1	Habitat fragmentation influences nestling growth in Mediterranean blue
2	and great tits
3	Javier Bueno-Enciso <sup>1*</sup> , Esperanza S. Ferrer <sup>1, 2</sup> , Rafael Barrientos <sup>1</sup> , Eva
4	Serrano-Davies <sup>1</sup> and Juan José Sanz <sup>3</sup> .
5	<sup>1</sup> Área de Zoología, Departamento de Ciencias Ambientales, Facultad de Ciencias del
6	Medio Ambiente, Universidad de Castilla-La Mancha, Avenida Carlos III, s/n, E-45071,
7	Toledo, Spain.
8	<sup>2</sup> Grupo de Investigación de la Biodiversidad Genética y Cultural, Instituto de Investigación
9	en Recursos Cinegéticos IREC (CSIC-UCLM-JCCM), Ronda de Toledo s/n, 13071,
10	Ciudad Real, Spain.
11	<sup>3</sup> Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), C/
12	José 13 Gutiérrez Abascal 2, 28006, Madrid, Spain.
13	*Corresponding author. E-mail: jbuenoenciso@gmail.com
14	ESF: <u>esperanza.sferrer@gmail.com</u> ; RF: <u>Rafael.barrientos@uclm.es</u> ; ESD:
15	eva.serrano@uclm.es; JJS: sanz@mncn.csic.es
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18	conducted fieldwork. JBE, ESF, RF and ESD analyzed diet recordings, while JBE analyzed
19	the data and wrote the manuscript. JJS and RF helped and contributed to improve last
20	version.
21	

## 22 Abstract

23 In patchy forest areas, the size of the forest patch where birds breed has a strong 24 influence on their breeding success. However, the proximate effects contributing to 25 lowering the breeding success in small forest patches remain unclear; and a shortage of crucial resources in those forest patches has been suggested to account in some degree for 26 27 this failure. With the aim to further investigate this issue, we have monitored the breeding cycle of blue and great tits in three 'large' forest patches (ranging between 26.5-29.6 ha) 28 and twelve 'small' forest patches (ranging between 1.1-2.1 ha) in a Mediterranean area in 29 central Spain, during three years (2011-2013). We also recorded the nestling diet inside the 30 nest-boxes with the aid of handy-cams. Only males significantly differed between forest 31 32 patch size categories; being on average younger and with better body condition in small patches for great and blue tits respectively. Reproductive traits did not vary between forest 33 patch size categories, but the body condition of blue tit nestlings and the size of great tit 34 35 nestlings did, being significantly better and larger respectively in large forest patches. The recruitment rate of blue tit nestlings was also higher in large patches. Regarding nestling 36 37 diet, blue tits did not differ but great tits did, delivering a larger amount of caterpillars in large forest patches. Most variation in the reproductive traits occurred between years, 38 probably due to annual differences in environmental conditions. This study suggests that 39 food supply could be limiting the breeding success of birds above all in small patches, but 40 also in large patches under particular environmental conditions. 41

42 Additional keywords: Forest patch; feeding behavior; recruitment; nestling diet; body
43 condition.

Habitat fragmentation is one of the major threats that forest biodiversity faces 45 46 (Laurance, 2010; Amos et al., 2013; Bregman et al., 2014), and its effects have been widely studied in forest birds (Fahrig, 2003). The ultimate effect of habitat fragmentation is the 47 decline of bird species richness and population abundances (Moller, 1987; Debinski and 48 Holt, 2000; Boulinier et al., 2001). These numerical responses may stem, at least in part, in 49 demographic changes, i.e. proximate effects given at a regional-scale (Lampila et al., 2005). 50 However, the mechanisms underlying these proximate effects remain unclear, and it is of 51 vital importance to light them in the sake of conservation biology (Boulinier et al., 2001; Le 52 Tortorec et al., 2012). One feature that affects the breeding success of birds, is the size of 53 54 the forest patch where they breed (Paton, 1995; Hinsley et al., 1999, 2009; Shochat et al., 2001; Loman, 2003; Zitsque et al., 2011, but see Nour et al., 1998), and a reduction of 55 crucial resources in small forest patches has been suggested to be a responsible cause 56 57 (Kuitunen and Makinen, 1993; Tremblay et al., 2005; Hinam and Clair, 2008).

58 In this regard, food supply could be a crucial resource limiting the breeding success of birds in small forest patches, as it is one of the most important limiting factors affecting 59 life-history in birds (Lack, 1968; Martin, 1987; but see Martin, 1995). Food supply could 60 be compromised in small forest patches just because their small surface area (Moller, 61 62 1991); but also because in small forest patches the proportion of forest edges increases (Helzer and Jelinski, 1999), which harsh the environmental conditions (Zanette et al., 2000) 63 and may drive to a decrease in the amount of invertebrates (Didham et al., 1996; Burke and 64 Nol, 1998). Furthermore, the process of habitat fragmentation typically implies 65

degradation, which changes the structure of the remaining habitat (Hinsley et al., 1999; 66 Fahrig, 2003). These changes in the vegetation structure usually involve microclimate 67 alterations too; which apart from its direct effects on the abundance of invertebrates, it 68 could promote a change in the composition of the vegetation which could also alter the 69 70 composition of invertebrates (Cramp and Perrins, 1993; Laurance et al., 2002). In addition, 71 for altricial bird species, breed in a small forest patch could be challenging due to they are 'central-place foragers', as they are attached to a fixed point when they breed, their nests 72 73 (Tremblay et al., 2005). If they are not able to cope with the food demand of their broods within the patch, they will be forced to travel longer distances to reach other foraging 74 75 patches, crossing unsuitable foraging habitats, which will limit their feeding rate (Bruun 76 and Smith, 2003). In other cases, in landscapes containing little habitat, the distance between forest patches may exceed a species gap-crossing tolerance, constraining the size 77 78 of the home ranges and limiting the availability of resources (Desrochers and Hannon, 1997). The ultimate effect of both scenarios is a reduction of the breeding success (Frey-79 Roos et al., 1995; Hinsley, 2000). 80

The aim of the present study was to test whether there is an effect of the forest patch 81 82 size on the breeding performance of two populations of blue (Cyanistes caeruleus) and great tits (*Parus major*). To do this, we studied the breeding performance of these two 83 species of tits in a fragmented landscape in central Spain during three years. Both species 84 are ideal to study this topic as they need an enormous supply of food when they breed. For 85 example great tits while feeding their chicks made up to 700 feeding visits per day, and 86 87 blue tits even more (Perrins, 1991). Because of this, it is crucial for tits to match the maximum food demand period of their chicks with the food peak in the forest (Naef-88

89	Daenzer and Keller, 1999; Matthysen et al., 2011); when they do not achieve this match,
90	their reproductive success can decrease (Svensson and Nilsson, 1995; Naef-Daenzer et al.,
91	2001; Tremblay et al., 2003). We hypothesized that in small patches the breeding
92	performance will be worse (Moller, 1991; Riddington and Gosler, 1995), and predict that
93	the lack of resources in small patches will be an important responsible factor, concretely
94	food supply (Burke and Nol, 1998; Zanette et al., 2000; Razeng and Watson, 2014).

