DEPARTAMENT DE VERTEBRATS TERRESTRES

FEEDING AND BREEDING ECOLOGY OF THREE INSECTIVOROUS BIRDS IN MEDITERRANEAN ECOSYSTEMS.

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Feeding and breeding ecology of three insectivorous birds in Mediterranean ecosystems

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Feeding and breeding ecology of three insectivorous birds in Mediterranean ecosystems

REPORT PRESENTED BY

FRANCISCO ATIÉNZAR NAVARRO

TO OBTAIN THE DEGREE OF DOCTOR IN BIOLOGY

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“*Sólo aquellos que se arriesgan a ir muy lejos,*

pueden llegar a saber lo lejos que pueden ir”

(T.S. Elliot)

Tesi presentada per FRANCISCO ATIÉNZAR NAVARRO per optar al grau de Doctor en Ciències Biològiques per la Universitat de València.

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I

GENERAL INTRODUCTION

One of the most exciting challenges of modern ecology is trying to understand the correspondence and the adaptations among different stages of the life cycle of organisms and the environment (e.g. Southwood 1977). Organisms are adapted to their environment in order to survive and reproduce successfully (Darwin 1859). Most of them cope simultaneously with numerous aspects or constraints of their environments (food phenology, physical environment, predation, intra and interspecific competition…), and have to trade-off conflicting demands (Pianka 1974). Predation is, for example, an important breeding constraint. Thus, for birds living in high predation-risk areas, having a paler colouration reduce the risk of predation, but also reduce their mating opportunities (see for instance, Lyon and Montgomerie 1985, Magnhagen 1991). Therefore, an adequate knowledge of these constraints is required for a better understanding of how animals are adapted to their environment and how coexisting species can occur. This knowledge achieves greater relevance in heavily seasonal and food-poor environments (e.g. Mediterranean evergreen forests, Blondel and Aronson 1999), where both seasonal fluctuation and scarcity of resources are considered the main factors influencing current and/or future reproductive success (Martin 1987, Barba et al. 1994, Rytkönen and Krams 2003). Moreover, the predictability of external circumstances, which limits reproduction, plays the most crucial role in heavily seasonal environments. This is related to the degree to which environmental resources or conditions can be utilized by an organism in order to maximize the number of recruits produced for the next generation (e.g. Kuitunen 1989).

In seasonal environments, with only a limited period in the year when conditions are favourable enough to successfully reproduce or grow, plants and animals exhibit seasonal patterns in their activities. Thus, negative fitness consequences are often found if reproduction or growth takes place outside the temporal window of favourable conditions (review in Visser and Both 2005). Moreover, if the phenology of a species is shifting at a different rate from that of the species that make-up its ecological conditions (e.g. prey, hosts, etc.), this will lead to mistiming of its seasonal activities (see Visser et al. 2006). In birds, where reproduction involves a high energy cost (review in Martin 1987), timing reproduction with prey phenology is crucial. For example, in insectivorous birds, such as Golden Plovers *Pluvialis apricaria*, reproductive success depends on the synchrony of hatching of their chicks with the period when adult tipulids, their main food, are more abundant. This poses a clear selection pressure on the timing of reproduction (see more examples on birds in Visser and

Both 2005). Therefore, birds should use cues to time reproduction (e.g. environmental temperature, Visser and Both 2005). However, asymmetrical dispersal movements among habitats may prevent populations from becoming adapted to heterogeneous environments. Dispersal movements occur from the most to the less common habitats causing an apparent maladaptation to local conditions. Therefore, birds living in such habitats are expected to mismatch the best period of food availability (e.g. Dias and Blondel 1996a). On the other hand, many herbivorous insect species can only develop on young plant material. For these species, the phenology of growth of leaves or growing tips can be used as a yardstick for the shifts in the phenology of their larval development. An example of this is the Winter Moth *Operophtera brumata*-oak interaction. Winter Moth eggs which hatch either before or after the oak bud burst have reduced fitness (van Asch 2007). There are also examples from aquatic systems: intertidal bivalve *Macoma balthica*, is under selection by temporal variation in its food resource, phytoplankton (see Visser and Both 2005 for a review).

Individuals are probably using environmental cues to adjust their reproductive investment in order to maximize their fitness. Nevertheless, within the same population, some individuals invest more than others. Taking into account that individuals investing more (e.g. bird females laying large clutches) tend to be more successful than those with smaller ones (e.g. Nur 1984a), why those differences in investment within population? In small passerines, two main hypotheses have been put forward trying to solve the above question: the Trade-Off (TOH) and the Individual Optimization (IOH) hypotheses. The TOH postulates that laying more eggs has reproductive costs (e.g. a decrease in future reproduction) and benefits (e.g. more fledglings are recruited in the following season, Werf 1992, Pettifor et al. 2001). Therefore, individuals would be laying a clutch size where benefits are higher than costs in the long term. Reproductive costs have been examined in a variety of animals and plant species, using observational and experimental methods (see for a review Harper and White 1974, Zera and Harshman 2001, Obeso 2002). On the other hand, the IOH postulates that individuals would be laying the number of eggs corresponding to the maximum number of chicks that they can feed successfully. Therefore, laying more or less eggs would be disadvantageous. The argument is that there are energetic and time constraints acting on the parents, so they could not invest more than they do. Some studies have supported the TOH (Nur 1984a, Both 1998, see more references in Chapter VI). The IOH has received less support to date (Both 1998, Pettifor et al. 2001, but see also Lindén 1990). Since investment strategies could depend on the costs and benefits actually experienced by birds, it would be expected that populations living under different environmental constraints show different strategies. Therefore, to understand the plasticity of the life-history strategy of a species, such hypotheses should be tested in all possible environments where species is able to reproduce successfully.

Animal behaviour can be studied from different angles, trying to answer how behaviour is caused, and by which mechanisms (Tinbergen 1963). Foraging behaviour in animals is one of the main themes in behavioural ecology, and animals can often respond in a number of ways to the situation in which they find themselves. Such behaviour is affected by some constraints (e.g. day length, Kuitunen 1989) being that translated into reproductive success. In altricial birds, where offspring are dependent on both parents, reproductive success can be constrained by the rate at which food is delivered to the nest, as well as by the quality and the amount of food.

