

Breeding performance of Blue tits *Cyanistes caeruleus* can be predicted from time since last logging in Mediterranean mixed oak forest

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Abstract – Logging can affect breeding performance and offspring survival in birds, but such effect can change over time. We investigated this question, deploying nest boxes for blue tits (*Cyanistes caeruleus*) in four forest stands, differing in the time since the last harvesting event occurred: 2, 10, 20 and 45 years ago. We recorded laying date, clutch and brood size and number of fledglings in the four stands over two years (2014-2015). We modelled reproductive success as a function of laying date and number of offspring. In the first year, the first laying date was about ten days earlier in the older stands, while in the second year the laying date did not differ among stands. Clutch size differed between stands in the first year but in the second year. Brood size dropped in 2015, except in one of the oldest stands. Reproductive success changed markedly between years and stands and was determined mainly by laying date. Though our results should be considered preliminary, we acknowledge that such year-to-year variability is likely attributed to climatic and structural differences between years and stands, respectively.

Key-words: forest bird, habitat selection, stand complexity, reproductive performance.

INTRODUCTION

In forest ecosystems, timber harvest can be a dramatic source of habitat alteration. Forestry shapes the environment at multiple spatial scales, from landscape to single stand. Acting on single stands, it provides a mosaic of younger, structurally simplified, smaller and isolated forest patches that generate, as a consequence, an altered landscape. Such altered conditions can increase the fitness of a few successfully competitive species (McKinney & Lockwood 1999), often generalists or invasive species that outcompete specialists that are affected negatively by habitat alteration.

Wildlife response to habitat alteration often depends on both biological intrinsic properties of the species and/or population and the magnitude of the alteration. The re-

sponse of wildlife, however, is time-dependent and can be quite different in the short- versus long-term. Soon after habitat has been modified (*e.g.* forest harvest) animal populations can exhibit resiliency and persist despite more sensitive and/or specialist taxa exhibiting some decline (Schmiegelow *et al.* 1997). In contrast, over a long period, a simplified forest structure can cause the loss of many species, whose ecological niches are often not filled even after a long period has elapsed (Thompson *et al.* 2003). Indeed, the intensity of forestry activities is a major driver in shaping the response of wildlife, exacerbating it in both positive and negative ways (Millington *et al.* 2011).

One of the most common habitat changes associated with timber harvest is the loss of cavities, used by birds for nesting or roosting (Newton 1994). Breeding activity is assumed to be the most sensitive biological process af-

ected by cavity limitation and habitat alteration (Suorsa et al. 2003). Both inter- and intraspecific overlap interference for resources often lead to a decrease in recruitment because of increased energetic demands required for reproduction (Robertson & Rendell 1990).

Food availability is dependent on habitat structure and thus affects both the phenology of laying and clutch size (Perrins 1965, Arriero et al. 2006), which in turn can have strong effects on reproductive success (Norris 1993). Therefore, habitat quality can affect breeding performance, offspring survival and recruitment. Moreover, habitat quality can change over time due to natural forest succession.

To explore how habitat quality change after timber harvest, we supplemented with nest boxes four forest stands, differing by the time since logging, targeting Blue tits *Cyanistes caeruleus*. We, thus, examined several reproductive traits that included laying date, clutch size and fledging rate by testing the following hypotheses:

- Birds lay eggs in older stands earlier in the season than in younger ones, due to more favourable site conditions.
- Birds have larger clutches in older stands.
- As for the hypotheses 2, we also expect that the fledging success is higher in older stands.

We seek to investigate how increasing degree of habitat alteration can affect the reproductive biology of a species. Our experiment, using nest boxes to improve habitat, was repeated in two consecutive years and yearly results compared.

MATERIALS AND METHODS

Study area

The experimental forest stands were in Abruzzo and Molise Regions (Central Italy) (Fig. 1). All stands were included in Turkey oak-dominated forests *Quercus cerris*, in which coppice has been the main forestry practice in recent times. Three forest stands were included in the Natura2000 site SCI IT7110104 Cerrete di Monte Pagano e Feudozzo (41°45'N, 14°11'E), and were separated from each other by approximately 300 m:

- the oldest forest stand ('70') was harvested in 1970. It was a late successional, mature forest structured in two layers, a dominant Turkey oak overstory and an understorey consisting mainly of European hornbeam *Carpinus betulus* and Common hazel *Corylus avellana*;
- the stand '95' was harvested in 1995 and consisted of a coppice in conversion to mature forest structured in

two-layers, a dominant Turkey oak overstory with a mixed species layer;

- the stand '05' was similar to the '95' stand but harvested in 2005.