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## 96 2. Material and Methods

97 2.1. Study area

The present study was conducted in the locality of San Pablo de los Montes situated 98 99 in Montes de Toledo (39°32'44"N, 4°19'41"W; Toledo, central Spain). This region presents 100 continental Mediterranean climate, characterized by pronounced summer droughts and a high daily thermal oscillation, with mean annual rainfall of 700-800 mm. The landscape of 101 102 this area has suffered an intense fragmentation due to human activities, mainly agriculture 103 and deforestation for raising cattle, as occurs in other regions of the Mediterranean basin (Blondel and Aronson, 1999). As a consequence, deciduous woodlands, considered the 104 most suitable breeding habitat for tits in this region (Atiénzar et al., 2012), are scattered and 105 patched in a matrix of less suitable habitat, mainly Mediterranean scrubland with low tree 106 107 cover and pastureland. Our study area consisted of fifteen oak (Quercus pyrenaica) forest 108 patches: three 'large' patches ranging between 26.5 and 29.6 ha, and twelve 'small' patches 109 ranging between 1.1 and 2.1 ha, separated from each other by a mean distance of 4.23 km 110 (range 0.53 - 9.84 km). Both oak forest patch size categories present a similar habitat

111 structure, with the oak as dominant plant accompanied by its typical shrub courtship: common hawthorn (*Crataegus monogyna*), elmleaf blackberry (*Rubus ulmifolius*), terebinth 112 113 (Pistacia terebinthus), and common broom (Cytisus scoparius). Large patches were provided with 80 wood nest-boxes (internal dimensions: 12 x 11.5 x 16.5 cm.) and small 114 115 ones with 5 wood nest-boxes; separated from each other by at least 30 m. All nestboxes were hung on the branches of oak trees at a height of 2.5-3 metres and oriented towards the 116 south. They were protected from predators (mustelids, woodpeckers) with wire mesh and a 117 118 polyvinyl chloride (PVC) pipe (length: 50-70 mm, diameter: 40 mm) fixed to the holeentrance. Because of this protection, the main predator in our study area was the ladder 119 120 snake (*Rhinechis scalaris*), a very common species in the area (Salvador and Pleguezuelos, 121 2002).

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#### 123 *2.2. Field work*

During the 2011-2013 breeding seasons (day 1= April 1), nest-boxes were 124 frequently inspected to obtain the basic reproductive parameters of our tit population, such 125 126 as laying date (the day of laying the first egg of the clutch), clutch size, hatching date and brood size. Body condition, size and age of parents were compared between patch size 127 categories because these variables are indicators of status and thus of dominance over 128 resources (Gosler, 1997; Stahl et al., 2001). To do this, parents were trapped and ringed 129 while feeding their nestlings (8-9 days old). The tarsus length of birds was measured with a 130 digital calliper to the nearest 0.01 mm; the body weight was measured with an electronic 131 balance (0.01 g) and the age of parents (yearling or older) was noted according to plumage 132 characteristics. Due to technical difficulties, adult great tits in 2011 were not trapped. 133

Nestlings were ringed, measured and weighted when they were 13 days old, and mean 134 values per brood were taken in the analyses. Tarsus length was employed as a surrogate of 135 body size, and the weight analyses were corrected by the tarsus length (added as a 136 covariate) to consider the body condition of birds. Nest-boxes were also visited on day 22 137 138 to assess the number of chicks fledged. We assumed that all chicks have fledged when we 139 did not find any chick dead inside the nest-boxes. Hatching success was calculated as the 140 ratio between the number of nestlings hatched and the clutch size; and fledgling success 141 was calculated as the ratio between nestlings fledged and hatched. To assess the breeding performance of each tit pair, seven variables were used (laying date, clutch size, hatching 142 143 success, fledgling success, nestling body condition, nestling size and fledgling recruitment). Fledgling recruitment was estimated by noting, for each yearling that we recaptured (i.e. 144 that was born in the study area); the forest patch ID where it was breeding and the forest 145 146 patch ID where it was born. Through this way, we could estimate the percentage of recruitments that were born in large or small patches and the percentage of them that 147 achieved to breed in large or small patches the next year. Apart from the seven breeding 148 variables mentioned above, we also estimated the nest-box occupation rate and the breeding 149 density to increase the comprehensive approach of this study. Nest-box occupation rate was 150 151 obtained for each species and year as the ratio between occupied nest-boxes and total availability of them in each forest patch. We also calculated the density of great and blue 152 tits in each breeding territory as the number of tit breeding pairs in a radius of 75 m around 153 154 each occupied nest-box with the aid of Quantum GIS 2.0.1, as it is an important trait 155 influencing breeding performance and recruitment rate (Both, 1998; Both et al., 1999).

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## 157 2.3. Feeding rate and Nestling diet

To evaluate potential differences in the breeding performance between patch size 158 categories, nestling diet was filmed by placing an infrared handy-cam (Sony DCR-SR290E-159 like) in an adapted nest box when nestlings were 11 days old (see García-Navas and Sanz, 160 161 2011, for details); that is, when nestling food requirements are maximum (Naef-Daenzer and Keller, 1999). All filming sessions were carried out during the first hours of the day 162 and in similar weather conditions. First hour of video of each recording was discarded to 163 164 allow parents to habituate to the disturbance that the video camera installation entails. The second hour of recording was analysed frame by frame using the software package Adobe 165 Premiere Elements 7.0. In a previous study performed in a nearby area, it was confirmed 166 that an hour is representative of the feeding behaviour in these species (García-Navas and 167 Sanz, 2012). A total of 247 film recordings were analysed, 186 belonged to blue tits (131 in 168 169 large patches and 55 in small ones. Table S2) and 61 from great tits (29 in large patches and 32 in small patches. Table S2). For each recording, we combined the number of feeding 170 events of each adult. Thus, the number of feeding events per hour was considered as a 171 surrogate of parental provisioning effort (hereafter 'feeding rate'). Diet of nestlings was 172 estimated from identified prevs of 6,017 feeding trips: 5,037 belonging to blue tits and 980 173 174 to great tits. Food items were firstly classified in two main trophic categories: Lepidoptera larvae (caterpillars) and "others". We further distinguish between caterpillars of the three 175 major Lepidoptera families presented in the study area: Tortricidae, Noctuidae and 176 Geometridae. The second group "others" include: 'spiders' (Aranea), 'imago' (belonging to 177 178 the orders Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera and Orthoptera), 'Chrysalides' and 'Miscellaneous' (heterogeneous group including plant tissues, fungus, 179

eggshell, snails and lichen). Size of preys was assessed using a scale bar attached above the 180 181 entrance of the nest box as a reference. Within each taxonomic category, items of prey were classified to three ordinal categories of body size [1 = small (length < 1.5 cm for ]182 caterpillars; <1.5 cm for imagos and abdomen diameter <0.2 cm for spiders); 2 = medium 183 184 (length 1.5-2.5 cm, 1.5-2 cm and diameter 0.2-0.6 cm, respectively); 3 = large (length >2.5 cm for both caterpillars and imagos and diameter >0.6 cm for spiders)] to make 185 individual prey volumes comparable among taxa (see García-Navas and Sanz, 2010). 186 Shannon index H' was calculated for each nest. 187