Different kind of animals living together in one place could interact and potentially compete for limiting resources such as food, space, etc. (Krebs 2001). Such competition is stronger in sibling species living in sympatry and making use of similar resources (Pianka 1974). There are two different modes of competition among animals: exploitation and interference. The first occurs when a number of organisms (of the same or different species) utilize common resources that are in short supply (e.g. lions and cheetahs competing for gazelles on the African plains). The second occurs directly between individuals via aggression, when individuals interfere with foraging, survival, reproduction of others, or by directly preventing their physical establishment in a portion of the habitat, even if the resource is not in short supply (Krebs 2001). For instance, territorial Red Grouses *Lagopus lagopus scoticus* defend the richest areas of the heather moors as breeding and feeding territories, while excluded birds have to go to exploit poor habitats where chances of survival are lower (Krebs and Davies 1993). Competition is, therefore, considered a reproductive constraint due to their fitness consequences on the worst competitor (e.g. Török 1987). The question raised now is how organisms living together in the same habitat have evolved within the context of competition. Differential use of food and/or habitat could allow the coexistence of putative competitors in the same environment. For instance, two similar bird species may coexist in the same forest by specializing in prey types (or size), or in where or how they feed (Pianka 1974). Hence, for a better understanding of animal coexistence, it is interesting to have an adequate knowledge of the constraints affecting it.

Food availability and predation are two reproductive constraints (see more below) related to the habitat in which a species lives (Sargent and Gebler 1980, Dobkin 1985, Kuitunen 1989, Stokes and Dee Boersma 1998). However, habitat-species relationships are often complex and dependent on the scale considered (e.g. habitat selection, WallisDeVries et al. 1999, Quevedo et al. 2006). Habitat may be defined at various spatial scales, from geographic or macrohabitat to local scale or microhabitat. Macrohabitat scale in birds is examined mostly at landscape level (Otter et al. 2007). This comprises some characteristics that may affect breeding success such as patch area and isolation, types of land uses within landscapes, or even the dominant vegetation type (e.g. deciduous vs. evergreen). Instead, microhabitat scale comprises structural complexity of surrounding nest features (e.g. stem density). Such features may affect breeding success. For instance, dense vegetation influences the ability and visibility of predators to find nests, increasing reproductive success (see for instance, Martin 1993, Tarvin and Garvin 2002). Therefore, analyses at several levels are important to understand the processes underlying how birds respond in a structured landscape, especially when floristic composition is not homogeneous, as well as to understand the constraints affecting reproduction.

In many systems, predation is one of the major selective forces in habitat selection and animal colouration because of its effects over reproductive success (Magnhagen 1991, Martin 1993, Godin and McDonough 2003). In birds, natural selection should favour birds that choose places with low incidence of nest predation or organisms with concealing colouration to mislead predators (e.g. Götmark 1997). For instance, birds breeding in dense foliage and increased structural heterogeneity showed lower predation rates (see for instance, Martin 1993). In some fishes (e.g. Trinidadian Guppies *Poecilia reticulata*), males become less colourful when predation risk was high. According with sexual selection, such males showed lower chances of mating (Magnhagen 1991). However, having conspicuous colouration implies also reproductive benefits by enhancing either male-male competition or female choice (Andersson 1994, Hill and McGraw 2006a). Male colouration signals some male traits, such as high contribution to the feeding of nestlings (Senar et al. 2002). Therefore, sexual selection should favour the development and maintenance of conspicuous colours that facilitates mating opportunities (Andersson 1994). Hence, predation is, through colouration, another important reproductive constraint to have into account in studies of breeding ecology.

Tits (Family Paridae) as model-systems

Species of the family *Paridae* are among the best known songbirds (e.g. Perrins 1979, Cramp and Perrins 1993). Since 1997 to date more than 1200 studies have been published directly or indirectly implying Great Tits *Parus major* (ISI Web of Knowledge) covering several research topics from genes to habitat selection. So, why did we plan to do a thesis about tit species when such a bulk of information is already available? Despite people have been talking about birds for as long as historical records exist, we still do not really understand life-history strategies of birds living under most ecological conditions. For instance, breeding strategies and life-history traits of Great Tits have been well studied in central and northern Europe (Perrins 1979, Gosler 1993), but they are poorly studied southern in their distribution range (Cramp and Perrins 1993). Indeed, it is important to study the individual and population characteristics and adaptations of a species throughout its distribution in all habitats able to be occupied by the species (Zink 1989). This reaches relevance if we take into account that relationships found at local scales may not be true when the whole distribution area is covered. For instance, Belda and Orell (2003) found that adult Great Tit survival was relatively high in the

Mediterranean area, and this characteristic could easily affect other life-history traits.

One of the most characteristic features of the tit family is its nesting habit. All the species build their nests in holes, often using existing holes in old trees or stumps, though some, as Crested and Willow Tits *Poecile montana*, usually excavate their own holes in rotten stumps (Perrins 1979, Denny and Summers 1996). Most tit species readily accept artificial nests (nest boxes) for breeding. Moreover, the use of nest boxes makes easier nest inspection as well as taking measurements of chicks. They lend themselves well to field experiments, particularly because of use of nest boxes, but also because they are easy to capture and mark. Tit species are broadly distributed, breeding in different habitats from gardens to forests (Cramp and Perrins 1993). Therefore, they experience different environmental conditions (food, climate, vegetation type, predation risk…), which makes them ideal for comparative studies on a large geographical scale (e.g. Visser et al. 2003, van den Steen et al. 2009).

Outline of the thesis

The general objective pursued in the present thesis was to achieve a better understanding of how birds are adapted to their environment. In particular, to examine the existence and the consequences of food limitation in Mediterranean evergreen habitats, through an adequate knowledge of the constraints affecting both feeding behaviour and breeding success. With it, most aspects related to the life span of an individual could be interpreted more properly.

Using tits from three eastern Spanish populations breeding in nest boxes as model species, the specific aims pursued in this thesis were as follows:

Chapter III. Developing a device to facilitate the filming of adult feeding behaviour from outside the nest box. This was required to get some of the objectives proposed in further chapters.

Chapter IV. Looking for the environmental cues that trigger reproduction in Great Tits, and how birds use such cues in order to syncronize food phenology and reproduction: fitness consequences of mistiming.

Chapter V. Describing the patterns of feeding behaviour in Great Tits and their consequences on both adults and nestlings.

Chapter VI. Testing, through experimental brood size manipulations, whether birds are optimizing clutch size.

Chapter VII. Investigating how landscape composition and vegetation structure affect nesting success: a multiscale approach.

Chapter VIII. Assessing mate choice in Great Tits under a scenario of high level of nest predation: the role of habitat quality in female choice.

Chapter IX. Describing nesting habitat characteristics in Crested Tits *Lophophanes cristatus* in untypical and typical forests for the species, also investigating how Crested Tits have adapted their reproduction to new environmental conditions, and how this might affect their life-history traits and nestling diet.

