



Original article

Habitat fragmentation influences nestling growth in Mediterranean blue and great tits



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ABSTRACT

In patchy forest areas, the size of the forest patch where birds breed has a strong influence on their breeding success. However, the proximate effects contributing to 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 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 and 29.6 ha) and twelve 'small' forest patches (ranging between 1.1 and 2.1 ha) in a Mediterranean area in central Spain, during three years (2011–2013). We also recorded the nestling diet inside the nest-boxes with the aid of handy-cams. Only males significantly differed between forest 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 patch size categories, but the body condition of blue tit nestlings and the size of great tit 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 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, probably due to annual differences in environmental conditions. This study suggests that food supply could be limiting the breeding success of birds above all in small patches, but also in large patches under particular environmental conditions.

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1. Introduction

Habitat fragmentation is one of the major threats that forest biodiversity faces (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 decline of bird species richness and population abundances (Moller, 1987; Debinski and Holt, 2000; Boulinier et al., 2001). These numerical responses may stem, at least in part, in demographic changes, i.e. proximate effects given at a regional-scale

(Lampila et al., 2005). However, the mechanisms underlying these proximate effects remain unclear, and it is of vital importance to light them in the sake of conservation biology (Boulinier et al., 2001; Le Tortorec et al., 2012). One feature that affects the breeding success of birds, is the size of the forest patch where they breed (Paton, 1995; Hinsley et al., 1999, 2009; Shochat et al., 2001; Loman, 2003; Zitsue et al., 2011; but see Nour et al., 1998), and a reduction of crucial resources in small forest patches has been suggested to be a responsible cause (Kuitunen and Mäkinen, 1993; Tremblay et al., 2005; Hinam and Clair, 2008).

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 life-history in birds (Lack, 1968; Martin, 1987; but see Martin, 1995). Food supply could be compromised in small forest patches just because their small

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surface area (Moller, 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) and may drive to a decrease in the amount of invertebrates (Didham et al., 1996; Burke and Nol, 1998). Furthermore, the process of habitat fragmentation typically implies degradation, which changes the structure of the remaining habitat (Hinsley et al., 1999; Fahrig, 2003). These changes in the vegetation structure usually involve microclimate alterations too; which apart from its direct effects on the abundance of invertebrates, it could promote a change in the composition of the vegetation which could also alter the composition of invertebrates (Cramp and Perrins, 1993; Laurance et al., 2002). In addition, 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 (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 patches, crossing unsuitable foraging habitats, which will limit their feeding rate (Bruun 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 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-Roos et al., 1995; Hinsley, 2000).

The aim of the present study was to test whether there is an effect of the forest patch 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 species of tits in a fragmented landscape in central Spain during three years. Both species are ideal to study this topic as they need an enormous supply of food when they breed. For example great tits while feeding their chicks made up to 700 feeding visits per day, and 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-Daenzer and Keller, 1999; Matthysen et al., 2011); when they do not achieve this match, their reproductive success can decrease (Svensson and Nilsson, 1995; Naef-Daenzer et al., 2001; Tremblay et al., 2003). We hypothesized that in small patches the breeding performance will be worse (Moller, 1991; Riddington and Gosler, 1995), and predict that the lack of resources in small patches will be an important responsible factor, concretely food supply (Burke and Nol, 1998; Zanette et al., 2000; Razeng and Watson, 2014).

2. Material and methods

2.1. Study area

The present study was conducted in the locality of San Pablo de los Montes situated in Montes de Toledo (39°32'44"N, 4°19'41"W; Toledo, central Spain). This region presents 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 this area has suffered an intense fragmentation due to human activities, mainly agriculture 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 most suitable breeding habitat for tits in this region (Ati  n  zar et al., 2012), are scattered and patched in a matrix of less suitable habitat, mainly Mediterranean scrubland with low tree cover and pastureland. Our study area consisted of fifteen oak (*Quercus pyrenaica*) forest patches: three 'large' patches ranging between 26.5 and 29.6 ha,

and twelve 'small' patches ranging between 1.1 and 2.1 ha, separated from each other by a mean distance of 4.23 km (range 0.53–9.84 km). Both oak forest patch size categories present a similar habitat structure, with the oak as dominant plant accompanied by its typical shrub courtship: common hawthorn (*Crataegus monogyna*), elmleaf blackberry (*Rubus ulmifolius*), terebinth (*Pistacia terebinthus*), and common broom (*Cytisus scoparius*). Large patches were provided with 80 wood nest-boxes (internal dimensions: 12 × 11.5 × 16.5 cm) and small 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 m and oriented towards the south. They were protected from predators (mustelids, woodpeckers) with wire mesh and a polyvinyl chloride (PVC) pipe (length: 50–70 mm, diameter: 40 mm) fixed to the hole-entrance. Because of this protection, the main predator in our study area was the ladder snake (*Rhinechis scalaris*), a very common species in the area (Salvador and Pleguezuelos, 2002).