The final forest stand was located in the Natura2000 site SCI IT 7212124 Bosco Monte di Mezzo - Monte Miglio - Pennataro - Monte Capraro - Monte Cavallerizzo (41°43'N, 14°11'E), at a distance of approximately 3 km from the Feudozzo Regional Forest:

- the youngest stand ('12') consisted of a coppice harvested in 2012 and 2013, with young and thinned Turkey oak stands sparsely distributed in combination with a layer of herbs and shrubs.

Data collection

Nest boxes consisted of a wedge-like box, with two entrance holes (width = 4 cm) on both upper-sides and a maximum depth of 24 cm (Fig. 2). Nest boxes were installed at 1.5 m height, facing south, and arranged in a grid-like fashion at 50-m intervals (Fig. 1). Each forest stand was supplemented with 36 nest boxes in February 2014. The majority of the nest boxes were occupied by Blue tits (Tab. 1), and therefore the main statistical analyses were focused on this taxon.

Nest boxes were checked every seven-ten days (depending on favourable weather conditions), starting from the beginning of April until early July. Surveys were carried out by two teams, so as to check all nest boxes within two consecutive days. Eggs and chicks were carefully weighted using a digital scale (precision ± 0.01 g).

Statistical analyses

Nest boxes were checked and grouped into 10-day aggregates. Dates of initial occupation and egg laying were recorded separately since birds can lay eggs several days after nest building has been initiated. Dates of initial occupation and laying were compared between years by means of a Wilcoxon rank sum test. Differences in the number of eggs and chicks between years were tested using *F* and *t* tests.

To address our three hypotheses, we did not consider nest boxes occupied but later abandoned (number of eggs = 0) and the statistical analyses were carried out as follows:

- Differences in laying dates in the four stands (grouped in 10-day increments beginning the 1st April) were tested using a Kruskal-Wallis test with a Conover-post-hoc test using Holm's p-value correction (Conover & Iman 1979)
- Clutch and brood size among the four forest stands

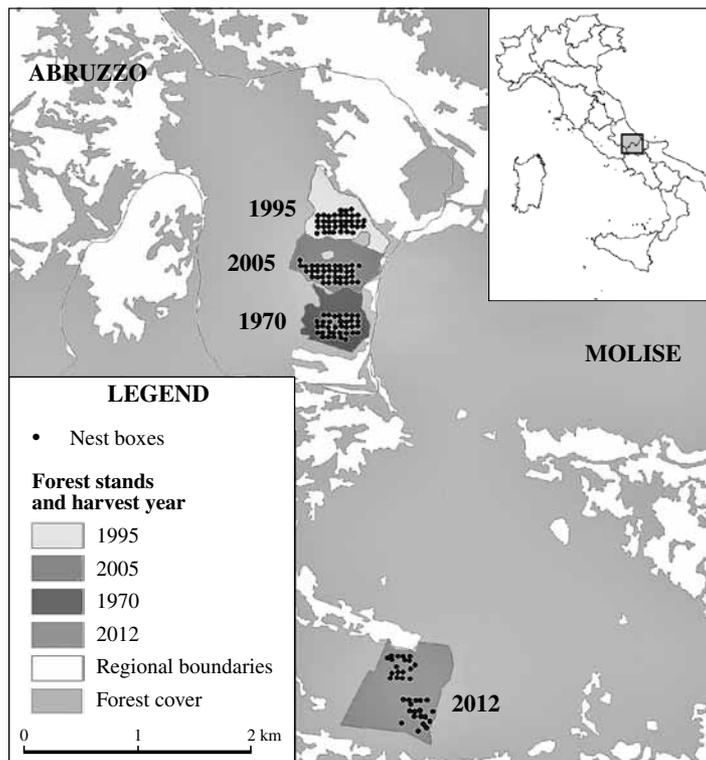


Figure 1. Study area.

were also tested using a Kruskal-Wallis test with a Conover-*post-hoc* test using Holm's p-value correction (Conover & Iman 1979). Mean egg weights per clutch were tested for difference among clutch sizes using ANOVA.

- Reproductive success, expressed as the proportion of a fledging brood relative to the clutch size, was modelled as a function of clutch size, brood size, laying date (10-day aggregates) and date of first disturbance (i.e. when a nest was found completed). This metric allowed us to determine if the disturbance associated with to nest box checking affected chick survival. Modelling considered as random effect, area and year, in order to account for unexplained variability between areas and years. Indeed, we implemented generalized linear mixed models (GLMM), via penalized quasi-likelihood, assuming a quasi-binomial error distribution. We first built a global model, including all the independent variables, then all the non-significant independent variables were thrown out and the model run again. A Levene test was employed to assess heteroscedasticity in the dataset and, where applicable, model correction was implemented. In this way, we can assess if the samples are comparable among stands and

years, by checking their variance. Therefore, GLMM modelling considered heteroscedasticity, by considering both year and stands as different additive random effects.