Chapter X. Analyzing some mechanisms of coexistence between putative competitors: Great, Crested and Coal Tits *Periparus ater*: food size, nesting habitat requirements and the timing of reproduction.

II

GENERAL METHODS

The present thesis is focused on well-studied species. This allows comparing results with information gathered in other regions with similar or different environmental characteristics, and exploring the evolutionary and ecological consequences in life-history strategies.

The Great Tit *Parus major* (Linnaeus, 1758) is the largest among tit species (Cramp and Perrins 1993). It is one of the most abundant small songbirds in Europe (Hagemeijer and Blair 1997), and is also present in Asia and North Africa. It inhabits several habitat types from urban gardens to forests. It commonly feeds on caterpillars during the breeding season (Cramp and Perrins 1993), although adult moths are their main prey in orange groves (Barba et al. 1994). Outside the breeding season it also feeds on fruits and seeds. Both sexes are similar in plumage, but males are usually markedly brighter than females, with richer yellow underparts and glossier black crown and throat. In addition, the black stripe down the underparts is wider and more intense in males than in females, not reaching the legs in the case of females (Perrins 1979, Cramp and Perrins 1993).

The Crested Tit *Lophophanes cristatus* (Linnaeus, 1758) is, among the tit species included in the present study, the less abundant in Europe (Martí and Del Moral 2003). Its distribution spans through Europe and Asia (Cramp and Perrins 1993). It preferably appears in coniferous forests, being scarcer in mixed and deciduous forests (Díaz et al. 1998, Tellería et al. 1999). Unlike other tits, a gap of knowledge still exists on what it feeds during the breeding season. Spiders and pine seeds compose its diet outside the breeding season. It is not sexually dimorphic in plumage colour.

Coal Tits *Periparus ater* (Linnaeus, 1758) have also Palaearctic and Oriental distribution. Among tits, this species is the smallest (Cramp and Perrins 1993). Habitat requirements are similar to those of Crested Tits, i.e. they occur mostly in coniferous forests. During the breeding season, adults prey on caterpillars, but other prey types, as spiders and Hemiptera, are also important (Cramp and Perrins 1993). All three species are sedentary, performing short movements mainly during the winter (Tellería et al. 1999).

Location and features of study areas

Three study areas, located in the Mediterranean basin in eastern Spain, were selected for the present study (Fig. II.1). Sierra Mariola and Font Roja natural parks were chosen because they were close to each other (c.a. 8 Km), but climatic conditions, orography and vegetation differed greatly (Chapter VII). This was relevant to test some aims proposed in

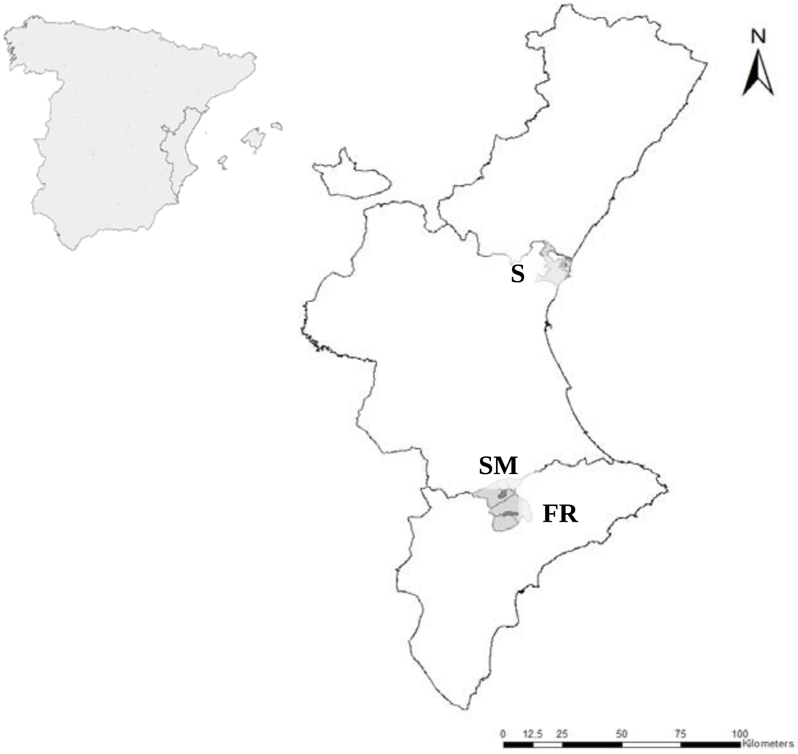


Figure II.1. Location of the three study areas, Sagunto (top, S) and the natural parks, Sierra Mariola (SM) and Font Roja (bottom, FR). Light grey color shows the boundary of both natural parks, and of the municipality of Sagunto. Dark grey colour indicates the area where nest boxes were placed.

Figura II.1. *Localització de les tres àrees d'estudi, Sagunt (dalt, S) i els parcs naturals, Serra Mariola (SM) i Font Roja (abaix, FR). Amb color gris clar es mostra els límits dels parcs naturals, i del municipi de Sagunt. El gris obscur és l'àrea ocupada per les caixes niu.*

the present thesis. The third study area, Sagunto, was chosen because a large data set on the feeding behaviour of Great Tits, including observational and experimental data, was already available (Chapters V and VI).

Sagunto is located at the northeast of the Province of Valencia (39º 42' N, 0º 15' W, 30 m a.s.l.). The study was performed in an area of c.a. 150 ha located within large orange plantations (Fig. II.2). The Great Tit was the only tit species breeding in this habitat. Climate is characterized by mild winters (mean temperature over 0 ºC during the coldest moths: January

Figure II.2. View of a nest box placed in an orange tree (top). Landscape view of the study area in an orange grove (bottom, Author: Jenifer Andreu).

Figura II.2. *Caixa niu penjada en un taronger (dalt). Visió paisatgística de l'àrea d'estudi als tarongerals (sota, Autora: Jenifer Andreu).*

and February) and warm summers, with maximum temperatures over 30 ºC (www.mapya.es/siar/Informacion.asp). Mean annual rainfall is about 420 mm, being more abundant during May and September. The dominant type of vegetation is the orange tree *Citrus* sp. with isolated fruit trees of other species and vegetable gardens. Vegetation under the canopy is composed mainly by Soursop *Oxalis pes-caprae*. In abandoned groves, the dominant species are *Avena sp*. and Nettles *Urtica urens*.