2.2. Field work

During the 2011–2013 breeding seasons (day 1 = April 1), nest-boxes were frequently inspected to obtain the basic reproductive parameters of our tit population, such 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 categories because these variables are indicators of status and thus of dominance over resources (Gosler, 1997; Stahl et al., 2001). To do this, parents were trapped and ringed while feeding their nestlings (8–9 days old). The tarsus length of birds was measured with a digital calliper to the nearest 0.01 mm; the body weight was measured with an electronic balance (0.01 g) and the age of parents (yearling or older) was noted according to plumage characteristics. Due to technical difficulties, adult great tits in 2011 were not trapped. Nestlings were ringed, measured and weighted when they were 13 days old, and mean values per brood were taken in the analyses. Tarsus length was employed as a surrogate of body size, and the weight analyses were corrected by the tarsus length (added as a covariate) to consider the body condition of birds. Nest-boxes were also visited on day 22 to assess the number of chicks fledged. We assumed that all chicks have fledged when we did not find any chick dead inside the nest-boxes. Hatching success was calculated as the ratio between the number of nestlings hatched and the clutch size; and fledgling success 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 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. that was born in the study area); the forest patch ID where it was breeding and the forest 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 achieved to breed in large or small patches the next year. Apart from the seven breeding variables mentioned above, we also estimated the nest-box occupation rate and the breeding density to increase the comprehensive approach of this study. Nest-box occupation rate was 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 tits in each breeding territory as the number of tit breeding pairs in a radius of 75 m around each occupied nest-box with the aid of Quantum GIS 2.0.1, as it is an important trait influencing breeding performance and recruitment rate (Both, 1998; Both et al., 1999).

2.3. Feeding rate and nestling diet

To evaluate potential differences in the breeding performance between patch size categories, nestling diet was filmed by placing an infrared handy-cam (Sony DCR-SR290E-like) in an adapted nest box when nestlings were 11 days old (see [García-Navas and Sanz, 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 and in similar weather conditions. First hour of video of each recording was discarded to 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 Premiere Elements 7.0. In a previous study performed in a nearby area, it was confirmed that an hour is representative of the feeding behavior in these species ([García-Navas and Sanz, 2012](#)). A total of 247 film recordings were analysed, 186 belonged to blue tits (131 in 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 events of each adult. Thus, the number of feeding events per hour was considered as a surrogate of parental provisioning effort (hereafter 'feeding rate'). Diet of nestlings was estimated from identified preys of 6017 feeding trips: 5037 belonging to blue tits and 980 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 major Lepidoptera families presented in the study area: Tortricidae, Noctuidae and Geometridae. The second group "others" include: 'spiders' (Aranea), 'imago' (belonging to the orders Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera and Orthoptera), 'Chrysalides' and 'Miscellaneous' (heterogeneous group including plant tissues, fungus, eggshell, snails and lichen). Size of preys was assessed using a scale bar attached above the 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 caterpillars; <1.5 cm for imagos and abdomen diameter <0.2 cm for spiders); 2 = medium (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 individual prey volumes comparable among taxa (see [García-Navas and Sanz, 2010](#)). Shannon index H' was calculated for each nest.

