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Authors: Ziane, Nadia, Chabi, Yassine, and Lambrechts, Marcel M.

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Breeding performance of Blue Tits *Cyanistes caeruleus ultramarinus* in relation to habitat richness of oak forest patches in north-eastern Algeria

Nadia ZIANE[1]*, Yassine CHABI[1] & Marcel M. LAMBRECHTS[2]

[1]Laboratoire d'Ecophysiologie animale, Département de Biologie, B.P. 12 2300 Annaba, ALGÉRIE
[2]Centre d'Ecologie Fonctionnelle et Evolutive (UMR 5175 du CNRS), 1919 route de Mende, F-34293 Montpellier cedex 05, FRANCE
*Corresponding author, e-mail: ziane23@yahoo.fr

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Abstract. Like many other seasonally breeding birds, Blue Tits raise their chicks mainly at the time when numerous caterpillars attack fresh oak leaves. This paper reports on the results of the first quantitative study of food ecology in combination with the breeding biology of a North African population of Blue Tits occupying distinct patches of oak habitat (high-altitude semi-evergreen zeen oak versus low-altitude evergreen cork oak). To check for between-habitat differences in intensities of nest parasites feeding on chicks, all nests monitored were heat-treated during the chick-raising stage. The peak demands of the chicks were found to coincide with the peak date of caterpillar availability in both habitat types. Food availability was much higher in the semi-evergreen habitat, and the diversity of prey delivered to the chicks was higher in the evergreen habitat. Surprisingly, breeding success was very low in both habitat types. It is suggested that several environmental constraints may cause maladapted avian breeding responses in heterogeneous Algerian habitat mosaics. Spatial variation in micro-climate may influence the capacity to adaptively adjust breeding responses to distinct habitat types.

Key words: Blue Tit, *Cyanistes caeruleus ultramarinus*, North Africa, habitat richness, *Quercus*, oak, reproduction, *Parus*

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INTRODUCTION

Any avian breeding trait is influenced by resource availability required for phenotype development and performance (Lack 1968, Martin 1987). In fast-growing avian species, raising offspring optimally requires large amounts of food. Food is not only invested in growth and reproduction, but also in maintenance and defense against potential enemies, such as pathogens (e.g. Fargallo & Merino 2004) and parasites exploiting adults and/or nestlings (Loye & Zuk 1991, Simon et al. 2004). Many seasonally breeding free-ranging birds are therefore challenged annually to match their reproductive performance with a narrow time window when food availability is at its maximum. Individuals reproducing outside this window often have lower breeding success, as expressed in the number and quality of the chicks produced (Van Balen 1973, Dias & Blondel 1996, Blondel et al. 2006).

Blue Tits produce the largest families of any nidicolous bird in the world (Perrins & McCleery 1989). The brood weight at 14 days post-hatching represents between 3–16 times the adults' body weight, depending on the territory and study population. Blue Tit breeding time and reproductive effort most probably evolved in response to the timing of maximal caterpillar biomass supply, key prey to raise chicks (e.g. Zandt et al. 1990, Dias & Blondel 1996, Bańbura et al. 1999, Grieco 1999, Blondel et al. 2006, but see e.g. Lambrechts et al. 2004). Lower breeding success and offspring survival is found in Blue Tits raising chicks well before or after the peak date of caterpillar availability (Dias & Blondel 1996, Blondel et al. 2006). Additional observations of food delivered to chicks in combination with experiments manipulating brood size, breeding time and/or food availability support the view that caterpillar availability in the territory influences parental feeding capacities and the types of prey delivered to

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chicks (e.g. Grieco 1999, Tremblay et al. 2003, 2005).