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189 *2.4. Statistical analysis* 

Only first clutches were used. A set of General Linear Mixed Models (GLMM) 190 were performed in all cases with year and patch size category as fixed factors and laying 191 192 date as a covariate. As mentioned above, body condition of birds was estimated by adding the tarsus length as another covariate, as advised by Darlington and Smulders (2001) and 193 García-Berthou (2001). In all models, nest ID nested in forest patch ID was included as the 194 195 random term. Normal distribution was assumed in all models, with the exceptions of proportions (occupation rate, hatching success, fledgling success and proportions of the 196 main prey). For these analyses, GLMMs with a binomial distribution and a binary response 197 variable were employed. In the occupation rate model the numerator of the binary response 198 variable was the number of occupied nest-boxes and the denominator was the total number 199 200 of available nest-boxes in each forest patch. In hatching and fledgling success models, the numerator was the number of hatchlings and fledglings respectively, and the denominator 201 was the clutch size and the number of hatchlings respectively. For proportions of the main 202

prey types, the numerator was the number of preys belonging to a specific prey type and the 203 204 denominator was the total number of prey. Age of parents and probability to recruit next year were also analysed fitting the GLMMs with a binomial distribution. In age models the 205 response variable was 0 for yearlings and 1 for adults; and in recruitment models the 206 207 response variable was 0 for nestlings non-recruited and 1 for nestlings recruited. Nestling 208 mass and nestling tarsus length were included as explanatory variables in the models of 209 recruitment. Because in a fragmented landscape an increase of nest predation in small forest patches due to edge effects may also drive a worsening in the breeding success (Robinson 210 et al., 1995; Chalfoun et al., 2002), we also tested the effect of the forest patch size on the 211 212 predation rate by the ladder snake in both tit populations. The former analysis was also 213 carried out fitting a GLMM with a binomial distribution, in which the dependent variable was 0 for non-predated nests and 1 for predated nests. When the interaction between the 214 215 factor 'Year' and 'Patch size' was significant, the main effects of both factors on the response variable were not considered (even when P < 005), in a similar way as MacDonald 216 et al. (2014). From the 329 blue tit nests used in this study, 28 females and 32 males were 217 218 duplicated among years; and from the 161 great tit nests used, the number of duplicated adults was 11 females and 6 males. We performed the analysis with and without these 219 220 duplicate adults and found no difference in the results. Thus, we decided to treat each adult 221 as independent in the analyses, in the same way as Camfield and Martin (2013).

Assumptions of homogeneity, normality and independence were visually verified plotting the residuals against fixed values, doing a histogram of the residuals and plotting the residuals against each explanatory variable respectively (Zuur et al., 2009). All models were firstly constructed with all explanatory terms fitted including interactions, and final models were selected following a backward procedure, by progressively eliminating nonsignificant terms starting with the interactions. Therefore, final models were those that explained the maximum variance with the least number of explanatory variables. All analyses were performed in R (R Core Team 2014) with the package lme4 (Bates et al., 2014). For non-parametric distributions Wald chi-square statistic ( $\chi^2$ ) is given. Mean ± SE (n) is given in the results.

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### 233 **3. Results**

# 234 *3.1. Occupation rate and breeding density*

Nest-box occupation rate was higher in blue tits than in great tits [GLMM: Estimate 235  $\pm$  SE= -0.98  $\pm$  0.12,  $\chi^2_{1,70}$ = 71.58, P< 0.001. Blue tits= 47.53 %  $\pm$  3.24 (41) and great tits= 236  $38.39 \% \pm 4.19 (35)$ ]. Regarding yearly variation, great tits increased their nest-box 237 occupation rate in 2012, while years 2011 and 2013 did not differ (GLMM:  $\chi^{2}_{2, 30}$ = 36.75, 238 P < 0.001. See Table 1). In contrast, nest-box occupation rate of blue tits did not change 239 among years (GLMM:  $\chi^{2}_{2, 36} = 0.03$ , P = 0.99. See Table 2). In both species, the nest-box 240 occupation rate was higher in small patches (Great tits, GLMM: Estimate  $\pm$  SE= 1.75  $\pm$ 241 0.27,  $\chi^{2}_{1,30}$ = 42.37, *P*< 0.001; large patches= 13.75 % ± 3.29 (9) and small patches= 46.92 242 % ± 4.43 (26). Blue tits, GLMM: Estimate ± SE= 0.71 ± 0.27,  $\chi^2_{1,38}$ = 6.92, P= 0.008; large 243 patches=  $34.31 \% \pm 3.36 (9)$  and small patches=  $51.25 \% \pm 3.80 (32)$ . See Table 1 and 2 244 245 respectively).

Regarding the density of breeding pairs, there was not difference between species [GLMM: Estimate  $\pm$  SE= 0.05  $\pm$  0.18, F<sub>1, 482</sub>= 0.08, *P*= 0.78. Blue tits= 5.40 %  $\pm$  0.14 (329)

and great tits= 5.52 %  $\pm$  0.21 (161)]; and both species increased their breeding density in 248 249 2012, whereas the breeding density between the years 2011 and 2013 did not differ (Great 250 tits, GLMM: F<sub>2, 153</sub>= 9.97, P< 0.001. Blue tits, GLMM: F<sub>2, 322</sub>= 32.97, P< 0.001; Table 1 and 2 respectively). Breeding density of great tits was also positively affected by the laying 251 252 date (GLMM: Estimate  $\pm$  SE= 0.03  $\pm$  0.01, F<sub>1, 153</sub>= 6.87, P= 0.01). As regards the forest patch size effect, both tit species presented a higher breeding density in large forest patches 253 than in small ones (Great tits, GLMM: Estimate  $\pm$  SE= -3.43  $\pm$  0.35, F<sub>1, 153</sub>= 98.61, P< 254 255 0.001; large patches= 6.89 %  $\pm$  0.24 (99) and small patches= 3.34 %  $\pm$  0.14 (62). Blue tits, GLMM: Estimate  $\pm$  SE= -3.30  $\pm$  0.44, F<sub>1, 322</sub>= 55.71, P< 0.001. Table 1 and 2 respectively). 256

**Table 1.** Summary of the occupation, density, predation, morphometric characteristics of adults and nestlings and reproductive parameters in a population of great tits (*Parus major*) breeding in large and small oak forest patches in San Pablo de los Montes (central Spain). Values given are Mean  $\pm$  SE (n). Sample sizes vary accordingly to nest failures and missing adults.