2.4. Statistical analysis

Only first clutches were used. A set of General Linear Mixed Models (GLMM) were performed in all cases with year and patch size category as fixed factors and laying 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 [García-Berthou \(2001\)](#). In all models, nest ID nested in forest patch ID was included as the random term. Normal distribution was assumed in all models, with the exceptions of proportions (occupation rate, hatching success, fledgling success and proportions of the main prey). For these analyses, GLMMs with a binomial distribution and a binary response variable were employed. In the occupation rate model the numerator of the binary response variable was the number of occupied nest-boxes and the denominator was the total number 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 was the clutch size and the number of hatchlings respectively. For proportions of the main prey types, the numerator was the number of preys belonging to a specific prey type and the 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 response variable was 0 for yearlings and 1 for adults; and in recruitment models the response variable was 0 for nestlings non-recruited and 1 for nestlings recruited. Nestling mass and nestling tarsus length were included as explanatory variables in the models of 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 et al., 1995](#); [Chalfoun et al., 2002](#)), we also tested the effect of the forest patch size on the predation rate by the ladder snake in both tit populations. The former analysis was also 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 factor 'Year' and 'Patch size' was significant, the main effects of both factors on the response variable were not considered (even when $P < 0.05$), in a similar way as [MacDonald et al. \(2014\)](#). From the 329 blue tit nests used in this study, 28 females and 32 males were 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 duplicate adults and found no difference in the results. Thus, we decided to treat each adult as independent in the analyses, in the same way as [Camfield and Martin \(2009\)](#).

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 non-significant 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 (χ^2) is given. Mean \pm SE (n) is given in the results.

3. Results

3.1. Occupation rate and breeding density

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

Regarding the density of breeding pairs, there was not difference between species [GLMM: Estimate \pm SE = 0.05 ± 0.18 , $F_{1, 482} = 0.08$, $P = 0.78$. 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 2012, whereas the breeding density between the years 2011 and 2013 did not differ (Great tits, GLMM: $F_{2, 153} = 9.97$, $P < 0.001$. Blue tits, GLMM: $F_{2, 322} = 32.97$, $P < 0.001$; [Tables 1 and 2](#) respectively). Breeding density of great tits was also positively affected by the laying date (GLMM: Estimate \pm SE = 0.03 ± 0.01 , $F_{1, 153} = 6.87$,

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						
	2011		2012		2013	
	Large patch	Small patch	Large patch	Small patch	Large patch	Small patch
Occupation rate (%)	5.42 \pm 2.20 (3)	37.14 \pm 6.80 (7)	23.75 \pm 6.16 (3)	60.00 \pm 8.94 (10)	12.08 \pm 1.10 (3)	40.00 \pm 3.33 (9)
Density (No. Pairs \times Ha ⁻¹)	5.85 \pm 0.88 (13)	3.23 \pm 0.34 (13)	7.75 \pm 0.29 (57)	3.52 \pm 0.19 (31)	5.66 \pm 0.31 (29)	3.11 \pm 0.23 (18)
Nest predation (%)	0 (13)	0 (13)	42.11 \pm 6.59 (57)	16.12 \pm 6.72 (31)	17.24 \pm 7.13 (29)	5.56 \pm 5.56 (18)
Female age	—	—	0.41 \pm 0.08 (32)	0.52 \pm 0.12 (17)	0.77 \pm 0.09 (22)	0.57 \pm 0.14 (14)
Male 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)
Female mass (g)	—	—	16.18 \pm 0.21 (32)	16.66 \pm 0.21 (17)	16.94 \pm 0.18 (22)	16.84 \pm 0.20 (14)
Male 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)
Female tarsus length (mm)	—	—	19.12 \pm 0.10 (32)	19.21 \pm 0.09 (17)	19.29 \pm 0.13 (22)	19.10 \pm 0.13 (14)
Male tarsus length (mm)	—	—	19.89 \pm 0.11 (29)	19.86 \pm 0.15 (16)	20.01 \pm 0.16 (19)	19.78 \pm 0.11 (13)
Laying date	16.15 \pm 2.87 (13)	13.62 \pm 3.25 (13)	27.59 \pm 2.00 (57)	23.87 \pm 3.01 (31)	22.72 \pm 1.32 (29)	21.72 \pm 1.45 (18)
Clutch size	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)
Hatching success (%)	78.07 \pm 5.96 (13)	84.08 \pm 7.42 (13)	65.82 \pm 4.95 (32)	76.46 \pm 6.26 (18)	66.12 \pm 7.94 (23)	75.83 \pm 6.76 (16)
Fledgling success (%)	91.88 \pm 5.51 (13)	87.71 \pm 8.28 (13)	86.67 \pm 6.31 (30)	86.58 \pm 6.63 (17)	96.60 \pm 2.29 (18)	77.71 \pm 10.50 (15)
Nestling mass (g)	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 tarsus length (mm)	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)
Recruitment (%)	—	—	4.83 \pm 1.26 (290)	4.20 \pm 1.84 (119)	0.88 \pm 0.62 (226)	0 (122)

Table 2
Summary of the occupation, density, predation, morphometric characteristics of adults and nestlings and reproductive parameters in a population of blue tits (*Cyanistes caeruleus*) 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.