Former investigations that linked spatial variation in breeding performance to habitat heterogeneity focused mainly on nest-box breeding European continental Blue Tit populations occupying "non-Mediterranean" broad-leaved deciduous or mixed forest patches (e.g. Blondel 1985, Clamens et al. 1986, Blondel et al. 1987, 1993, Fargallo & Johnston 1997, Massa et al. 2004, Arriero et al. 2006, Garcia-Del-Rey et al. 2006). Comparative analyses of breeding biology in distinct habitat types at the southern edge of the distribution range reported lower breeding success in European Mediterranean evergreen habitat, often attributed to a significant reduction in caterpillar availability and/or higher loads of nest ectoparasites attacking chicks in these populations (Blondel et al. 1991, Chabi et al. 1995, Hurtrez-Boussès et al. 1997, Tremblay et al. 2003, 2005, Bańbura et al. 2004, Charmantier et al. 2004, Massa et al. 2004, Arriero et al. 2006, Garcia-Del-Rey et al. 2006). Studies that controlled for altitude and latitude also reported significantly later adaptive breeding dates in evergreen than in summergreen oak patches (e.g. Lambrechts et al. 1997a, Blondel et al. 1999, 2006).

Habitat and altitude influence breeding parameters in North African Blue Tits (e.g. Chabi et al. 1995, Chabi & Isenmann 1997, Chabi et al. 2000), but a quantitative study of breeding performance in relation to food available to the chicks has not been reported before. Here we present the first results of a study of nestling feeding ecology in relation to some measures of Blue Tit breeding success in two distinct Algerian oak forest patches. We focused research on a mountain semi-evergreen zeen oak *Quercus faginea* patch and a lowland habitat dominated by the evergreen cork oak *Q. suber*. Based on findings from former investigations in tits (e.g. Chabi et al. 1995), we predicted: a) parents feeding chicks around the peak date of caterpillar availability in both habitat types, b) higher food availability in the semi-evergreen habitat, and c) higher prey diversity in the evergreen habitat. With the aim to reduce effects of spatial variation in parasite attack on chicks we removed parasites in nests from both habitat types between hatching and 14 days post-hatching, using nest heat treatment following Bouslama et al. (2001). If food availability would have an important impact on breeding success, we predicted lower success in "poor" evergreen habitat than in "rich" semi-evergreen one, despite nest parasite removal.

MATERIAL AND METHODS

Study plots

Studies were conducted in north-eastern Algeria in the region of El-Kala (National Park of El-Kala). The evergreen oak patch is at 30 m a.s.l. near the Djebel Arassa (Brabtia 36°51N, 8°19E, 30 ha), mainly covered by cork oak 8 m height and a well-developed under-story with *Phillyrea angustifolia*, *Pistacia lentiscus*, *Erica arborea*. The semi-evergreen patch is at 875 m a.s.l. at the Djebel Ghorra (36°36N, 8°23E, 10 ha), mainly covered by zeen oak 17.5 m height. Both habitat types have been described by Chabi et al. (1995), Chabi & Isenmann (1997) and Chabi et al. (2000). In 2002 and 2003, 30 nest boxes suitable for Blue Tits were erected in each study plot, from end-February onwards in the evergreen site, and from mid-March onwards in the semi-evergreen site.

Blue Tit breeding data and chick features

The nest boxes were visited at least once a week to get background data on the onset of egg laying, clutch size, brood size, and the number of offspring fledged. Two breeding success measurements (young fledged of eggs laid, young fledged of eggs hatched) were calculated. Chicks were weighed from 13 days post hatching onwards to obtain a reliable measure of fledging quality (cf. Bouslama et al. 2001). The field protocols have been applied with success in former studies in the same study sites (e.g. Bouslama et al. 2001).

Anti-parasite treatment

Following the procedures of Richner et al. (1993), Hurtrez-Boussès et al. (1997), and Bouslama et al. (2001), nests were treated during three minutes using a microwave oven (830 W). Heat-treated nests were replaced twice a week from the onset of egg hatching onwards. This is an efficient method to reduce the ectoparasite loads in Algerian Blue Tit nests (Bouslama et al. 2001). The same protocol was applied during the two years of study. Because the proportion of nest boxes occupied by Blue Tits was relatively low in both habitat types, the yearly sample sizes of heat-treated nests were relatively small (Table 1).

