differ sig-

Breeding success

We used three-way ANOVAs to compare clutch size, brood size, and mean fledging weight between areas, species and years. A logistic regression was used to compare proportion of chicks that fledged in relation to the same variable.

Clutch size differed significantly between areas, species and years. However, both effects of area and species on clutch size differed between 1994 and 1995 (area \times year, $F_{3,598} = 2.92$, $P = 0.03$; species \times year, $F_{1,598} = 5.60$, $P = 0.02$). None of the other interactions were found to be significant (all $P > 0.1$). Separate analyses per year (least square means test, $P < 0.05$) showed that in 1994 differences between areas were not significant while in 1995, clutch size was significantly smaller in area 2 than in the other areas (Table 4a). Blue tits had significantly larger clutches (11.68 ± 1.73) than great tits (9.19 ± 1.37) (means for both years combined).

Mean fledging weight differed between species ($F_{1,588} = 5787.8$, $P = 0.0001$) and years. The effect of area however, differed between years (area \times year interaction effect; $F_{3,588} = 5.72$, $P = 0.0007$). Separate analyses per year show that in 1994 great and blue tit fledglings were on average the heaviest in areas 1 and 3 (least square means test) and lightest in areas 4 and 2. In 1995, fledging weights were still the lightest in area 2 but

nificantly (least square means test per year, on the two species combined in **a** and **b**; per species, on the two years combined in **c** and **d**). Sample sizes in Table 1

Area classes	1994		1995	
	Great tit	Blue tit	Great tit	Blue tit
a Clutch size				
1 (c. 200 ha)	8.77 \pm 1.25	10.75 \pm 1.65 ^a	9.33 \pm 1.64	11.67 \pm 1.35 ^a
2 (17 ha)	8.67 \pm 1.19	11.22 \pm 1.75 ^a	8.16 \pm 1.42	11.67 \pm 1.55 ^b
3 (10 ha)	9.23 \pm 1.30	11.27 \pm 1.99 ^a	9.46 \pm 1.41	12.65 \pm 1.43 ^a
4 (\leq 3 ha)	8.83 \pm 1.65	12.00 \pm 1.60 ^a	9.31 \pm 1.25	11.93 \pm 1.70 ^a
b Fledging weight				
1 (c. 200 ha)	17.96 \pm 0.99	11.38 \pm 0.76 ^a	17.85 \pm 0.89	11.22 \pm 0.65 ^a
2 (17 ha)	16.63 \pm 1.21	10.55 \pm 0.79 ^b	17.36 \pm 1.06	10.98 \pm 0.82 ^b
3 (10 ha)	17.65 \pm 1.01	11.25 \pm 0.67 ^a	18.27 \pm 0.99	11.81 \pm 0.62 ^a
4 (\leq 3 ha)	16.96 \pm 1.57	10.95 \pm 0.96 ^b	18.23 \pm 1.32	11.36 \pm 0.97 ^a
c Brood size				
1 (c. 200 ha)	7.91 \pm 1.49	8.44 \pm 1.68 ^a	8.55 \pm 2.82	9.26 \pm 1.94 ^a
2 (17 ha)	7.74 \pm 1.32	7.33 \pm 1.57 ^b	9.28 \pm 2.88	9.75 \pm 3.07 ^{ba}
3 (10 ha)	8.22 \pm 2.05	8.75 \pm 1.83 ^a	9.86 \pm 2.39	11.21 \pm 2.12 ^{cb}
4 (\leq 3 ha)	8.00 \pm 1.67	8.28 \pm 2.06 ^a	10.27 \pm 3.35	10.43 \pm 2.36 ^{dc}
d Fledging success				
1 (c. 200 ha)	0.90 \pm 0.12	0.91 \pm 0.09 ^a	0.79 \pm 0.19	0.81 \pm 1.19 ^a
2 (17 ha)	0.90 \pm 0.14	0.90 \pm 0.12 ^a	0.83 \pm 0.21	0.83 \pm 0.26 ^a
3 (10 ha)	0.88 \pm 0.17	0.92 \pm 0.12 ^a	0.87 \pm 0.14	0.88 \pm 0.11 ^a
4 (\leq 3 ha)	0.91 \pm 0.13	0.89 \pm 0.15 ^a	0.85 \pm 0.24	0.88 \pm 0.16 ^a

did not differ significantly between the three other areas (see also Table 4b).