Blue tits						
	2011		2012		2013	
	Large patch	Small patch	Large patch	Small patch	Large patch	Small patch
Occupation rate (%)	32.92 \pm 3.97 (3)	56.67 \pm 6.89 (12)	34.58 \pm 9.02 (3)	52.50 \pm 7.50 (8)	35.42 \pm 6.05 (3)	45.00 \pm 5.57 (12)
Density (No. Pairs \times Ha ⁻¹)	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 \pm 2.75 (79)	2.94 \pm 2.94 (34)	24.09 \pm 0.05 (83)	19.05 \pm 8.78 (21)	0.12 \pm 3.52 (85)	14.81 \pm 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 \pm 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 \pm 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 \pm 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 \pm 3.47 (22)
Fledgling success (%)	92.42 \pm 3.01 (72)	96.67 \pm 3.33 (30)	84.62 \pm 4.19 (55)	75.38 \pm 10.38 (13)	89.61 \pm 2.94 (68)	83.33 \pm 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 \pm 1.27 (570)	2.61 \pm 1.05 (230)	1.97 \pm 0.69 (406)	1.41 \pm 1.41 (71)

$P = 0.01$). As regards the forest patch size effect, both tit species presented a higher breeding density in large forest patches than in small ones (Great tits, GLMM: Estimate \pm SE = -3.43 ± 0.35 , $F_{1, 153} = 98.61$, $P < 0.001$; 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 ± 0.44 , $F_{1, 322} = 55.71$, $P < 0.001$. [Tables 1 and 2](#) respectively).

3.2. Parents

The body condition of blue and great tits decreased in 2012 (GLMM: Estimate \pm SE = 0.49 ± 0.20 , $F_{1, 74} = 6.12$, $P = 0.02$ and GLMM: Estimate \pm SE = 0.51 ± 0.21 , $F_{1, 68} = 5.97$, $P = 0.02$ for great tit females and males respectively, and GLMM: $F_{2, 255} = 4.37$, $P = 0.01$ and GLMM: $F_{2, 211} = 8.46$, $P < 0.001$ for blue tit females and males respectively. See [Tables 1 and 2](#)). In 2012, the proportion of yearlings to adults of female great tits increased (GLMM: Estimate \pm SE = 1.09 ± 0.49 , $\chi^2_{1, 78} = 5.09$, $P = 0.02$. [Table 1](#)), the same as the proportion of blue tit male yearlings (GLMM: $\chi^2_{1, 227} = 8.21$, $P = 0.02$. [Table 2](#)).

Attending the forest patch size effect, only males differed between patch size categories, although in a different way in each species. The proportion of old great tit males was higher in large patches (GLMM: Estimate \pm SE = -1.19 ± 0.52 , $\chi^2_{1, 69} = 5.16$, $P = 0.02$. [Table 1](#)), while blue tit males had a better body condition in small patches (GLMM: Estimate \pm SE = 0.29 ± 0.08 , $F_{1, 211} = 11.91$, $P < 0.001$. [Table 2](#)).

3.3. Breeding performance

The greatest differences in the breeding performance of tits were given among years ([Table 3](#)). Blue tit laying date was delayed year after year ([Table 2](#). Tukey HSD test < 0.05), and their hatching success, nestling condition, nestling size and recruitment decreased in 2012 ([Tables 2 and 3](#). Tukey HSD test < 0.05); contrary to nest predation, which increased in 2012 ([Tables 2 and 3](#)). Great tits showed a similar phenology than blue tits, and their laying date was also delayed in 2012 and 2013, although there were not differences between these latter years ([Tables 1 and 3](#). Tukey HSD

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 χ^2 statistic is used for Hatching and Fledgling success, Predation rate and Recruitment. Statistics of non-significant terms are shown in Table S1.