Food availability and feeding frequency measurements

Food availability measurements were obtained with two techniques. Frass fall is considered to be a reliable estimate of caterpillars available to Blue Tits, especially in between-study site comparisons

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Table 1. Blue Tit (mean ± SD) breeding traits in a cork and zeen oak patch. Number of nests sampled are in parentheses. * — p = 0.05, ** — p = 0.001, *** — p < 0.001.

Traits	Cork Oak	Zeen Oak
Onset of egg laying	37.2 ± 8.41 (9)	52.80 ± 6.29 (17)***
Clutch size	6.11 ± 0.78 (9)	6.47 ± 1.12 (17)
Number of hatchlings	5.88 ± 1.05 (9)	5.05 ± 1.51 (17)
Chick body mass	9.92 ± 0.45 (9)	10.65 ± 0.51 (17)*
Number of fledglings	4.66 ± 1.22 (9)	3.94 ± 1.51 (17)
Feeding frequency (days after hatching)		
4–5	0.47 ± 0.25 (7)	1.04 ± 0.17 (7)**
8–10	1.71 ± 0.47 (7)	3.1 ± 0.34 (7)***
14–17	1.00 ± 0.24 (7)	2.53 ± 0.27 (7)***

expressing large differences in peak caterpillar abundance between distinct habitat types (Tremblay et al. 2003). We therefore collected frass in 0.25 m^2 tissue collectors under the tree canopy to obtain a proxy of habitat richness (cf. Zandt et al. 1990, Tremblay et al. 2003, Wesołowski & Rowiński 2006). Ten collectors per study site were visited once a week during the breeding season. In addition, prey delivered to chicks were collected twice a week between 5 and 15 days post hatching using telephone wire necklace preventing swallowing prey, following the so-called "neck-collar method" (Willson 1966, Auger & Faivre 1993) (4 hours per chick per nest).

The total number of nest-box visits by parents delivering prey was determined with binoculars in the morning following Bouslama et al. (2002). The total observation time was 15 h 30 min. for the evergreen site, and 24 h for the semi-evergreen site. Observations were carried out at 4–5 days post-hatching, 8–10 days post hatching, and 14–17 days post hatching. All observations on feeding frequencies were carried out by the same person (NZ).

For the calculation of the average peak demand of chicks at 10 days post hatching at 28 days after the onset of egg laying, we assume that females lay, on average, 6 eggs (one egg / day) and incubate for 12 days.

Statistical analyses

Statistical analyses were carried out using SAS (1998) or Statistica 1997 (version 5.1) following Bouslama et al. (2001, 2002). Effects of year (2002, 2003), or the interactions "year*habitat" investigated were statistically not significant. We therefore pooled the data from 2002 and 2003 in all statistical analyses that focused on relationships with breeding traits.

RESULTS

Breeding and nestling traits

The percentage of boxes occupied by nesting Blue Tits was somewhat higher in the zeen oak (53.3%) than in the cork oak patch (40.0%). Some nests were exposed to treatment against ectoparasites (sample sizes in Table 1).

Blue Tits from the high altitude zeen oak habitat started egg laying statistically significantly later ($F_{3,25} = 29.97$, $p < 0.0001$) and also produced significantly heavier chicks ($F_{3,25} = 13.95$, $p < 0.05$) than Blue Tits from the low altitude cork oak habitat (Table 1). Clutch size ($F_{3,25} = 0.62$, $p > 0.10$) and number of chicks fledged ($F_{3,25} = 1.85$, $p > 0.10$) did not differ statistically significantly between the two habitat types. Surprisingly, number of young fledged of the number of eggs laid was statistically significantly higher in the evergreen cork oak habitat ($F_{3,25} = 5.06$, $p < 0.05$). The number of young fledged of the number of hatchlings produced did not differ statistically significantly between the two habitat types ($F_{3,25} = 2.56$, $p > 0.05$), although the egg hatching success was quite low in the zeen oak patch in 2002 (0.67).

Caterpillar frass

The mean peak caterpillar frass fall was about 5 times higher and occurred consistently later in the zeen oak than in the cork oak patch (1076 ± 62 mg/m^2/day versus 213 ± 0.7 mg/m^2/day) (Fig. 1). Also, chicks were in the nest near the peak date of caterpillar availability in both habitat types, so the supply of optimal prey for raising chicks was considerably higher in the semi-evergreen than in the evergreen habitat investigated, as predicted.