Great tits 2012 2013 2011 Large patch Small patch Large patch Small patch Large patch Small patch  $60.00 \pm 8.94$  (10)  $5.42 \pm 2.20(3)$  $37.14 \pm 6.80(7)$  $23.75 \pm 6.16(3)$  $12.08 \pm 1.10(3)$  $40.00 \pm 3.33$  (9) Occupation rate (%)  $5.85 \pm 0.88$  (13)  $3.23 \pm 0.34$  (13)  $3.52 \pm 0.19$  (31)  $3.11 \pm 0.23$  (18)  $7.75 \pm 0.29$  (57)  $5.66 \pm 0.31$  (29) Density (No. Pairs x Ha<sup>-1</sup>) 0(13)0 (13)  $16.12 \pm 6.72 (31)$  $17.24 \pm 7.13$  (29) Nest predation (%)  $42.11 \pm 6.59(57)$  $5.56 \pm 5.56$  (18)  $0.41 \pm 0.08$  (32)  $0.52 \pm 0.12$  (17)  $0.77 \pm 0.09$  (22)  $0.57 \pm 0.14$  (14) Female age \_  $0.69 \pm 0.09$  (29)  $0.44 \pm 0.13$  (16)  $0.89 \pm 0.07$  (19)  $0.54 \pm 0.14$  (13) Male age - $16.18 \pm 0.21$  (32)  $16.66 \pm 0.21$  (17)  $16.94 \pm 0.18$  (22)  $16.84 \pm 0.20$  (14) Female mass (g)  $17.12 \pm 0.19$  (29)  $17.22 \pm 0.25$  (16)  $17.77 \pm 0.14$  (19)  $17.46 \pm 0.22$  (13) Male mass (g)  $19.21 \pm 0.09$  (17)  $19.29 \pm 0.13$  (22)  $19.10 \pm 0.13$  (14) Female tarsus length (mm)  $19.12 \pm 0.10$  (32)  $19.89 \pm 0.11$  (29)  $19.86 \pm 0.15$  (16) Male tarsus length (mm)  $20.01 \pm 0.16$  (19)  $19.78 \pm 0.11$  (13)  $27.59 \pm 2.00(57)$ 23.87 ± 3.01 (31)  $16.15 \pm 2.87$  (13)  $13.62 \pm 3.25$  (13)  $22.72 \pm 1.32$  (29)  $21.72 \pm 1.45$  (18) Laying date  $9.46 \pm 0.44$  (13)  $9.62 \pm 0.35$  (13)  $8.84 \pm 0.26$  (57)  $8.19 \pm 0.34$  (31)  $9.62 \pm 0.35$  (29)  $9.11 \pm 0.43$  (18) Clutch size  $78.07 \pm 5.96$  (13)  $84.08 \pm 7.42$  (13)  $76.46 \pm 6.26$  (18) Hatching success (%)  $65.82 \pm 4.95$  (32)  $66.12 \pm 7.94$  (23)  $75.83 \pm 6.76$  (16) 86.67 ± 6.31 (30 91.88 ± 5.51 (13) 87.71 ± 8.28 (13) 86.58 ± 6.63 (17)  $96.60 \pm 2.29$  (18)  $77.71 \pm 10.50 (15)$ Fledgling success (%)  $17.21 \pm 0.27$  (13)  $16.87 \pm 0.24$  (13)  $16.34 \pm 0.19$  (30)  $16.02 \pm 0.21$  (18)  $17.23 \pm 0.18$  (22)  $16.96 \pm 0.19$  (12) Nestling mass (g)  $19.63 \pm 0.12$  (13)  $19.44 \pm 0.12$  (13)  $19.33 \pm 0.09$  (30)  $19.19 \pm 0.12$  (18)  $19.45 \pm 0.07$  (22)  $19.10 \pm 0.12$  (12) Nestling tarsus length (mm)  $4.83 \pm 1.26$  (290)  $4.20 \pm 1.84$  (119)  $0.88 \pm 0.62$  (226) 0 (122) Recruitment (%)

The body condition of blue and great tits decreased in 2012 (GLMM: Estimate  $\pm$ 261 262 SE= 0.49  $\pm$  0.20,  $F_{1, 74}$ = 6.12, P= 0.02 and GLMM: Estimate  $\pm$  SE= 0.51  $\pm$  0.21,  $F_{1, 68}$ = 5.97, P=0.02 for great tit females and males respectively, and GLMM:  $F_{2, 255}=4.37$ , P=263 0.01 and GLMM:  $F_{2, 211}$  = 8.46, P< 0.001 for blue tit females and males respectively. See 264 Tables 1 and 2). In 2012, the proportion of yearlings to adults of female great tits increased 265 (GLMM: Estimate  $\pm$  SE= 1.09  $\pm$  0.49,  $\chi^2_{1, 78}$ = 5.09, P= 0.02. Table 1), the same as the 266 proportion of blue tit male yearlings (GLMM:  $\chi^{2}_{1, 227}$ = 8.21, P= 0.02. Table 2). Attending 267 the forest patch size effect, only males differed between patch size categories, although in a 268 different way in each species. The proportion of old great tit males was higher in large 269 patches (GLMM: Estimate  $\pm$  SE= -1.19  $\pm$  0.52,  $\chi^{2}_{1, 69}$ = 5.16, P= 0.02. Table 1), while blue 270 tit males had a better body condition in small patches (GLMM: Estimate  $\pm$  SE= 0.29  $\pm$ 271 0.08,  $F_{1,211}$ = 11.91, P < 0.001. Table 2). 272

273 Table 2. Summary of the occupation, density, predation, morphometric characteristics of adults and nestlings and reproductive

274 parameters in a population of blue tits (*Cyanistes caeruleus*) breeding in large and small oak forest patches in San Pablo de los Montes

275 (central Spain). Values given are Mean  $\pm$  SE (n). Sample sizes vary accordingly to nest failures and missing adults.