Parameter	Blue tit				Parameter	Great tit			
	Effect	d.f.	Test	P		Effect	d.f.	Test	P
Laying date	Year	320	32.2	<0.001	Laying date	Year	150	8.1	<0.001
Rejected effects: Patch size and Year* Patch size.					Rejected effects: Patch 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: Patch size.					Rejected effects: Year, Patch size and Year* Patch size.				
Hatch. success	Year	296	6.9	0.03	Hatch. success				
Rejected effects: Patch size, Laying date and Year* Patch size.					Rejected effects: All.				
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: Patch size.					Rejected effects: Patch size, Laying date and Year* Patch size.				
Nest predation	Year	320	15.77	<0.001	Nest predation				
Rejected effects: Patch size, Laying date and Year* Patch size.					Rejected effects: All				
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.				
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: Patch size and Year* Patch size.					Rejected effects: Laying date and Year* Patch 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: Nestling mass, Tarsus length, Laying date and Year* Patch size.					Rejected effects: Patch size, Tarsus length, Laying date and Year* Patch size.				

test > 0.05). The clutch size in this species did not differ among years (Table 3). Rest of the reproductive variables varied among years in a similar way as blue tits, i.e. decreasing in 2012 (see Table 1. Tukey HSD test < 0.05), except for the hatching success and nest predation (Table 3).

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 conspecifics in small patches all years (large patches: 19.43 ± 0.06 (65), small patches: 19.23 ± 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: $9.94 \text{ g} \pm 0.05$ (189), small patches: $9.72 \text{ g} \pm 0.08$ (61). Tables 2 and 3). The nestling body condition in both species was also positively affected by their tarsus length (Table 3). Regarding recruitment, 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 related to their body mass (Table 3). Almost none other trait of breeding performance differed between patch size categories, although there were some significant interactions between year and patch size category in blue tits (Table 3). Concretely, the clutch size and fledgling success differed in 2012, being smaller in small patches (Table 2), in rest of years these variables did not differ between patch size categories.

3.4. Nestling diet

Table S2 resumes the nestling diet of each species in each forest patch size category 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 2013 in relation to 2011 (Tukey HSD test < 0.05, Table 4), but these increases were sustained by different caterpillar families in each year. In 2012 the increase in the 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 < 0.05). This increase in the consumption of

noctuids in 2012 was probably the cause of the increase in the prey size this year (Tukey HSD test < 0.05). In 2013 the proportion of noctuids diminished, but the proportion of tortricids increased with respect to the former 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 < 0.05). In this species, the forest patch size did not affect the nestling diet (Table 4). 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 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 tortricids was positively affected (Table 4). Diet diversity (*H'*) in this species did not vary between patch sizes or years, but was positively affected by both laying date and brood size (GLMM: Estimate \pm SE: 0.009 ± 0.03 , $F_{1, 177} = 9.12$, $P = 0.003$ and GLMM: Estimate \pm SE: 0.04 ± 0.01 , $F_{1, 177} = 6.26$, $P = 0.01$).

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

4. Discussion

The nest-box occupation rate was higher in small forest patches

Table 4
Results of the GLMMs analyzing the effects of the year, patch size, laying date and brood size on blue tit nestlings diet (*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 (χ^2) statistic is given with non-parametric distributions. Significant results are highlighted in bold.

Response variable	Explanatory term	Estimate \pm SE	Test	P	Response variable	Explanatory term	Estimate \pm SE	Test	P
Feeding rate	Intercept	8.44 \pm 3.04			Tortricidae	Intercept	-2.00 \pm 0.32		
	Year		$F_{2, 175} = 1.84$	0.16		Year		$\chi^2_{2, 176} = 37.57$	<0.001
	Patch size	-4.02 \pm 2.47	$F_{1, 176} = 2.64$	0.13		Patch size	0.08 \pm 0.20	$\chi^2_{1, 175} = 0.17$	0.68
	Laying date	-0.08 \pm 0.09	$F_{1, 174} = 0.74$	0.40		laying date	-0.01 \pm 0.005	$\chi^2_{1, 176} = 5.13$	0.02
	Brood size	2.50 \pm 0.39	$F_{1, 177} = 40.31$	<0.001		Brood size	0.08 \pm 0.03	$\chi^2_{1, 176} = 5.52$	0.02
Caterpillars	Year*Patch size		$F_{2, 172} = 0.09$	0.92	Aranea	Year*Patch size		$\chi^2_{2, 173} = 4.24$	0.12
	Intercept	1.48 \pm 0.13				Intercept	-1.93 \pm 0.10		
	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	-0.07 \pm 0.10	$\chi^2_{1, 175} = 0.40$	0.52
	laying date	-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
Noctuidae	Brood size	-0.007 \pm 0.03	$\chi^2_{1, 175} = 0.08$	0.78	Prey size	Brood size	-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
	Intercept	0.51 \pm 0.23				Intercept	1.99 \pm 0.08		
	Year		$\chi^2_{2, 176} = 16.38$	<0.001		Year		$F_{2, 176} = 18.30$	<0.001
	Patch size	-0.09 \pm 0.17	$\chi^2_{1, 175} = 0.32$	0.57		Patch size	-0.008 \pm 0.08	$F_{1, 175} = 0.01$	0.92
	laying date	-0.02 \pm 0.004	$\chi^2_{1, 176} = 12.48$	<0.001		laying date	-0.007 \pm 0.003	$F_{1, 176} = 4.52$	0.04
	Brood size	-0.05 \pm 0.02	$\chi^2_{1, 176} = 4.35$	0.03		Brood size	-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