Food availability and feeding frequencies

If the caterpillar frass fall data would nicely reflect the amount of caterpillars available for parents and chicks, we should find a significantly higher proportion of caterpillars in the chicks' diet in the zeen oak than in the cork oak patch. This was indeed the case. The percentage of caterpillars delivered to chicks was statistically significantly higher in the former habitat (zeen oak: 90.1%, n = 131 versus cork oak: 64.1%, n = 64) ($\chi^2 = 20.48$, df = 1, $p < 0.0001$). As predicted, the percentage of prey other than caterpillars was higher in the cork oak patch (Spiders: 18.7%, Orthoptera: 12%) than in the zeen oak patch (Spiders: 4.6%, Orthoptera: 1.5%) (Fig. 2), therefore expressing a higher prey diversity in the

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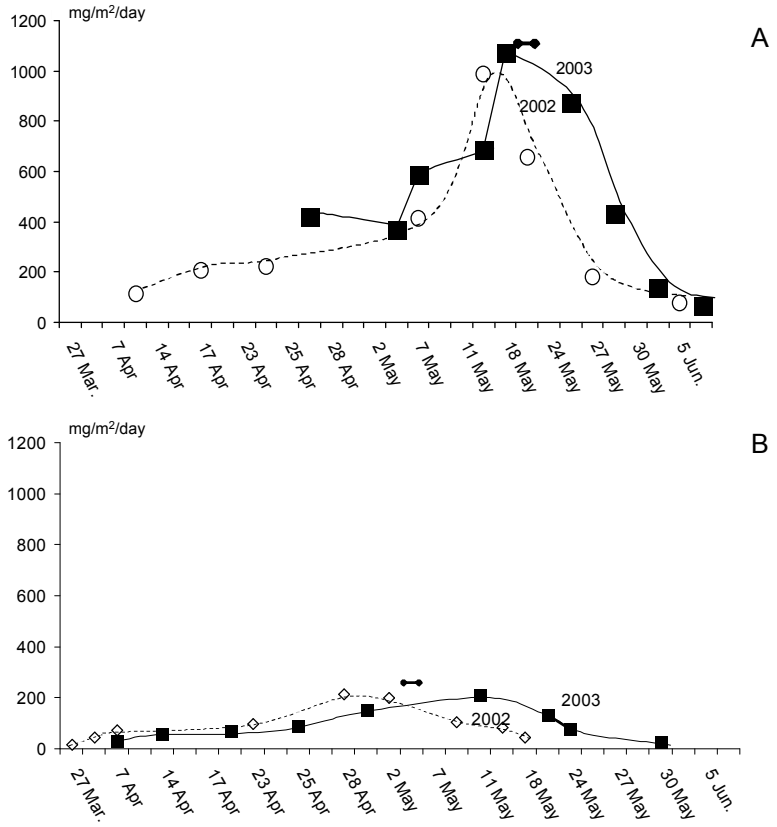


Fig. 1. Changes in caterpillar frassfall during two consecutive years (2002, 2003), in a zeen oak (A) and cork oak (B) patch (••, represent the average calculated peak demand at 10 days post hatching in each habitat, 3 May in cork oak and 20 May in zeen oak).

chicks' diet in the evergreen than in the semi-evergreen patch ($\chi^2 = 23.61$, df = 4, $p < 0.0001$).

Feeding frequencies were consistently higher in the zeen oak patch than in the cork oak patch, and this for different age classes (Table 1).