Blue tits							
	20	11	20	12	2013		
	Large patch	Small patch	Large patch	Small patch	Large patch	Small patch	
Occupation rate (%)	$32.92 \pm 3.97$ (3)	56.67 ± 6.89 (12)	$34.58 \pm 9.02$ (3)	$52.50 \pm 7.50$ (8)	$35.42 \pm 6.05$ (3)	45.00 ± 5.57 (12)	
Density (No. Pairs x Ha <sup>-1</sup> )	$5.52 \pm 0.26 \ (79)$	$2.85 \pm 0.21$ (34)	$7.40 \pm 0.24$ (83)	$2.90 \pm 0.21 \ (21)$	$5.87 \pm 0.20 \ (85)$	$2.63 \pm 0.22$ (27)	
Nest predation (%)	6.32 ± 2.75 (79)	2.94 ± 2.94 (34)	$24.09 \pm 0.05 \ (83)$	$19.05 \pm 8.78 \ (21)$	$0.12 \pm 3.52$ (85)	14.81 ± 6.97 (27)	
Female age	$0.51 \pm 0.06 \ (73)$	$0.61 \pm 0.09 \ (31)$	$0.61 \pm 0.07 \ (57)$	$0.60 \pm 0.13 \ (15)$	$0.64 \pm 0.05 \ (73)$	0.57 ± 0.11 (23)	
Male age	$0.81 \pm 0.05 \ (57)$	$0.70 \pm 0.09 \ (27)$	$0.59 \pm 0.07 \ (51)$	$0.83 \pm 0.11$ (12)	$0.85 \pm 0.04 \ (66)$	$0.85 \pm 0.08 \ (20)$	
Female mass (g)	$9.66 \pm 0.06 \ (73)$	$9.51 \pm 0.10$ (31)	$9.22 \pm 0.13$ (57)	$9.62 \pm 0.10 \ (15)$	$9.69 \pm 0.06 \ (73)$	$9.55 \pm 0.09 \ (23)$	
Male mass (g)	$9.80 \pm 0.06 \ (57)$	$9.83 \pm 0.09 \ (27)$	$9.18 \pm 0.11 \ (51)$	$9.82 \pm 0.10 \ (12)$	$9.71 \pm 0.05 \ (66)$	$10.15 \pm 0.22$ (20)	
Female tarsus length (mm)	$15.81 \pm 0.06 \ (73)$	$15.66 \pm 0.11 \ (31)$	$15.79 \pm 0.06 \ (57)$	$16.21 \pm 0.16 \ (15)$	$15.86 \pm 0.05 \; (73)$	$16.00 \pm 0.11$ (23)	
Male tarsus length (mm)	$16.29 \pm 0.07 \ (57)$	$16.23 \pm 0.10 \ (27)$	$16.30 \pm 0.07 \ (51)$	$16.34 \pm 0.14$ (12)	$16.32 \pm 0.06 \ (66)$	$16.30 \pm 0.09 \ (20)$	
Laying date	$18.63 \pm 1.36 \ (79)$	$14.59 \pm 2.11 \ (34)$	$24.82 \pm 1.24 \ (83)$	26.95 ± 2.97 (21)	$29.13 \pm 1.5 \ (85)$	$28.44 \pm 1.89$ (27)	
Clutch size	$8.14 \pm 0.24 \ (79)$	$9.03 \pm 0.32$ (34)	8.63 ± 0.24 (83)	$7.43 \pm 0.51$ (21)	$8.19 \pm 0.19 \ (85)$	$8.89 \pm 0.34 \ (27)$	
Hatching success (%)	$82.23 \pm 2.34 \ (73)$	$74.97 \pm 5.05 \ (33)$	$69.79 \pm 3.84 \ (62)$	$75.39 \pm 6.30 \ (13)$	$79.07 \pm 3.35 \ (72)$	85.83 ± 3.47 (22)	
Fledgling success (%)	92.42 ± 3.01 (72)	96.67 ± 3.33 (30)	$84.62 \pm 4.19$ (55)	$75.38 \pm 10.38  (13)$	$89.61 \pm 2.94$ (68)	83.33 ± 7.60 (22)	
Nestling mass (g)	$10.10 \pm 0.07$ (67)	$9.85 \pm 0.08 \ (29)$	$9.34 \pm 0.13 \ (53)$	$9.36 \pm 0.28 \ (11)$	$10.24 \pm 0.07$ (69)	$10.03 \pm 0.16  (21)$	
Nestling tarsus length (mm)	$15.90 \pm 0.06 \ (67)$	$15.82 \pm 0.07$ (29)	$15.67 \pm 0.05$ (53)	$15.75 \pm 0.21$ (11)	$15.88 \pm 0.05 \ (69)$	$16.03 \pm 0.12$ (21)	
Recruitment (%)	-	-	10.18 ± 1.27 (570)	$2.61 \pm 1.05$ (230)	$1.97 \pm 0.69 \ (406)$	1.41 ± 1.41 (71)	

### 276 *3.3. Breeding performance*

The greatest differences in the breeding performance of tits were given among years 277 278 (Table 3). Blue tit laying date was delayed year after year (Table 2. Tukey HSD test< 0.05), 279 and their hatching success, nestling condition, nestling size and recruitment decreased in 2012 (Table 2 and 3. Tukey HSD test < 0.05); contrary to nest predation, which increased in 280 281 2012 (Table 2 and 3). Great tits showed a similar phenology than blue tits, and their laying 282 date was also delayed in 2012 and 2013, although there were not differences between these latter years (Table 1 and 3. Tukey HSD test> 0.05). The clutch size in this species did not 283 differ among years (Table 3). Rest of the reproductive variables varied among years in a 284 similar way as blue tits, i.e. decreasing in 2012 (see Table 1. Tukey HSD test< 0.05), 285 286 except for the hatching success and nest predation (Table 3).

287 In both species, the main difference found between forest patch size categories was at nestling stage. The tarsi of great tit nestlings in large patches was longer than the tarsi of 288 289 conspecifics in small patches all years (large patches:  $19.43 \pm 0.06$  (65), small patches: 290  $19.23 \pm 0.07$  (42). Tables 1 and 3), while the body condition of blue tit nestlings in large patches was better than conspecifics in small patches (large patches: 9.94 g  $\pm$  0.05 (189), 291 small patches: 9.72 g  $\pm$  0.08 (61). Tables 2 and 3). The nestling body condition in both 292 293 species was also positively affected by their tarsus length (Table 3). Regarding recruitment, 294 the probability of a blue tit yearling that was born in the study area to breed the next year, was higher for those that were born in large patches; whereas in great tits, it was positively 295 related to their body mass (Table 3). Almost none other trait of breeding performance 296 differed between patch size categories, although there were some significant interactions 297

- between year and patch size category in blue tits (Table3). Concretely, the clutch size and
- fledgling success differed in 2012, being smaller in small patches (Table 2), in rest of years
- 300 these variables did not differ between patch size categories.

**Table 3.** Results of the GLMMs showing the effects of year, patch size and laying date on the breeding performance of blue (*Cyanistes caeruleus*) and great tits (*Parus major*) in Montes de Toledo, central Spain. The ID nest localized in ID forest patch is included in all models as the random effect. *F* statistic is used for Laying date, Clutch size and Nestling condition and size; while  $\chi^2$  statistic is used for Hatching and Fledgling success, Predation rate and Recruitment. Statistics of non-significant terms are shown in Table S1.