Figure 2. Nest box employed in the study. Entrance hole (on opposite side, only one shown in figures) diameter = 4 cm, maximum depth = 24 cm.

Statistical analyses were carried out in R (R Core Team 2015), using the packages ‘PMCMR’ (Pohlert 2014), ‘spdep’ (Bivand & Piras 2015) and ‘MASS’ (Venables & Ripley 2002).

RESULTS

The field seasons in each of 2014 and 2015 were divided into 7 x 10-day intervals. In 2014, 119 out of 144 nest boxes were suitable for nesting, *i.e.* un-broken or not occupied by other species. Among them, 30 were never occupied and 27 boxes were initially occupied but later abandoned before any egg was laid. Most of the nest boxes were occupied in the first interval with laying following in the subsequent interval (Fig. 3). A total of 467 eggs and 398 nestlings were recorded, with a mean clutch size of 5.3 (range = 0–11) and a mean brood size of 4.5 (range = 0–10). In 2015, the number of suitable nest boxes decreased to 115, of which 16 remained unoccupied and 30 were abandoned prior to egg laying. Surprisingly, few nest boxes were occupied in the first 10-day interval, with a clear delay in the onset of the breeding season and the peak of occupation overlapped with the peak of laying in the third 10-day interval (Fig. 3).

A total of 429 eggs and 245 nestlings were found, with a mean clutch size of 4.4 (range = 0–10) and a mean brood size of 2.5 (range = 0–9). Indeed, initial occupation and laying periods differed significantly between years (occupation: $W = 3380$; $p < 0.001$; laying: $W = 5156$; $p = 0.001$), with 2014 showing early laying dates. Also, brood size was significantly larger in 2014 ($F = 1.40$, $p = 0.07$; $t = 2.46$, $p = 0.02$) but clutch size did not differ between years ($F = 1.30$, $p = 0.16$; $t = 0.25$, d.f. = 230, $p = 0.81$).

Difference in laying dates

Because laying date differed between years, laying dates were analysed separately (Tab. 1). In 2014, a significant difference emerged among stands ($K = 10.40$, d.f. = 3, $p = 0.02$) whereby a significantly higher portion of Blue tits in stand ‘70’ laid earlier (Fig. 4) than in stand ‘12’ ($p_{\text{adj}} = 0.037$). In contrast, there was no difference among stands in 2015 ($K = 1.13$, d.f. = 3, $p = 0.77$).

Difference in clutch and brood size

We used a similar approach to examine how clutch and brood size differed between years (Tab. 1). A difference in clutch size among stands emerged only in 2014 ($K = 10.46$, d.f. = 3, $p = 0.02$) and only between the oldest (*i.e.* ‘70’) and the youngest stands (*i.e.* ‘12’) ($p_{\text{adj}} = 0.03$). The mean egg weight did not differ significantly among clutches of different stands ($F = 1.514$; d.f. = 3; $p = 0.22$). There was significant difference in brood size between 2014 ($K = 8.11$, d.f. = 3, $p = 0.04$) and 2015 but only one significant difference among stands ‘70’ and ‘05’ ($p_{\text{adj}} = 0.05$).

Difference in reproductive success

We found evidence for heteroscedasticity ($p < 0.01$) when testing for differences in the variability among forest stands and years. Indeed, these two variables contributed to the random error, when modelling the reproductive success: ‘year’ explained 39% of the variation, of which 22% was due to ‘area’. The model explained the reproductive success as a function of both the laying date (1.08 ± 0.11 se, $t = 9.63$, d.f. = 222, $p < 0.001$) and the brood size (0.96 ± 0.06 se, $t = 17.49$, d.f. = 222, $p < 0.001$). Both variables had a positive effect on reproductive success, with any differences accounted for by year and stand effects (Fig. 5). In contrast, clutch size and the first date at which the nest