DISCUSSION

We report that Blue Tit chicks are raised when caterpillars are most plentiful, both in the Algerian semi-evergreen and evergreen oak habitat investigated. It supports conclusions from European investigations that caterpillars are key prey to raise chicks optimally (see Introduction). Surprisingly, Blue Tits in Algeria seem to be able to adapt their breeding time responses to very distinct oak habitat types. Local genetic specialization (cf. Dias 1996, Blondel et al. 2006) of Blue Tit breeding dates to the Algerian semi-evergreen oak habitat is probably unlikely, as this habitat supports very small effective populations sizes (zeen oak: 4325 ha versus cork oak: 34167 ha, Bureau National des Etudes Forestières 1984) (e.g. cf. Dias 1996, Dadci 2005). If this is true, Algerian Blue Tits occupying semi-evergreen oak habitat most probably originate from genetic lines adapted to evergreen oak (Dadci 2005). But why then do the Algerian Blue Tits selected in evergreen oak habitat also match the local peak-date in semi-evergreen oak habitat? In mainland southern France, for instance, Blue Tits closely match the early peak-date of caterpillar availability in habitat dominated by summergreen oak, but also settle for breeding in nearby patches dominated by evergreen oak where caterpillar abundances

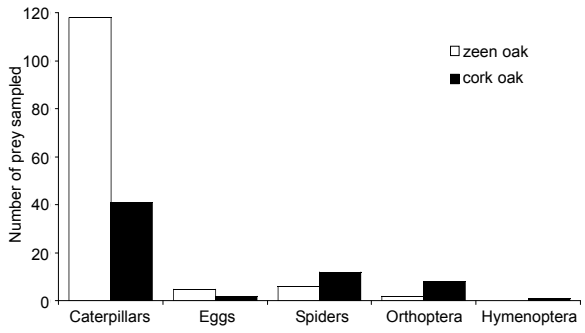


Fig. 2. Nestling diet in Algerian Blue Tits, in zeen oak and cork oak habitat.

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usually peak about 5 weeks later (Zandt et al. 1990, Dias & Blondel 1996). Gene flow from summergreen towards evergreen oak patches are causing so-called "maladaptive" breeding dates where Blue Tit chicks are raised well before the peak-date in caterpillar availability in evergreen habitat (Dias & Blondel 1996). Thus, in these heterogeneous landscapes, where the different oak habitats are situated at similar altitude and exposed to similar ambient temperatures, the reproductive system of Blue Tits (e.g. see Caro et al. 2006) does not seem to be sufficiently plastic to allow adaptive breeding time responses to very contrasting oak habitat types, most probably caused by maladapted photoperiodic responses in evergreen habitat (Lambrechts et al. 1997b, Lambrechts & Perret 2000). However, the oak-caterpillar-tit ecosystem is known to be temperature-sensitive (e.g. Buse et al. 1999, Visser et al. 2004), which can cause retarded development in phenology of up to 3–4 weeks in very cold compared to hot spring conditions. The semi-evergreen Algerian zeen oak habitat is situated at high altitude and thus exposed to cold climate, presumably causing the significant delay in the developmental onset and/or speed of this "oak-caterpillar-tit" ecosystem. This delay is such that the between-oak habitat type differences in optimal breeding dates are reduced by about 2 weeks only, and later in the semi-evergreen than in evergreen habitat. This may allow well-timed reproduction in both habitats through phenotypic plasticity alone. It would also imply that spatial variation in micro-climatic conditions may have an important impact on the abilities to adjust the reproductive system to distinct habitat types.

Our results also support previous findings in European tits that evergreen oak patches contain less and more diversified food than other oak species (e.g. Blondel et al. 1991, Bańbura et al. 1994, Lambrechts et al. 1997a). Frass fall values obtained for the Algerian zeen oak patch matches those observed in summergreen oak patches on Corsica and in some study sites in the Netherlands, and considerably exceeds values reported in mainland southern France and Switzerland (Dias & Blondel 1996, Tremblay et al. 2003). In addition, the proportion of caterpillars in the chick diet, the parental provisioning rates, and the average chick body mass, were significantly higher in the Algerian semi-evergreen than in the evergreen oak patch. The spatial variations in frass fall values measured therefore also reflect spatial habitat-specific differences in the quantities of caterpillar available to the tits (but see Tremblay et al. 2005).