Table 5
Results of the GLMMs analyzing the effects of the year, patch size, laying date and brood size on great tit nestlings diet (*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. Wald chi-square (χ^2) statistic is given with non-parametric distributions. Significant results are highlighted in bold.

Response variable	Explanatory term	Estimate \pm SE	Test	P	Response variable	Explanatory term	Estimate \pm SE	Test	P
Feeding rate	Intercept	8.40 \pm 3.68			Tortricidae	Intercept	-2.45 \pm 0.19		
	Year		$F_{2, 49} = 0.09$	0.91		Year		$\chi^2_{2, 53} = 0.97$	0.61
	Patch size	-0.83 \pm 5.78	$F_{1, 49} = 0.03$	0.87		Patch size	-0.32 \pm 0.33	$\chi^2_{1, 55} = 0.96$	0.32
	laying date	-0.09 \pm 0.09	$F_{1, 54} = 1.07$	0.30		laying date	-0.02 \pm 0.01	$\chi^2_{1, 54} = 1.63$	0.20
	Brood size	1.02 \pm 0.45	$F_{1, 55} = 5.15$	0.03		Brood size	-0.01 \pm 0.07	$\chi^2_{1, 52} = 0.03$	0.87
Caterpillars	Year*Patch size		$F_{5, 49} = 2.71$	0.06	Aranea	Year*Patch size		$\chi^2_{2, 50} = 2.00$	0.37
	Intercept	2.28 \pm 0.52				Intercept	-2.34 \pm 0.34		
	Year		$\chi^2_{2, 53} = 20.80$	<0.001		Year		$\chi^2_{2, 55} = 13.10$	0.001
	Patch size	-1.01 \pm 0.41	$\chi^2_{1, 53} = 5.93$	0.01		Patch size	0.14 \pm 0.43	$\chi^2_{1, 53} = 0.10$	0.75
	laying date	-0.05 \pm 0.001	$\chi^2_{1, 53} = 10.17$	0.001		laying date	0.001 \pm 0.02	$\chi^2_{1, 52} = 0.005$	0.95
Noctuidae	Brood size	-0.01 \pm 0.08	$\chi^2_{1, 52} = 0.02$	0.89	Prey size	Brood size	-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
	Intercept	0.93 \pm 0.41				Intercept	2.15 \pm 0.08		
	Year		$\chi^2_{2, 51} = 21.93$	<0.001		Year		$F_{2, 54} = 1.65$	0.21
	Patch size	-0.60 \pm 0.31	$\chi^2_{1, 51} = 4.34$	0.03		Patch size	0.05 \pm 0.15	$F_{1, 51} = 0.11$	0.75
	laying date	-0.04 \pm 0.01	$\chi^2_{1, 51} = 8.82$	0.002		laying date	-0.007 \pm 0.01	$F_{1, 53} = 1.71$	0.20
	Brood size	0.02 \pm 0.06	$\chi^2_{1, 50} = 0.09$	0.76		Brood size	-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

for both species in all years, probably because the lower availability of nest-boxes in such forest patches 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 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 important trait that negatively influences the breeding performance and recruitment of birds because of the competition over resources (Both, 1998; Both et al., 1999). However, the nestling growth was better and the blue tit recruitment was higher in large patches, despite the higher breeding density in those patches; which reinforces the idea that large forest patches offer better conditions for breeding tits than small patches.

As we said before, patch size affected nestling growth in both species (Table 3). Great tit nestlings in large patches were bigger than those from small patches, which 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 factor of nestling growth (Van Noordwijk et al., 1988).