Breeding success as measured by fledging success, did not differ between years (also no significant interactions of year with area or species, $P > 0.1$) but was influenced by a species \times area interaction ($\chi^2 = 8.8$, $df = 3$, $P = 0.03$). There was no area effect in great tits, while in blue tits fledging success was smaller in area 1 (least square means test, see also Table 4c, d).

Provisioning rates and breeding success parameters

To test the relationship between breeding success (mean fledging weight and fledging success at focal nests) and provisioning variables, we performed an analysis of covariance (per species) with area as a class and volume per chick (1995 data only) or percentage of caterpillars as a covariate.

In neither species did the relationship between provisioning rate and breeding success differ between areas, as revealed by non-significant interactions terms between provisioning variables and area (all $P > 0.1$). Surprisingly, we found no evidence that fledging success or weight were related to total prey volume per chick (1995 data only; $P > 0.1$). Neither did the percentage of caterpillars in the diet contribute to any of these components of breeding success ($P > 0.1$). The latter result remained the same when analyses were separated per year.

Discussion

The aim of this study was to investigate to what extent a presumed reduction of the quantity or the quality of arthropods in smaller or more isolated forest fragments would be reflected in chick feeding rates and nestling diet, and to what extent these expected effects would be reflected in the fledging weight and breeding success. Our study involved two closely related species that to a large extent use the same prey, but that differ in their degree of specialization: the more specialised blue tit was expected to be more strongly affected by a depleted resource base in fragments than the less specialised great tit (Dhondt 1987).

Knowing that arthropod prey populations fluctuate widely between years (McCauley 1989) and that this is likely to be reflected in nestling diet (Royama 1970; Banbura et al. 1994), we repeated our study in a second year. Such fluctuations may be more acute in smaller fragments due to the increased likelihood of stochastic extinctions and colonisations or the greater vulnerability of prey populations to external influences (Soulé and Simberloff 1986; Saunders et al. 1991; Opdam 1991). One might therefore predict lower and more variable abundance of prey in smaller forest fragments.

Our study certainly does not provide a simple answer. Some results, in fact, are quite different from what we predicted. In the following sections we will discuss the results in more detail.

Provisioning rates

Feeding rates differed between study sites in different-sized forests: in both years and for both species feeding rates were highest in the smallest fragments (area 4) and lowest in the large forest (area 1) (Table 2). Feeding frequencies are considered a poor indication of the amount of food given to nestlings due to variation in load size between feeds (Gibb and Betts 1963; Royama 1966; Van Balen 1973; Blondel et al. 1991). It is generally assumed that higher feeding rates correlate with smaller prey items, and therefore may actually result in less food being delivered rather than more. In our case, feeding rates were indeed negatively related to prey size, suggesting that total volume delivered to the chicks may be less variable than either prey size or feeding rates by themselves. Since there was no consistent trend for prey size to change with forest size, the higher provisioning rates in the smallest fragments resulted in these chicks receiving on average a larger volume of prey, but these differences were not significant (Table 3).

Food availability

The lack of correlation between frass fall and the total number of caterpillars in the diet suggests that (1) prey items were not limited in abundance during the period of filming, or (2) that frass fall, as measured in this study, is not a reliable estimator of food availability. Indeed, frass fall counts may overestimate prey caterpillar density due to the inclusion of non-prey species.

Differences in vegetation between area 2 (with a lower proportion of oak trees) and the other forests may account for the lower frass fall collected in this area (see also below). It should be stressed, however, that frass was collected under oak trees at all study sites.

Frass fall decreased throughout the period of filming in the small (area 3) and the very small (area 4) fragments, probably due to between-area differences in timing and duration of caterpillar peaks. However, parents in these areas did not decrease their feeding frequency throughout the same period, suggesting that changes in frass fall cannot explain changes in feeding rates.