Sierra Mariola is a forest extended across 12000 ha in the north of the Province of Alicante (Fig. II.3). The peak of the mountain is at 1390 m a.s.l. Nest boxes were located by 800 m a.s.l. It was close to Font Roja, and both places constituted a Special Zone for Bird Protection across 22531 ha. Great, Crested and Coal Tits inhabited both forests. Climate is mainly Mediterranean, although slightly continental owing to its altitude. Moreover, there is a great variety of microclimates depending on the altitude and orientation. During winter, average temperature reaches 6 ºC. It snows almost every year. In summer, average temperature increases till 26 ºC. Mean annual rainfall ranges from 350 to 900 mm. The dominant type of vegetation is the Aleppo Pine *Pinus halepensis*. Other tree species such as Holm Oaks *Quercus ilex* and deciduous Portuguese Oaks *Quercus faginea* ssp. *valentina*, Italian Maples *Acer opalus* ssp. *granatense* and Flowering Ashes *Fraxinus ornus* are present but relatively scarce. As much as 1200 plant species have been identified, many of them endemic (http://www.cma.gva.es/).

Font Roja is also a forest extended across 2298 ha (Fig. II.4). The peak of the mountain is at 1356 m a.s.l., and nest boxes are located at around 1000 m a.s.l. This area is located at the north of the Province of Alicante. It also shows Mediterranean climate with continental influences. Average temperature during winter is 4 ºC, with punctual lower temperatures (-8 ºC), whilst in summer temperature increases till 24 ºC. Mean annual rainfall is about 700 mm (Boronat el al. 1989). Font Roja is one of the scarce places where natural vegetation has been conserved in the Community of Valencia (Boronat et al. 1989). Holm Oaks are the most abundant tree species, mainly in the north side of the mountain. Aleppo Pine trees are also common but at lower altitude, replacing the ancient Holm Oaks disappeared after intense clearings. Deciduous trees, as Portuguese Oaks, Flowering Ashes, Italian Maples, Whitebeams *Sorbus aria* and Yews *Taxus baccata*, are mixed with evergreen vegetation. The tree undergrowth is plentiful, with many different species such as Ivy *Hedera helix*, Honeysuckle *Lonicera implexa* and *L. etrusca*, Wild Madder *Rubia peregrina*, Laurustinus *Viburnum tinus* or the Hawthorn *Crataegus monogyna* (see more in www.cma.gva.es/).

Figure II.3. Landscape view of the Sierra Mariola natural park (top). View of the study area within the natural park (bottom).

Figura II.3. *Visió paisatgística del parc natural de la Serra de Mariola (dalt). Vista de l'àrea d'estudi dins del parc natural (sota).*

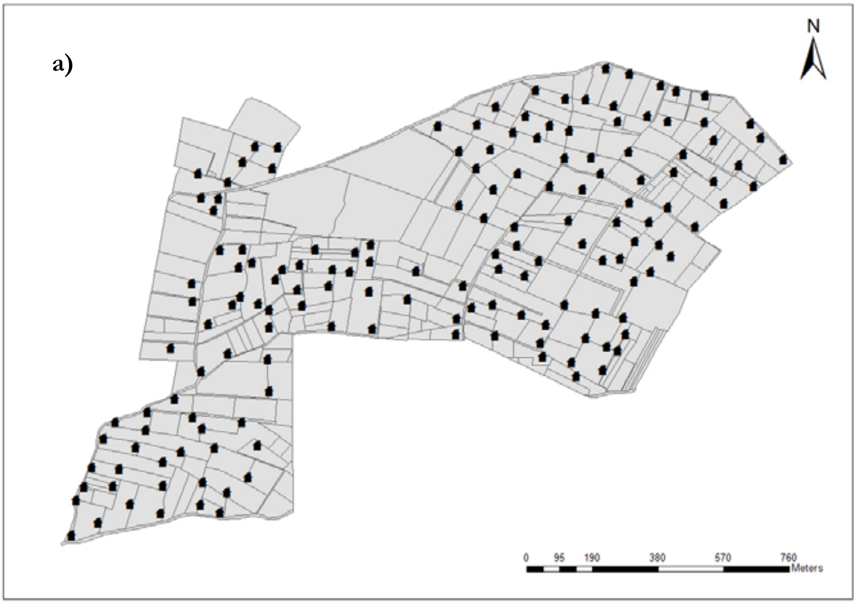
Figure II.4. Landscape view of the Font Roja natural park (top, Author: Pep Cantó). View of the study area within the natural park (bottom).

Figura II.4. *Visió paisatgística del parc natural de la Font Roja (dalt, Autor: Pep Cantó). Vista de l'àrea d'estudi dins del parc natural (sota).*

Breeding data collection

The nest box Great Tit population of Sagunto is being monitored since 1985. In this population, several aspects, as nest quality, egg size variation, laying date and clutch size, nestling diet and prey preparation, postfledging survival and adult breeding dispersal, have been studied previously (http://www.uv.es/~barba/Publications.htm). The study of the tit population breeding in Sierra Mariola was started in 2002, and that of Font Roja in 1995. Both areas were established with the aim of performing long-term studies, especially those related to survival, though little information has been published to date (López and Cantó 2003).

Nest boxes available varied from 156 in Sagunto, to 140 in Font Roja or 121 in Sierra Mariola. In Sagunto, nest boxes were placed every year in the same places by the end of February, and removed after the breeding season (Monrós et al. 2002). Nest boxes occupied a surface of c.a. 150 ha in the orange grove, 442 ha in the pine forest and of 355 ha in the Holm Oak forest (Fig. II.5). Nest boxes were similar in size. They were hung at a similar height (around 2 m) near pathways about 75-100 m away from each other in both forests. In Sagunto, we had to remove them after each breeding season mainly to avoid overwinter occupation by small mammals as Black Rats *Rattus rattus* or Garden Dormice *Eliomys quercinus* (Barba and Gil-Delgado 1990a, Gil-Delgado et al. 2006). Those from the other two places remained in the field throughout the year. Nest box inspections started in March, initially once per week.