		Blue tit	t		Great tit					
Parameter	Effect	d.f.	test	Р	Parameter	Effect	d.f.	test	Р	
Laying date	Year	320	32.2	< 0.001	Laying date	Year	150	8.1	< 0.001	
Rejected effects: I	Patch size and Year	r * Patch	ı size.		Rejected effects: P	atch size and Year	* Patch	size.		
Clutch size	Laying date	316	164.5	< 0.001	Clutch size	Laying date	149	13.3	< 0.001	
	Year*Patch size	316	3.3	0.02						
Rejected effects: I	Patch size.				Rejected effects: Y	ear, Patch size and	Year *	Patch si	ze.	
Hatch. success	Year	296	6.9	0.03	Hatch. success					
Rejected effects: I	Patch size, Laying da	te and Ye	ear * Patch	n size.	Rejected effects: A	.11.				
Fledg. success	Laying date	251	35.2	< 0.001	Fledg. success	Year	100	11.8	0.003	
	Year*Patch size	251	13.7	0.003						
Rejected effects: I	Patch size.				Rejected effects: Patch size, Laying date and Year * Patch size.					
Nest predation	Year	320	15.77	<0.001	Nest predation					
Rejected effects: I	Patch size. Laving da	te and Ye	ar * Patch	n size.	Rejected effects: All					
	allen sille, Laying da									
Nest. condition	Year	224	26.4	< 0.001	Nest. condition	Year	94	11.5	< 0.001	
	Patch size	224	5.5	0.02		Tarsus length	95	36.1	< 0.001	
	Laying date	224	5.5	< 0.001						
	Tarsus length	224	28.6	< 0.001						
Rejected effects: `	Year * Patch size.				Rejected effects: Patch size, Laying date and Year * Patch size.					
NT	V	225	6.0	0.001	N	V	07	25	0.02	
Nestling size	Year	225	6.9	0.001	Nestling size	Year	95	3.5	0.03	
	Laying date	225	5.3	0.02		Patch size	95	4.9	0.03	
Rejected effects: I	Patch size and Year	r * Patch	sıze.		Rejected effects: L	aying date and Yea	ir ↑ Patc	en size.		
Recruitment	Year	1274	20.9	< 0.001	Recruitment	Year	787	6.1	0.01	
	Patch size	1274	6.3	0.01		Nestling mass	787	5.9	0.02	
Rejected effects: 1 Year * Patch size.	Nestling mass, Tars	sus lengt	h, Laying	g date and	Rejected effects: Patch size, Tarsus length, Laying date and Year * Patch size.					

Table S2 resumes the nestling diet of each species in each forest patch size category 308 309 and year. Regarding the nestling diet of each species, the greatest differences were given among years. The proportion of caterpillars in blue tit nestling diet increased in 2012 and 310 2013 in relation to 2011 (Tukey HSD test< 0.05, Table 4), but these increases were 311 312 sustained by different caterpillar families in each year. In 2012 the increase in the 313 proportion of caterpillars delivered by blue tits was above all due to an increase in the intake of noctuids, while the proportion of tortricids this year decreased (Tukey HSD test< 314 0.05). This increase in the consumption of noctuids in 2012 was probably the cause of the 315 316 increase in the prey size this year (Tukey HSD test <0.05). In 2013 the proportion of 317 noctuids diminished, but the proportion of tortricids increased with respect to the former 318 years (Tukey HSD test <0.05, Table 4), resulting in the highest proportion of caterpillar in nestling diet this year. The proportion of spiders decreased in 2013 (Tukey HSD test 319 <0.05). In this species, the forest patch size did not affect the nestling diet (Table 4). 320 321 However, the proportions of total caterpillars, noctuids, tortricids and prey size were negatively affected by the date, while proportion of spiders increased with the date; both in 322 323 a linear way (Table 4). Feeding rate was only positively affected by the brood size. Finally, the proportion of noctuids was negatively affected by brood size, whereas the proportion of 324 tortricids was positively affected (Table 4). Diet diversity (H') in this species did not vary 325 between patch sizes or years, but was positively affected by both laying date and brood size 326 (GLMM: Estimate  $\pm$  SE: 0.009  $\pm$  0.03,  $F_{1,177}$ = 9.12, P= 0.003 and GLMM: Estimate  $\pm$  SE: 327  $0.04 \pm 0.01$ ,  $F_{1, 177} = 6.26$ , P = 0.01). 328

**Table 4.** Results of the GLMMs analyzing the effects of the year, patch size, laying date and brood size on blue tit nestlings diet

330 (*Cyanistes caeruleus*) in Montes de Toledo, central Spain. The ID nest nested in ID forest patch is included in all models as the random

term. Wald chi-square  $(\chi^2)$  statistic is given with non-parametric distributions. Significant results are highlighted in bold.

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Response variable	Explanatory term	$Estimate \pm SE$	test	Р	Response variable	Explanatory term	$Estimate \pm SE$	test	Р
Feeding rate	Intercept	$8.44 \pm 3.04$			Tortricidae	Intercept	$-2.00\pm0.32$		
	Year		$F_{2, 175} = 1.84$	0.16		Year		$\chi^2_{2,176} = 37.57$	<0.001
	Patch size	$-4.02\pm2.47$	$F_{1, 176} = 2.64$	0.13		Patch size	$0.08\pm0.20$	$\chi^2_{1, 175} = 0.17$	0.68
	Laying date	$\textbf{-0.08} \pm 0.09$	$F_{1, 174} = 0.74$	0.40		laying date	$\textbf{-0.01} \pm 0.005$	$\chi^2_{1,176} = 5.13$	0.02
	Brood size	$2.50\pm0.39$	$F_{1, 177} = 40.31$	<0.001		Brood size	$0.08\pm0.03$	$\chi^2$ 1, 176= 5.52	0.02
	Year*Patch size		$F_{2, 172} = 0.09$	0.92		Year*Patch size		$\chi^2_{2,173} = 4.24$	0.12
Caterpillars	Intercept	$1.48\pm0.13$			Aranea	Intercept	$-1.93\pm0.10$		
	Year		$\chi^2_{2, 177} = 11.32$	0.003		Year		$\chi^2_{2,177} = 24.33$	<0.001
	Patch size	$-0.11 \pm 0.16$	$\chi^2_{1, 176} = 0.50$	0.48		Patch size	$\textbf{-0.07} \pm 0.10$	$\chi^2_{1, 175} = 0.40$	0.52
	laying date	$\textbf{-0.03} \pm 0.004$	$\chi^2$ 1, 177= 38.87	<0.001		laying date	$0.009 \pm 0.004$	$\chi^2$ 1, 177= 5.21	0.02
	Brood size	$\textbf{-0.007} \pm 0.03$	$\chi^2_{1, 175} = 0.08$	0.78		Brood size	$\textbf{-0.03} \pm 0.004$	$\chi^2_{1, 176} = 1.67$	0.20
	Year*Patch size		$\chi^{2}_{2, 173} = 3.02$	0.22		Year*Patch size		$\chi^2_{2,173} = 4.22$	0.12
Noctuidae	Intercept	$0.51\pm0.23$			Prey size	Intercept	$1.99\pm0.08$		
	Year		$\chi^2_{2, 176} = 16.38$	<0.001		Year		$F_{2, 176} = 18.30$	<0.001
	Patch size	$\textbf{-0.09} \pm 0.17$	$\chi^2_{1, 175} = 0.32$	0.57		Patch size	$\textbf{-0.008} \pm 0.08$	$F_{1, 175} = 0.01$	0.92
	laying date	$\textbf{-0.02} \pm 0.004$	$\chi^2_{1, 176} = 12.48$	<0.001		laying date	$\textbf{-0.007} \pm 0.003$	$F_{1, 176} = 4.52$	0.04
	Brood size	$\textbf{-0.05} \pm 0.02$	$\chi^2_{1, 176} = 4.35$	0.03		Brood size	$\textbf{-0.002} \pm 0.02$	$F_{1, 172} = 0.02$	0.89
	Year*Patch size		$\chi^2_{2,173} = 0.36$	0.84		Year*Patch size		$F_{2, 173} = 2.56$	0.08