In fact, the analysis of great tit nestling diet revealed key differences between patch size categories (Table 5). Great tits delivered more caterpillars to their 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., 2013). The possibility to feed with a higher proportion of their preferred prey in large patches may not go unnoticed for great tits, and males may compete to settle there, as the age pattern suggests. This difference in the average age of great tits between large and 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 acquisition of a territory (Riddington and Gosler, 1995). In this species, the patch size did not affect their recruitment; although it was positively affected by the nestling mass; as other previous studies have shown (Tinbergen and Boerlijst, 1990; Verhulst et al., 1997). 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 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); which suggests that blue tit nestlings did not have the limitations in their development that 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, 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 composition of them. Great tits are more specialists on caterpillars, being highly selective 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 spiders in their diet (García-Navas et al., 2013). The particular feeding behavior of each 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 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 with the increase in diet diversity (Table 4). An example of this switch in blue tit diet according to the degree of parental effort, is what happens with the two most abundant caterpillar families in our study area, noctuids and tortricids. The first ones, despite they are a high quality prey, are scarce and more difficult to find. In contrast, tortricids are smaller but their higher abundance, gregarious behavior and leaf-roller habits make them easy to find (Naef-Daenzer and Keller, 1999; García-Navas et al., 2013). With small broods, blue 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 change in the composition of the diet allows them to increase their feeding rate (Table 4). This switch in blue tit diet accordingly to the degree of parental effort was experimentally demonstrated by García-Navas and Sanz (2010). Great tits with larger broods did feed more frequently but they did not change their nestling's diet composition (Table 5).

This wider trophic niche of blue tits (Matthysen et al., 2011), may allow them to 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 did not change between patch size categories; which means that they in general find their 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 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, this does not mean that little differences in composition, even at species level (García-Navas et al., 2013 and references there-in), influence the body condition of their nestlings due to differences in food quality, as food is the main limiting factor in nestling body condition (Naef-Daenzer and Keller, 1999; Kuliński et al., 2014). In fact, for blue tit 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 yearlings that achieved to breed were born in large patches, and the 97% of them did it in large patches. Surprisingly, blue tit males were heavier in small patches; which a priori goes against expectation. However, Riddington and Gosler (1995) found a similar result 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 uncertainty (McNamara and Houston, 1990; Higginson et al., 2012). This could be 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 found in this study contrasts with the results obtained by Nour et al. (1998), where they did 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 a similar habitat structure, the small patches support a greater influx of people and the passage of cattle; which could have contributed for the worse breeding performance of tits in those forest patches due to annoyances.

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, favoring 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 because of the different environmental conditions in each year; which had a large influence 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 extremely delayed (some patches did not bud until mid-May, J. Bueno-Enciso pers. obs.). This probably caused caterpillars hatched before this date to starve, as they only can survive a few days without food (Durant et al., 2007). As a consequence, the abundance of 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 2012, due to the 'reproductive stress' hypothesis (Nagy et al., 2007; Neto and Gosler, 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 year, probably in an attempt to synchronize the period of maximum food demand of their 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., 2011). Blue tits, but not great tits, had a smaller clutch size and a worse breeding success in small patches in 2012. This result may suggest that for some species, the effects of habitat fragmentation only arise in certain years under particular conditions, such as a food 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 increased. This increase in the proportion of yearlings in 2012 was probably due to the effect of increasing the number of nest sites the former year, joined with the good environmental conditions prevailing in 2011; which allowed a higher recruitment rate in 2012 (Newton, 1994; Robles et al., 2012). Blue tit nestling diet varied among years probably in consonance with the prey availability in each year, because of their more flexible feeding behavior (Matthysen et al., 2011). This was not the case of great tits, which actively selected noctuids, the consumption of which increased each year (Table 3). Consumption of spiders decreased in 2013 in both species, probably due to a sudden decline of this type of prey in the forest this year (Tables 4 and 5).

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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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.actao.2015.12.008>.

Author contributions

JJS originally formulated the idea; JBE, ESF, RF and JJS conducted fieldwork. JBE, ESF, RF and ESD analyzed diet recordings, while JBE analyzed the data and wrote the manuscript. JJS and RF helped and contributed to improve last version.

Conflicts of interest

The authors declare that they have no conflict of interest.

Ethical approval

All applicable institutional and/or national guidelines for the care and use of animals were followed.

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