If clutch size, and thus brood size, would be nicely adapted to the local food conditions, we initially predicted a large clutch and brood size in the Algerian semi-evergreen patch, with comparable values to those reported in continental Europe (10–11 eggs/clutch on average, e.g. Blondel et al. 1993). We thus assume that tits should be able to adjust clutch size to caterpillar availability (e.g. Perrins 1990, 1991), also allowing parents raising larger broods more efficiently in rich habitat. Surprisingly, average clutch sizes were small in both Algerian oak habitat patches monitored, reflecting values observed in Corsican evergreen habitat, and in North African study sites in general (e.g. Chabi & Isenmann 1997). "Nonadaptive" clutch sizes, not matched to the amount of food available to the chicks, have also been suggested to occur in a Corsican summergreen oak habitat (Lambrechts et al. 1997a) and European mainland populations (e.g. Perrins 1989, Dhondt et al. 1990, Postma & van Noordwijk 2005a). The existence of these maladapted clutch sizes assumes a strong genetic basis for clutch size, as reported in Great Tits *Parus major* (e.g. Postma & van Noordwijk 2005b), and gene flow from tits specialised to breed in poor evergreen oak habitat towards rich semi-evergreen oak habitat in Algeria (see above).

More surprisingly, brood sizes and number of young fledged were very low in both habitat types, despite the anti-parasite treatments, and smaller than in most, if not all European oak study sites (e.g. Fargallo & Johnstone 1997, Massa et al. 2004, Arriero et al. 2006, Blondel et al. 2006). This suggests that factors other than food or nest parasites cause the low breeding success in the rich, ectoparasite-free, nest environment in the Algerian semi-evergreen oak habitat. One of these key factors could be the elevated level of nest predation observed in both study sites, especially the semi-evergreen site. Tits are known to adjust life-history decisions to nest predator pressures (e.g. Julliard et al. 1997). Also, tits are sensitive to changes in the chemical nest environment (e.g. Petit et al. 2002), and thus may perceive subtle chemical changes caused by heat-treatment of nests. Interestingly, parents in Algerian Blue Tits are known to be reluctant to visit the nest boxes in the presence of human observers, which could explain why the observed feeding frequencies to chicks reported in this study are much lower than those reported in other Blue Tit studies (e.g. Hurtrez-Boussès et al. 1998). We therefore cannot

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exclude that the presence of nest predators in combination with the intensive monitoring of the nests may have altered parental behaviour with potential negative effects on nestling survival.

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STRESZCZENIE

[Biologia lęgowa modraszki w zależności od zasobności środowiska w dąbrowach północno-wschodniej Algierii]

Badania prowadzono w latach 2002–2003 w wysokogórskich, częściowo wiecznie-zielonych dąbrowach tworzonych przez *Quercus faginea* oraz nizinnych wiecznie-zielonych drzewostanach dębu korkowego w północnej Afryce. W obu środowiskach rozwieszono po 30 skrzynek lęgowych. Opisywano biologię lęgów oraz określano obfitość gąsienic i jej dynamikę w obu środowiskach. Aby zniwelować ewentualny wpływ ektopasożytów na wyniki lęgów eliminowano je poprzez poddawanie gniazd działaniom wysokich temperatur. Stwierdzono, że szczytowe zapotrzebowanie na pokarm przypadało na szczyt liczebności gąsienic w obu środowiskach, a dostępność pokarmu była większa w częściowo wiecznie-zielonych drzewostanach *Quercus faginea* (Fig. 1). Natomiast zróżnicowanie pokarmu przynoszonego pisklętom było większe w wiecznie-zielonych dąbrowach dębu korkowego (Fig. 2). Z różnicami w dostępności pokarmu wiązały się także różnice w terminach przystępowania do lęgu, masie piskląt i częstotliwości karmień (Tab. 1). Liczba wyprowadzanych piskląt była niska w obu środowiskach. W związku z tym wydaje się, że na wyniki lęgów w tych środowiskach wpływają inne czynniki niż pokarm i ektopasożyty. Autorzy sugerują, że jednym z nich może być wysokie drapieżnictwo. Także intensywne badania połączone z manipulacjami gniazdami i częstymi obserwacjami mogły wpływać na uzyskane wyniki.

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