333	Attending great tit nestling diet, they showed a similar yearly pattern than blue tits.
334	The proportion of caterpillars increased in 2012 and 2013, although it did not differ
335	between the latter years (Tukey HSD test> 0.05); in the same way as the proportion of
336	noctuids (Table 5). The proportion of spiders also diminished in 2013 in this species
337	(Tukey HSD test< 0.05). Opposite to blue tits, proportion of tortricids and prey size were
338	not affected by any explanatory variable (Table 5). In this species, the forest patch size did
339	affect the nestling diet. Concretely, the proportions of caterpillars and noctuids were higher
340	in large patches (Table 5 and S2). These two prey types were also negatively affected by
341	the date. As in blue tits, feeding rate was positively affected by the brood size, but no prey
342	type was (Table 5). Diet diversity (H') in this species was only affected by the patch size,
343	being higher in large patches (GLMM: Estimate $\pm$ SE: 0.32 $\pm$ 0.15, $F_{1,56}$ = 4.37, $P$ = 0.04).
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**Table 5.** Results of the GLMMs analyzing the effects of the year, patch size, laying date and brood size on great tit nestlings diet

350 (*Parus major*) in Montes de Toledo, central Spain. The ID nest nested in ID forest patch is included in all models as the random term.

351 Wald chi-square ( $\chi^2$ ) statistic is given with non-parametric distributions. Significant results are highlighted in bold.

Response variable	Explanatory term	$Estimate \pm SE$	test	Р	Response variable	Explanatory term	$Estimate \pm SE$	test	Р
Feeding rate	Intercept	$8.40\pm3.68$			Tortricidae	Intercept	$-2.45\pm0.19$		
	Year		$F_{2, 49} = 0.09$	0.91		Year		$\chi^2_{2,53} = 0.97$	0.61
	Patch size	$-0.83\pm5.78$	$F_{1, 49} = 0.03$	0.87		Patch size	$\textbf{-0.32} \pm 0.33$	$\chi^2_{1,55} = 0.96$	0.32
	laying date	$\textbf{-0.09} \pm 0.09$	$F_{1, 54} = 1.07$	0.30		laying date	$\textbf{-0.02} \pm 0.01$	$\chi^2_{1,54} = 1.63$	0.20
	Brood size	$1.02\pm0.45$	$F_{1,55} = 5.15$	0.03		Brood size	$\textbf{-0.01} \pm 0.07$	$\chi^2_{1,52} = 0.03$	0.87
	Year*Patch size		$F_{5, 49} = 2.71$	0.06		Year*Patch size		$\chi^2$ 2, 50= 2.00	0.37
Caterpillars	Intercept	$2.28\pm0.52$			Aranea	Intercept	$-2.34\pm0.34$		
	Year		$\chi^2_{2,53} = 20.80$	<0.001		Year		$\chi^2_{2,55} = 13.10$	0.001
	Patch size	$\textbf{-1.01} \pm 0.41$	$\chi^2_{1,53} = 5.93$	0.01		Patch size	$0.14\pm0.43$	$\chi^2_{1,53} = 0.10$	0.75
	laying date	$\textbf{-0.05} \pm 0.001$	$\chi^2_{1,53} = 10.17$	0.001		laying date	$0.001\pm0.02$	$\chi^2_{1,52} = 0.005$	0.95
	Brood size	$\textbf{-0.01} \pm 0.08$	$\chi^2_{1,52} = 0.02$	0.89		Brood size	$\textbf{-0.03} \pm 0.10$	$\chi^2_{1,54} = 0.13$	0.72
	Year*Patch size		$\chi^{2}_{2, 50} = 0.95$	0.62		Year*Patch size		$\chi^2_{2,50} = 0.51$	0.77
Noctuidae	Intercept	$0.93 \pm 0.41$			Prey size	Intercept	$2.15\pm0.08$		
	Year		$\chi^2_{2,51} = 21.93$	<0.001		Year		$F_{2, 54} = 1.65$	0.21
	Patch size	$\textbf{-0.60} \pm 0.31$	$\chi^2_{1,51} = 4.34$	0.03		Patch size	$0.05\pm0.15$	$F_{1, 51} = 0.11$	0.75
	laying date	$\textbf{-0.04} \pm 0.01$	$\chi^2_{1,51} = 8.82$	0.002		laying date	$\textbf{-0.007} \pm 0.01$	$F_{1, 53} = 1.71$	0.20
	Brood size	$0.02\pm0.06$	$\chi^2$ 1, 50= 0.09	0.76		Brood size	$\textbf{-0.02} \pm 0.03$	$F_{1, 52} = 0.83$	0.37
	Year*Patch size		$\chi^2_{2,48} = 2.17$	0.34		Year*Patch size		$F_{2, 49} = 0.85$	0.44

### 353 4. Discussion

The nest-box occupation rate was higher in small forest patches for both species in 354 355 all years, probably because the lower availability of nest-boxes in such forest patches 356 limited the nest choice of tits (Barrientos et al., 2015). However, contrary to nest-box occupation rate, the density of tit breeding pairs around each territory was higher in large 357 358 forest patches. This forest patch size effect on the breeding density was possibly due to the greater availability of nest-boxes in the large forest patches. Breeding density is an 359 important trait that negatively influences the breeding performance and recruitment of birds 360 361 because of the competition over resources (Both, 1988; Both et al., 1999). However, the nestling growth was better and the blue tit recruitment was higher in large patches, despite 362 363 the higher breeding density in those patches; which reinforces the idea that large forest patches offer better conditions for breeding tits than small patches . 364

As we said before, patch size affected nestling growth in both species (Table 3). 365 366 Great tit nestlings in large patches were bigger than those from small patches, which 367 suggest that nestling growing conditions were better in large patches. Worse feeding conditions in small patches may be behind the former result, as food is the main limiting 368 factor of nestling growth (Van Noordwijk et al., 1988). In fact, the analysis of great tit 369 370 nestling diet revealed key differences between patch size categories (Table 5). Great tits 371 delivered more caterpillars to theirs broods in large patches, in particular noctuids (Table S2), which are the preferred prey of this species in the study area (García-Navas et al., 372 2013). The possibility to feed with a higher proportion of their preferred prey in large 373 patches may not go unnoticed for great tits, and males may compete to settle there, as the 374

375 age pattern suggests. This difference in the average age of great tits between large and 376 small patches has been also shown in other studies with this species (Moller, 1991; Riddington and Gosler, 1995) and other species (Burke and Nol, 1998); and is related to the 377 acquisition of a territory (Riddington and Gosler, 1995). In this species, the patch size did 378 379 not affect their recruitment; although it was positively affected by the nestling mass; as 380 other previous studies have shown (Tinbergen and Boerlijst, 1990; Verhulst et al., 1997). 381 Nonetheless, from all great tit fledglings that achieved to breed in the next year, 82% were born in large patches (data not shown for brevity); and the 78% of them bred again in large 382 383 patches, versus the 50% of the nestlings that were born in small patches.