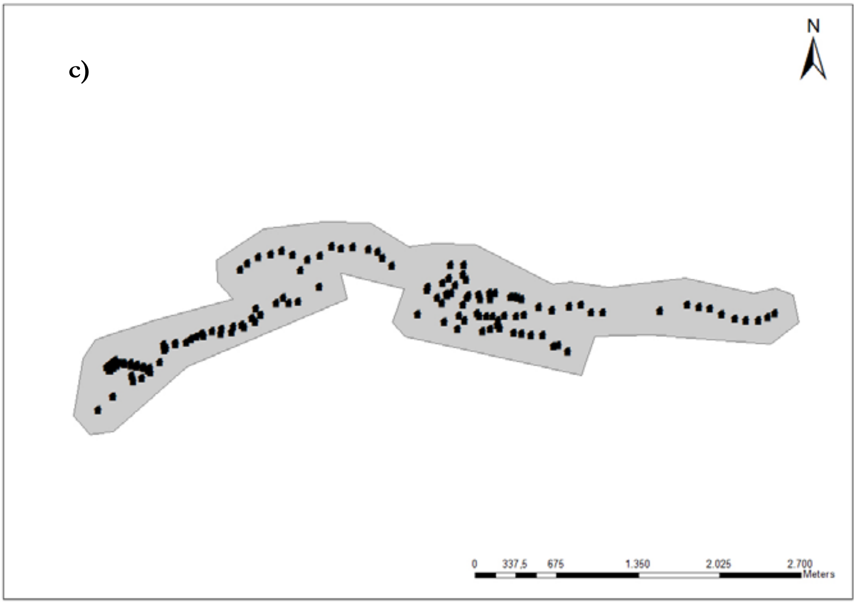


Figure II.5. Maps of nest box distribution for the three ecosystems: orange grove (a), pine forest (b), and Holm Oak forest (c).

Figura II.5. *Mapes de distribució de les caixes niu als tres ecosistemes: tarongeral (a), bosc de pi, i bosc de Carrasca (c).*

Once eggs were detected in a nest, the pattern of visits was arranged to allow us to assess the parameters of interest for each nest. These varied depending on the species, population, and year of study, and will be described in detail in each chapter.

Adults were trapped and individually ringed during the second half of the nesting period. Biometric and colour measures were taken depending on the species and population. We used several techniques for trapping adults, such as mist nets, door-traps or by fitting a blackcard in the inside part of the nest box door. Chicks were ringed and measured prior to fledging. Specific protocols for each species and population are explained in detail in each chapter.

Food abundance and phenology

Food availability and phenology was studied in the two forests by monitoring caterpillar frass-fall weight through time. The abundance of caterpillars was estimated by collecting their droppings once a week during the breeding season using frass-collectors randomly erected under the canopy of Holm Oaks and pine trees. A piece of filter paper was attached to the lower narrow end of the funnel, into which frass droppings rolled (Fischbacher et al. 1998, see more in Chapter IV).

Vegetation description: structure and composition

In the two forests, structural features (cover) and vegetation composition of the breeding territories were quantified performing line intercept transects in a sampling plot centred on the nest box with a radius of 50 m. Other structural traits, as number of trunks 5-10 cm and > 30 cm were estimated by eye, and average diameter of the five thickest trunks by using a metric tape within this plot (see more in Chapter VII).

III

A WIRE CAGE FOR FILMING PARENTAL BEHAVIOUR OF HOLE-NESTING PASSERINES

SUMMARY

Several techniques have been used to record details of feeding ecology in altricial birds. However, they often fail to provide the number, identity and size of prey, and/or the relative contribution of males and females. We designed and tested a handmade wire cage for filming nests in nest boxes (or natural holes) that allowed us to accurately (1) determine the sex and relative contribution of each parent and (2) identify each prey item and its size in a Great Tit *Parus major* population. The sex of adults was recorded successfully for all entries into the nest. The rate at which parents brought food and prey sizes were within the range obtained with other techniques in the same area. None of the nests were deserted and no detrimental effects on chick weight were found. A number of advantages compared to a previous design are discussed.

RESUM

Hi ha diferents tècniques per enregistrar l'ecologia tròfica en aus nidícoles, però sovint fracassen a l'hora d'identificar les preses i mesurar la seva mida amb precisió. En aquest estudi es mostra el disseny i aplicació d'una estructura metàl·lica per a la filmació de nius de la Mallerenga Carbonera Parus major *que permet identificar el sexe dels individus adults, la seva contribució relativa a l'alimentació dels polls, i la identificació del tipus i mida de les preses. El sexe fou identificat en tots els casos. La taxa a la que els adults duien aliment així com la seva grandària van estar dins de l'interval obtingut mitjançant d'altres tècniques a la mateixa població. No hi va haver abandonament de nius en cap ocasió on es va provar l'estructura metàl·lica, ni tampoc efectes sobre el pes dels polls, fet que suggereix que les mallerengues s'acostumen perfectament a l'estructura dissenyada. Es discuteixen els avantatges sobre d'altres dissenys previs*

INTRODUCTION

A number of different methods including direct behavioural observations (Karlsson 1994), automatic recorders (Kluijver 1950), video recording (Blondel et al. 1991), radiotelemetry (Licht et al. 1989) and passive integrated transponders (González-Solís et al. 2000) have been used in the past to assess parental feeding behaviour in birds. To register simultaneously the number and type of prey delivered to nestlings, however, requires direct observation or video recording (Barba and Monrós 1999). In species that readily occupy nest boxes filming can be done either from inside or outside the box: inside filming implies modifying the nest box to accommodate a video camera and to ensure adequate light conditions, which limits the number of nest boxes that can be filmed (Blondel et al. 1991). On the other hand, filming from outside does not require significant modifications to the nest box itself and many different nests can be recorded at once (see Currie et al. 1996). However, filming from outside may not always be suitable (e.g. in studies of nest predation rates) because the camera equipment may affect the behaviour of predators (Richardson et al. 2009).

A video camera placed outside a nest box does not usually allow the prey types brought to nestlings to be identified because adults tend to enter the box too fast. Currie et al. (1996) solved this problem by building a wire structure that momentarily stopped birds (Great Tits *Parus major* and Blue Tits *Cyanistes caeruleus*) before they entered the nest box, thereby allowing more time for observers to identify prey. This structure, however, had some disadvantages: (1) it only permitted filming from one direction, which may be a problem in unsuitable light conditions and (2) was inappropriate for identifying the sex of the parents since Currie et al. (1996) had to trap and mark birds prior to filming.

Our objective thus was to design a cage that would allow the prey brought to nestlings, the sex of the adults, and the rate at which parents visited the nest to be accurately identified and measured. We tested the performance of our cage by filming nesting Great Tits, a species for which previous data of nestling diet and feeding rates were available for the study area (Barba and Gil-Delgado 1990b, Barba et al. 2009).