Diet

Tits exhibit a preference for caterpillars whenever possible (Perrins 1965; Perrins and McCleery 1989). A relatively low proportion of caterpillars in the diet is characteristic of suboptimal environments such as pine forests (Gibb and Betts 1963; Van Balen 1973), suburban gardens (Cowie and Hinsley 1987; Riddington and Gosler 1995), sclerophyllous habitats (Blondel et al. 1991) and forest fragments (Riddington and Gosler 1995). In this study, caterpillars dominated the nestling diet in both species regardless of forest size. There was

also no evidence that the contribution of different caterpillar families varied with forest size (authors, unpublished work). Thus, we cannot conclude that fragmentation caused a reduction of chick food quality expressed as proportion of caterpillars in the diet. Differences in proportion of caterpillars and prey size between the areas did not suggest a consistent effect of forest fragmentation, but may rather be the result of small vegetational differences between study areas, which have been shown to have a significant effect on nestling's diet (Royama 1970; Van Balen 1973; see also Cramp and Perrins 1993).

Despite its presumed importance in the diet of nestling tits (Betts 1955; Van Balen 1973; Perrins 1979; but see Royama 1970) winter moths made up a surprisingly low proportion of the diet (11.8%). This cannot be explained by a low abundance, since adult densities were comparable with other studies (S. Van Dongen, personal communication). Contrary to expectation (Van Dongen et al. 1984) the proportion of winter moths in the diet was actually highest in the smallest fragments (authors, unpublished work), which provides no clue to explain the overall low presence in the diet.

Breeding success

In this study, there is no evidence to suggest that breeding success, as measured by clutch size, brood size, fledging weight and fledging success, is affected by habitat fragmentation for either great or blue tit. These observations support the provisioning data which indicated no adverse effects of breeding in small fragments as concerns the volume of prey delivered to the nestlings or the quality of chick diet.

Dhondt et al. (1990) used fledging success (fledglings per eggs in successful first broods) as a measure of habitat quality. They found a strong positive correlation between fledging success and 15-day chick weight. Since we do not find lower fledging success or weight in smaller forests, our results probably reflect an overall similarity of habitat conditions between the study areas, and show that conditions for successful breeding of tits are not inferior in small fragments.

Other studies on tits, in contrast to this one, did find a reduction in breeding success in small forest fragments. For instance, Riddington and Gosler (1995) concluded that great tit reproductive success was poorer in presumed marginal habitats which included small woodlots but also gardens and hedgerows, and suggested that environmental quality was the primary constraint. Similarly Dhondt et al. (1990) found lower fledging success and fledging weight in a beech forest fragment (their plot H). However, it is important to underline that in our case, in contrast to these studies, vegetation was very similar between the large forest (area 1) and the small fragments (areas 3 and 4) in particular.

The lower fledging weights in area 2 (significant in blue tits only) are consistent with earlier results from the

same area (Dhondt et al. 1990), but cannot be explained by an effect of forest size per se. Frass fall was lower in this area, but this did not result in lower feeding rates or food volume per chick. However, this area diverged most from the others in the relative frequency of different caterpillar families in the diet (authors, unpublished work). Therefore both the difference in frass production and in fledging weight may be a consequence of a difference in diet rather than food quantity.

In conclusion, our data do not suggest suboptimal foraging or breeding conditions in small fragments compared to a nearby large forest. Parallel studies, on the same or similar study sites, show fragmentation to have a more profound effect on dispersal patterns and population structure than on reproductive success and survival of birds and squirrels (see review in Matthysen et al. 1995). Redpath (1995) concluded that bird species that are least likely to be affected by fragmentation are small, abundant generalists of low trophic status, which is a good description of both great and blue tit. It is therefore not surprising that even in strongly fragmented habitats (excluding the confounding effect of vegetation differences), reproductive success in either great or blue tit is not lower than in the continuous large forest.

Acknowledgements Many thanks to S. Van Dongen for statistical advice, to F. Adriaensen and F. Fierens for assistance in the field and in data analysis, and to T. Van de Castele for commenting on an earlier version of the manuscript. D.C. was supported by an EC-Training and Mobility network "Dispersal and local adaptation in man-made habitats". E.M. and R.V.D. are research associate and senior research assistant with the Fund for Scientific Research – Flanders.

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