Blue tit nestlings did not differ in body size between patch size categories (Table 3); 384 which suggests that blue tit nestlings did not have the limitations in their development that 385 386 the great tit nestlings seem to suffer in small patches. The reason of this dissimilarity in the results could rely in the different feeding habits of both species. Blue and great tits, 387 388 although they share a similar trophic ecology predating above all on Lepidoptera caterpillars (Perrins, 1991), differ in the global amount of caterpillars in their diet and the 389 390 composition of them. Great tits are more specialists on caterpillars, being highly selective 391 for larger ones (Naef-Daenzer et al., 2001); which in our study area are chiefly noctuids. Blue tits additionally, feed abundantly on tortricids and also incorporate a great amount of 392 spiders in their diet (García-Navas et al., 2013). The particular feeding behaviour of each 393 394 species was also highlighted when an increase in the parental effort was given. Both species increased their feeding rate with large broods, but in a different way. Blue tits faced this 395 396 burden on parental effort through a change in the composition of their diet. This is partly shown with the reduction in the proportion of caterpillar as broods become larger and also 397

with the increase in diet diversity (Table 4). An example of this switch in blue tit diet 398 according to the degree of parental effort, is what happens with the two most abundant 399 caterpillar families in our study area, noctuids and tortricids. The first ones, despite they are 400 a high quality prey, are scarce and more difficult to find. In contrast, tortricids are smaller 401 402 but their higher abundance, gregarious behaviour and leaf-roller habits make them easy to find (Naef-Daenzer and Keller, 1999; García-Navas et al., 2013). With small broods, blue 403 404 tits feed their nestlings with a high proportion of noctuids but, as the broods become larger, they start incorporating a higher proportion of tortricids at the expense of noctuids. This 405 change in the composition of the diet allows them to increase their feeding rate (Table 4). 406 This switch in blue tit diet accordingly to the degree of parental effort was experimentally 407 demonstrated by García-Navas and Sanz (2010). Great tits with larger broods did feed more 408 frequently but they did not change their nestling's diet composition (Table 5). 409

This wider trophic niche of blue tits (Matthysen et al., 2011), may allow them to 410 411 face more efficiently the food limitation conditions in small forest patches, and to better satisfy the energetic demands of their broods in such patches. Indeed, their diet diversity 412 did not change between patch size categories; which means that they in general find their 413 414 food requisites in both patch size categories. This was not the case of great tits, which increased their diet diversity in small patches, probably because they are not able to achieve 415 416 their preferred diet in those patches and are forced to shift to secondary low-quality preys. Although the elementary feeding requisites of blue tits may be satisfied in small patches, 417 this does not mean that little differences in composition, even at species level (García-418 419 Navas et al., 2013 and references there-in), influence the body condition of their nestlings 420 due to differences in food quality, as food is the main limiting factor in nestling body

condition (Naef-Daenzer and Keller, 1999; Kaliński et al., 2014). In fact, for blue tit 421 422 nestlings was better to be born in large patches, because the probability to breed next year was higher in those patches (Table 3). In the same way as great tits, the 81% of the blue tit 423 vearlings that achieved to breed were born in large patches, and the 97% of them did it in 424 425 large patches. Surprisingly, blue tit males were heavier in small patches; which a priori 426 goes against expectation. However, Riddington and Gosler (1995) found a similar result 427 with great tit males breeding in good and poor habitats. The former authors discussed that in poor habitats, due to the scarcity of food, birds increase their fat reserves to face this 428 uncertainty (McNamara and Houston, 1990; Higginson et al., 2012). This could be 429 430 happening in our study area, although we could not confirm this, as we did not measured the fat score levels (Gosler, 1997). The forest patch size effect on nestling characteristics 431 432 found in this study contrasts with the results obtained by Nour et al., (1998), where they did 433 not find differences in the breeding success, diet or caterpillar abundances among a gradient of forest patch size categories. In our study area, although both patch size categories present 434 a similar habitat structure, the small patches support a greater influx of people and the 435 passage of cattle; which could have contributed for the worse breeding performance of tits 436 in those forest patches due to annovances. 437

Besides food supply, nest predation has been seen an important feature driving the worse breeding success of forest birds in small forest patches (Robinson et al., 1995; Chalfoun et al., 2002; Batáry et al., 2014). Nonetheless in this study, the forest patch size did not affect the predation rate of nests, probably because we protected the nest-boxes against most predator species; leading the ladder snake as the main predator in our study area. The snake was present in all forest patches, making the predation rate homogeneous in the whole study area. The increase of the predation rate in 2012 could be related with the increase of the breeding density this year, favouring an increase in the encounter rate of the snakes with occupied nest-boxes.

Other feature that strongly marked this study was the yearly variation, probably 447 because of the different environmental conditions in each year; which had a large influence 448 449 on the abundance of caterpillars as temperature is the primary factor influencing their phenology (Visser and Holleman, 2001). In year 2012, the budding of the oaks was 450 extremely delayed (some patches did not bud until mid-May, J. Bueno-Enciso pers. obs.). 451 This probably caused caterpillars hatched before this date to starve, as they only can 452 survive a few days without food (Durant et al., 2007). As a consequence, the abundance of 453 454 caterpillars this year likely decreased in comparison with the others; which probably accounted for the decrease in the body condition and breeding performance of birds in 455 2012, due to the 'reproductive stress' hypothesis (Nagy et al., 2007; Neto and Gosler, 456 457 2010). This variation in the breeding performance among years is well documented in bird population studies (Perrins, 1965, Lack, 1966). Tits also delayed their laying date in each 458 year, probably in an attempt to synchronize the period of maximum food demand of their 459 460 chicks with the peak of food (Van Noordwijk et al., 1995), a feature that enhances their reproductive success (Visser et al., 2006; Cresswell and McCleery, 2003; Matthysen et al., 461 2011). Blue tits, but not great tits, had a smaller clutch size and a worse breeding success in 462 small patches in 2012. This result may suggest that for some species, the effects of habitat 463 fragmentation only arise in certain years under particular conditions, such as a food 464 465 shortage; as other authors have pointed out (Riddington and Gosler, 1995; Nour et al., 1998). In 2012, the proportion of yearlings to adults of blue tit males and great tit females 466

increased. This increase in the proportion of yearlings in 2012 was probably due to the 467 effect of increasing the number of nest sites the former year, joined with the good 468 environmental conditions prevailing in 2011; which allowed a higher recruitment rate in 469 2012 (Newton, 1994; Robles et al., 2012). Blue tit nestling diet varied among years 470 471 probably in consonance with the prey availability in each year, because of their more flexible feeding behaviour (Matthysen et al., 2011). This was not the case of great tits, 472 which actively selected noctuids, the consumption of which increased each year (Table 3). 473 Consumption of spiders decreased in 2013 in both species, probably due to a sudden 474 decline of this type of prey in the forest this year (Tables 4 and 5). 475

476 *4.1. Conclusions* 

This study suggests that food supply in small forest patches could be hampering the growing conditions of tits in such forest patches, and consequently, their recruitment rate. However, the observational nature of this study does not allow firm conclusions to be drawn, and experiments of cross-fostering between large and small forest patches would be necessary to confirm the factors involved in the reduced breeding performance of tits in small forest patches.

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496 Ethical approval: All applicable institutional and/or national guidelines for the care and497 use of animals were followed.

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