METHODS

Our study site was an extensive orange plantation in Sagunto, eastern Spain (39º 42' N, 0º 15' W, 30 m a.s.l.). Wooden nest boxes available for Great Tits (e.g. Andreu and Barba 2006) were visited to assess laying dates (assuming that one egg was laid per day), clutch size and hatching dates (with visits every day or every other day around the expected hatching dates) as a means of determining a schedule for filming each nest. We filmed when nestlings were 10 days-old (hatching date was day 0) since nestling age may affect parental feeding behaviour (Barba et al. 2009). Nestling weights were measured at day 14 using an electronic balance (± 0.1 g).

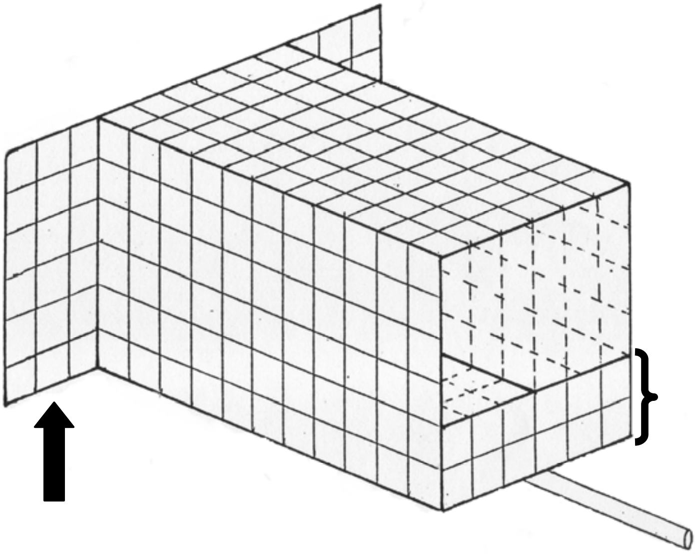


Figure III.1. Fronto-lateral view of the wire cage used for filming Great Tits. The arrow shows one of two "wings". The bracket gives an idea of the height of the fence.

Figura III.1. *Visió fronto-lateral de l'estructura metàl·lica emprada per a filmar les Mallerengues Carboneres. La fletxa mostra una de les dues "ales" de l'estructura metàl·lica. El corxet dóna una idea sobre l'altura de la tanca.*

We hand-built 7.8 x 7.8 x 14.3 cm wire cages (1 mm thick, 1.1 cm mesh) with a front entrance to which we attached a wooden perch (6-cm long, Fig. III.1). The cage had small wire 'wings' that were attached to the nest box with an elastic strap using the metal part of clothes pegs as a hook, thereby keeping the cage in place. The main difference between our cage (see Fig. III.1) and that of Currie et al. (1996) was that ours was designed to be attached to the front of the nest box so that the entrance was perpendicular to the direction of filming. Another important element was a wire 'fence' that we added to the cage entrance, which was one third of the height of the structure and kept birds on the perch (Fig. III.1), thereby allowing for more observation time for sex determination and the identification and measurement of prey items. We strapped cages onto the nest boxes 2-4 days before filming so that birds could get used to them and removed them after filming.

During 2005 and 2006 breeding seasons, we used video cameras (Sony DCR-DVD 203), which were placed on a tripod about 1 m from the nest a couple of hours prior to filming. Each nest was filmed for about 1 hour and the recordings were played and analyzed frame-by-frame on a computer. For each visit, we recorded the time when the parent entered and left the nest box, the sex of the parent, and prey type and size. The hourly provisioning rate was calculated by dividing the number of visits by the time elapsed from the first visit to the end of the filming separately for both the total number of visits and for each sex. If the time and angle of observation is adequate, the width of the black breast patch (tie) and the black neck-band, both of which are narrower in females (Cramp and Perrins 1993), can be used for sex identification. We measured the size of prey (length and width, ignoring appendages) using graph paper on a computer screen. The mean bill length of this Great Tit population (mean 11.94 mm, *SD* 0.78, $n = 17$; authors' unpublished data) used to scale prey measurements on the screen. Only the measurements for the main prey items brought to nests are reported here.

The percentage of visits of each sex to the nest and the percentage of prey items brought by each sex were analyzed with tests based on χ^2 values. The possible effects of the absence of one or both members of the pair feeding the chicks were tested using an ANCOVA, with brood size and hatching date as covariates, and year as fixed factor.

RESULTS

In ten out of the 28 nests filmed both adults entered the box during the filming period. In 14 nests only one member of the pair entered and there was no significant tendency for it to be either the male (43% of nests) or the female (57% of nests; $\chi^2_1 = 0.29$; $P > 0.05$). Neither of the adults entered in the remaining four nests. All sampled nests were successful (i.e. at least one chick fledged). On the basis of plumage dimorphism, the sexes were identified successfully in 100% of the entries for all nests in which at least one adult entered.

Since for some nests we only had data for the male or the female we checked whether prey types brought to the nest differed between sexes at the ten nests for which we had data for both parents.

The percentage of the two main prey types brought by males or females did not differ significantly ($\chi^2_1 = 0.66$; $P = 0.414$; Table III.1) and so we were able to use data from all nests in diet analyses. For those ten nests, the hourly provisioning rate was 12.70 visits $\cdot h^{-1}$ (*SD* 4.03) and when only one member of the pair entered, this rate was 7.39 visits $\cdot h^{-1}$ (*SD* 3.73). Feeding rates for each sex did not differ significantly (females 5.22 visits $\cdot h^{-1}$, *SD* 2.76; males 7.05 visits $\cdot h^{-1}$, *SD* 4.74) between nest boxes in which either one or both members of the pair entered, and the interaction was also non-significant ($P > 0.05$). The mean time elapsed between the installation of the camera and the first visit by a parent was 11.39 min (*SD* 4.74), showing that birds became quickly accustomed to its presence.

Of 158 prey items observed at the 24 nest boxes, 56.9% were moths (adult nocturnal Lepidoptera), 17.1% caterpillars, 3.8% pupae, 3.8% spiders and 15.2% other prey, including Coleoptera,

Table III.1. Percentage of prey brought by males ($n = 73$) and females ($n = 85$).

Taula III.1. *Percentatge de preses dutes pels mascles* ($n = 73$) *i per les femelles* ($n = 85$).

	Male	Female
Lepidoptera adult	67.12	48.24
Lepidoptera larvae	16.44	17.65
Pupae	4.11	3.53
Spiders	2.74	4.71
Coleoptera	0.0	1.18
Hymenoptera	1.37	16.47
Miriapoda	0.0	1.18
Orange pieces	6.85	2.35
Not identified	1.37	4.71

Hymenoptera, Miriapoda and pieces of oranges (see Table III.1). We failed to identify only 3.2% of the prey items. All identified prey items were measured and data on the main prey types are shown in Table III.2.