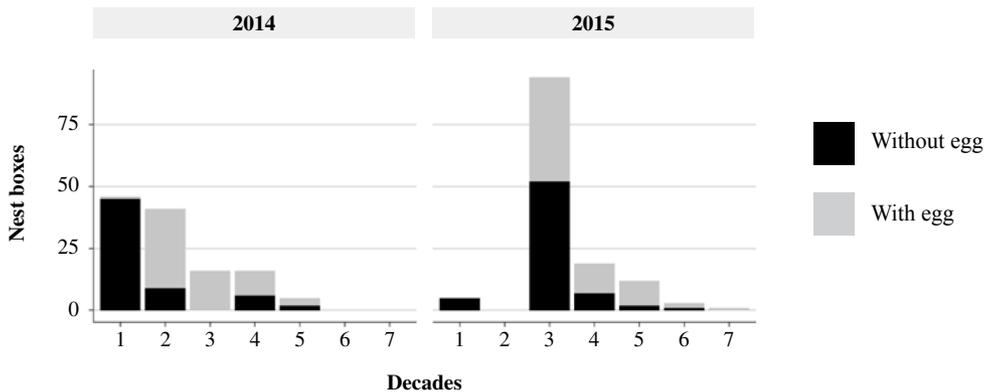


Figure 3. Chronology of nest box colonisation by Blue tits *Cyanistes caeruleus* in two consecutive years (2014 - 2015). Simple occupation of the nest box (black) is differentiated from the actual oviposition (grey). Each bar represent a period of ten days. Starting time = April 1st. Black = nest boxes occupied but with any eggs; grey = nest boxes with eggs.

Table 1. Reproductive parameters in each stand and year. Value are shown as mean (\pm sd) Survival is showed as fitted mean value.

* significant difference ($p_{adj} < 0.05$) between mean values of the parameter when compared between the two years. + = near significant difference ($p_{adj} = 0.05$) between mean values.

	Year 2014				Year 2015			
	1970	1995	2005	2012	1970	1995	2005	2012
Laying	2.45*	2.47	3.07	3.20*	3.78	3.65	3.40	3.71
Eggs	(0.90)	(0.83)	(1.00)	(0.79)	(1.17)	(0.93)	(0.68)	(0.95)
Chicks	8.78*	7.27	7.00	5.80*	6.57	5.88	6.60	6.57
Survival	(2.07)	(1.98)	(2.72)	(3.22)	(2.68)	(2.03)	(2.54)	(3.05)
	7.74+	6.67	4.43	5.80+	3.26	3.88	3.10	3.43
	(2.28)	(1.91)	(4.20)	(3.26)	(3.66)	(3.62)	(3.40)	(4.08)
	0.60	0.42	0.36	0.23	0.36	0.28	0.30	0.10

was completed did not have any significant effect on reproductive success.

DISCUSSION

Temperate forests have been intensively managed, so that forest structure and the relative bird responses are highly dependent on silvicultural practices (Guénette & Villard 2005). Although avian numerical responses to stand structural complexity are widely known, less investigated is the functional response of individuals (e.g. Duguay *et al.*

2001, Suorsa *et al.* 2004, Bellia 2005). Our results provide more insight on the functional response of birds to forest age, a metric of forest structure, though the results provided come from only two years of monitoring and should be considered as preliminary.

Difference in laying dates

Small passerines tend to lay eggs as soon as possible in the season, they can adjust their timing to better profit from local environmental conditions (Drent 2006). For instance, in food-rich areas, a delay in laying date to match a concomitant food availability peak, may be irrelevant in terms of brood survival, and thus laying date may only be constrained by environmental (weather) conditions (Wesołowski & Rowiński 2014). Moreover, in less productive habitat, laying date can be delayed, as females in worse condition are usually confined to suboptimal habitats, and constrained to wait for more favourable weather conditions (later in the season) to initiate laying (Arriero *et al.* 2006). In our study system, Blue tits laid eggs earlier in the two more mature stands, likely because of more stable microclimatic and environmental conditions (Chen *et al.* 1993).

A ten-day difference in the mean laying date between the oldest and the youngest stands, in 2014, may appear to be a large difference, yet this difference is even more pronounced when one examines the actual dates of laying. During the peak of laying in each stand, we found nest boxes with 11 eggs in stand ‘70’ on 16 April and 9 eggs in stand ‘12’ on 14 May 2014. Assuming that under favourable weather conditions, Blue tits can lay one egg per day (Yom-Tov & Wright 1993), we can suppose that nearly a month delay occurred in stand ‘12’. At the same time, we did not observe such differences in the second study year (2015), when laying times were more synchronous among