Table III.2. Measurements (length and width) of the main prey types delivered by parents to 10 day-old Great Tit nestlings.

Taula III.2. *Mides (longitut i amplària) de les principals preses dutes pels pares a polls de Mallerenga Carbonera de 10 dies de vida.*

	Length (mm)		Width (mm)		
	Mean	*SE*	Mean	*SE*	*n*
Lepidoptera adult	22.44	0.68	4.27	0.37	89
Lepidoptera larvae	19.12	1.58	4.11	0.47	27
Pupae	14.56	3.43	5.24	1.46	6
Spiders	10.87	4.44	2.37	0.93	6

There were no differences in the nestling weight in the nests in which both parents entered (16.54 ± 1.59 g) and those in which only one or none (15.50 ± 1.21 g) entered during the filming period (ANCOVA: $F_{1,21} = 0.20$, $P = 0.659$, brood size (covariate): $F_{1,21} = 0.02$, $P = 0.969$, hatching date (covariate): $F_{1,21} = 0.06$, $P = 0.816$, year: $F_{1,21} = 0.31$, $P = 0.583$). Additionally, mean nestling weight was similar in filmed (15.81 ± 1.30 g) to that of unfilmed nest boxes (15.89 ± 1.42 g, ANCOVA: $F_{1,35} = 0.02$, $P = 0.901$, brood size (covariate): $F_{1,35} = 0.03$, $P = 0.856$, hatching date (covariate): $F_{1,35} = 0.10$, $P = 0.749$, year: $F_{1,35} = 0.09$, $P = 0.762$).

DISCUSSION

Because the study site was open to the public, we could not leave the video camera (or even a tripod with a dummy camera) unattended for any length of time before filming as a means of allowing birds to get used to its presence; this may have caused some birds to refuse to enter the nest box during the filming period. We based this conclusion on two facts. Firstly, wire cages were placed on nest boxes a couple of days before filming and so if one or both parents had avoided entering the nest during this period we would expect to have detected detrimental effects on the nestling weight. However, no statistical significant differences were observed on nestling weight between nests and no nest box was deserted. Secondly, as part of another study, we attempted to trap both parents at the nest box a few days after filming and in 98% (*n* = 56 individuals) of the cases both the male and the female were trapped, thus indicating that neither had abandoned the brood as a consequence of the wire structure. As well, the hourly provisioning rate obtained with the video cameras at the nests in which both parents were feeding was within the range of that registered in another study of the same population where we used mechanical counters (12-16 visits per hour; Barba et al. 2009). Thus, the rate of visits to the boxes was seemingly unaffected by the wire structure.

The sex of the bird entering the nest box could be determined in all cases on the basis of plumage dimorphism. This is very advantageous and meant that trapping and marking birds prior to filming, as reported by Currie et al. (1996), was not necessary. In those nests in which both parents entered, their contribution in terms of feeding visits and prey types was similar and in accordance with that expected in monogamous birds (Perrins 1979).

Nestling diet and prey size obtained with the video cameras agreed with those previously reported for this population using neck collars (see e.g. Barba and Gil-Delgado 1990b, Iglesias et al. 1993). Barba and Gil-Delgado (1990b) studied the whole breeding season and included prey brought to nestlings of different ages (2-13 days-old) in contrast with our study, in which all nestlings sampled were 10 days-old and only from first clutches. Nevertheless, both studies agree that moths were the most abundant prey (50% in Barba and Gil-Delgado 1990b, 57% here), followed by caterpillars (24% vs. 17%). We also identified here other prey items such as pupae, spiders and even pieces of orange that also appear in the study by Barba and Gil-Delgado (1990b), even though our sample size was much lower (158 vs. 566 prey items) and more restricted in terms of time and range of nestling ages. We therefore conclude that the results obtained with the video cameras provide a good overview of nestling diet in these Great Tits since most items were successfully identified.

Previous data on prey size in this population consisted only of caterpillar length (mean 18.5 mm, *SD* 4.10 mm, $n = 118$; Iglesias et al. 1993). The mean caterpillar length found here (Table III.2) did not differ from that previously found (t_{145} = 0.57, $P > 0.05$). Measurements of the rest of the prey items were within the range reported for other habitats (Cramp and Perrins 1993; see also Monrós et al. 1997). We therefore conclude that this method allows accurate prey measurements to be made.

Further advantages of the wire cage used here include the fact that (a) it is easy to move from one nest box to another, thereby allowing a number of nest boxes to be sampled without any prior preparation or modification, that (b) filming could be done from both sides of the box, and that (c) because of the elastic strap the cage may be easily adapted for use on natural tree cavities. That filming could be done from both sides of the box is important for obtaining good quality film, since we were able to choose the direction of filming when we placed the camera once birds had got used to the wire structure. This allowed us to make a better use of the light conditions at the time of filming. The wire cage design used by Currie et al. (1996) established the direction of filming once the cage was placed on the nest box at least one day before filming and there were problems with prey identification when birds entered opposite the camera. Other factors may make our device even more attractive for future studies. Firstly, the material used is cheap and it does not require much time to make the cages and as many as necessary can be built without problems of cost. Secondly, the design of the cage prevents small mammals reaching either the adults or chicks from outside the nest box. Thirdly, this type of cage may be used for other hole nesters and indeed we have used it (authors' unpublished data) on the nests of Coal Tits *Periparus ater*, Crested Tits *Lophophanes cristatus* and Blue Tits breeding in Aleppo Pine *Pinus halepensis* and Holm Oak *Quercus ilex* forests and have found no effects on parental behaviour.

IV

FOOD PHENOLOGY AND BIRD REPRODUCTION IN MEDITERRANEAN FORESTS: FITNESS CONSEQUENCES

SUMMARY

Ambient temperature is one of the most important cues used for birds to trigger reproduction. Moreover, timing reproduction with food phenology has great effects on fitness. This is well reported in birds breeding in temperate deciduous forests, but poorly known in Mediterranean evergreen forests. The present study tries to fill in this gap using as bird model two Mediterranean Great Tit *Parus major* populations breeding in a Holm Oak *Quercus ilex* and in a pine forest. We first focused on examining factors affecting the timing of breeding and clutch size. Then, we described the food phenology, analyzing afterwards whether birds timed their period of maximum food demand with that of maximum food availability, looking for fitness consequences. Birds started reproduction earlier in warm years in both forests, and clutch size decreased with increasing laying date only in the pine forest. The pulse of food abundance lasted two weeks in the pine forest and only one in the Holm Oak forest. Mean frass-fall during the pulse of food abundance was six-fold higher in the Holm Oak than in the pine forest. Peaks of maximum food demand by the nestlings and of food availability matched in the pine, but not in the Holm Oak forest. Clutch size for those birds that timed in the pine forest was larger, and chicks from both forests weighed more, than those that mistimed. Some reasons for these differences in timing between forests are discussed.