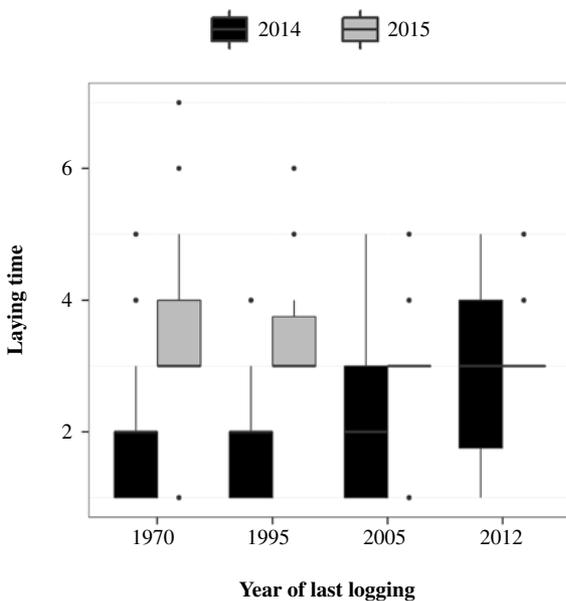


Figure 4. Difference in the laying date (referring to ten days period) between stands in two consecutive years: 2014 (black) and 2015 (grey).

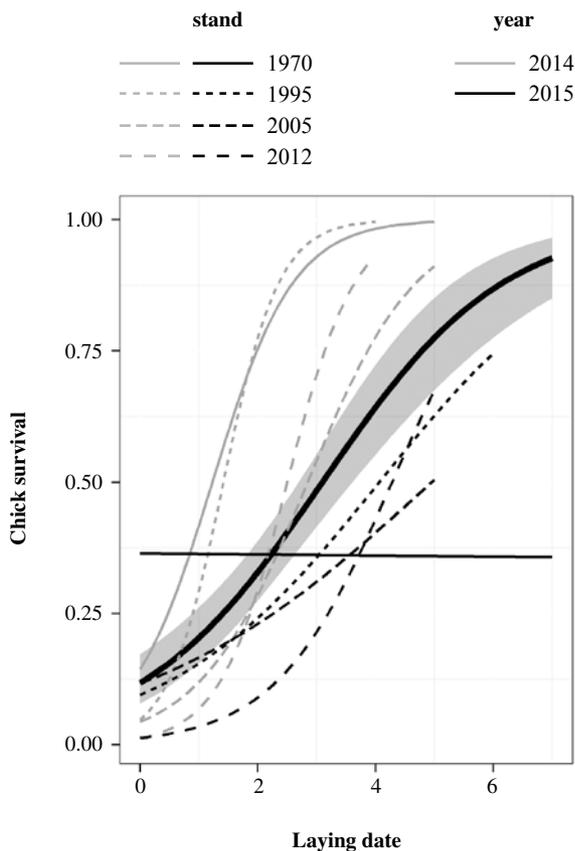


Figure 5. Effect of deposition time on chick survival. The thickest line show the average effect with standard error (shaded area). Other lines show the effect of stand age and year.

stands. Such difference among stands has been already observed in Mediterranean forests, where natural forests tend to have earlier breeder than secondary forests (Massa *et al.* 2011).

Difference in clutch and brood size

The individual optimization hypothesis shows that birds are capable of adjusting not only laying date but also clutch size, relative to their body condition (Pettifor *et al.* 1988). Again, our results are concordant with theory, as larger clutches were found in the more favourable year and stand. Both clutch size and laying date covary and are largely dependent on adult body condition (Drent 2006). However, the decline in brood size was not consistent among stands, suggesting other causes beyond unsuitable weather conditions. We did not record predation events in our study, even though we observed several signs of (attempted) predation during the field work, *e.g.* dead adult, dead or missing chick, broken or missing eggs, holes in the nest box excavated by a woodpecker, especially in 2015.

Difference in reproductive success

As already stated, several factors can affect the variability in the reproductive outcomes among years and stands, *i.e.* weather, forest structure, interference or female body condition. These variables might have acted in synchrony in our forest stands, causing a general decrease in reproductive success in the colder year (climate), a difference among structurally different stands (forest structure) and a different pattern of reproductive success among stand and year (degree of competition and female body condition). Tit density can naturally decrease in more open or structurally simplified stands, indicating a preference for more natural stands (Balestrieri *et al.* 2015) but we, indeed, observed a higher performance in stand ‘95’ than in stand ‘70’ (*i.e.* the older one). While it is known that in structurally simplified or disturbed habitats, interspecific interference can increase (Robillard *et al.* 2012) due to an overabundance of nest boxes, exacerbating intraspecific (or intra-guild) interference may ultimately lead to an ecological trap (Mänd *et al.* 2005).

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