RESUM

La temperatura ambiental és una de les senyals més importants emprades per les aus per a iniciar la reproducció. A més, ajustar la reproducció amb la fenologia de l'aliment té efectes importants sobre l'èxit reproductor. Açò està ben documentat en aus que es reproduixen als boscos caducifolis de les zones templades, sent poc conegut als boscos perennifolis del Mediterrani. El present estudi pretén plenar eixe buit d'informació emprant com a model dos poblacions Mediterrànies de Mallerenga Carbonera Parus major *a un bosc de Carrasca* Quercus ilex *i a un bosc de pi. Inicialment, ens vam centrar en examinar aquells factors que podrien afectar l'inici de la reproducció i el tamany de posta. Després, vam descriure la fenologia de l'aliment, analitzant posteriorment si els individus ajustaren el moment de màxima demanda d'aliment dels polls amb el de màxima disponibilitat d'aliment a l'ambient, buscant possibles efectes sobre l'èxit reproductor. Els individus dels dos boscos avançaren la reproducció en anys càlids, i el tamany de*

posta va disminuir amb la data de posta però sols al bosc de pi. El pols d'abundància d'aliment va durar dos setmanes al bosc de pi i sols una al de Carrasca. La biomasa promig d'orugues durant el pols d'abundància fou sis vegades major al bosc de Carrasca que al de pi. Els pics de demanda màxima d'aliment dels polls i el d'abundància d'aliment coincidiren al bosc de pi, però no al bosc de Carrasca. El tamany de posta per aquells individus que ajustaren fou major al bosc de pi, i els polls als dos boscos pesaren més. Mentre que aquells procedents de nius que no ajustaren amb l'aliment pesaren menys. Es discutixen algunes de les diferències en l'ajust entre boscos.

INTRODUCTION

In those environments with clear seasonality in the suitability of resources or conditions, animals exhibit seasonal patterns in their activities (e.g. Visser and Both 2005). Reproduction is the most demanding activity for an organism, and there is often only a limited period in the year when conditions are favourable enough to reproduce successfully. Individuals that time their breeding activities so that peaks of both nestling food demand and food supply are synchronized, usually show higher fitness (e.g. Perrins 1991). Thus, it is important for birds to recognise and respond to environmental cues which enable them to breed at a favourable period of the year. For example, prelaying temperatures are used by females of many passerines to trigger reproduction (e.g. Perrins and McCleery 1989, Nilsson and Källander 2006, Visser et al. 2006).

This situation is exemplified by the relation between Great Tits *Parus major* breeding in deciduous forests in northern and central Europe and their caterpillar prey (Visser et al. 2006). Tits tend to lay eggs so that the maximum nestling food demand, which occurs at 10-11 day-old nestlings (Perrins 1991), coincides with the spring peak in caterpillar abundance, which lasts about 24 days in such forests (van Balen 1973, Naef-Daenzer and Keller 1999, Visser et al. 2006). Birds breeding too early or too late relative to the caterpillar peak (i.e. mistiming) may experience lower food supply than needed, thus having their fitness reduced (Nager and van Noordwijk 1995, Naef-

Daenzer and Keller 1999). Several cues are known to be used by birds to start their breeding activities (see Nilsson and Källander 2006). Among them, laying date has been found to correlate negatively with spring temperature (van Balen 1973, Slagsvold 1976, Perrins and McCleerly 1989), so birds are probably using this cue to start laying eggs. Spring temperatures directly affect the leafing process of trees (e.g. Buse et al. 1999), and therefore the phenology of phytophagous insects, a basic food resource for insectivorous birds.

Evergreen trees renew no more than 30% of the foliage each year (Tremblay et al. 2003), so the abundance of phytophagous insects is lower than in deciduous trees (e.g. Blondel et al. 1991, 1993). Another important food constraint in evergreen forests is that the period when food is plentiful is narrower (e.g. roughly two weeks length in Holm Oak *Quercus ilex* forests, Dias and Blondel 1996b) than in deciduous ones (see above). The predictability of food conditions would be another trouble for Mediterranean breeding birds. Budburst is more noticeable in deciduous forests, because they renew the whole foliage, and this may be used as a cue by birds. Indeed, Nilssson and Källander (2006) found that laying date of Great and Blue Tits *Cyanistes caeruleus* was related to budburst in deciduous forests, while Blondel et al. (1993) did not find such relationship in evergreen oaks.

The relationship between reproduction and food in the Mediterranean region is better known for Blue Tits (e.g. Blondel et al. 1993, Dias and Blondel 1996b, Tremblay et al. 2003). It has been shown that Blue Tits breeding in deciduous forests timed reproduction to food phenology better than those breeding in Holm Oaks (Blondel et al. 1993, Iglesias 1996). Furthermore, the general pattern found for the relationship between temperature and laying date in central European populations may not be as evident in the Mediterranean area. For instance, laying date in Corsican Blue Tit populations was not affected by spring temperatures (Blondel 1985).

Though breeding areas of tit species reach as south as northern Africa (Cramp and Perrins 1993), response to food phenology in the southern European limits, and especially in evergreen forests, is poorly understood in Great Tits (e.g. Iglesias 1996). We studied Great Tit populations breeding in pine and Holm Oak forests in the Mediterranean region to (1) examine factors affecting the timing of breeding and clutch size; (2) describe the caterpillar phenology and abundance in both forests; and (3) assess the possible fitness consequences of mistiming reproduction with the time of maximum food availability.

METHODS

The study was carried out in two natural parks, 8 Km apart from each other, in eastern Spain: Sierra Mariola (38º 44' N, 0º 33' W, 900 m a.s.l.) and Font Roja (38º 39' N, 0º 32' W, 1090 m a.s.l.).

Font Roja is an evergreen Holm Oak forest, a remnant of the ancient forest which covered vast extensions in south-eastern Iberian Peninsula.

Sierra Mariola is a pine forest composed almost exclusively of Aleppo (the most abundant species), Umbrella and Maritime Pines (*P. pinea* and *P. pinaster* respectively). Isolated patches of Holm Oaks were also present. Detailed descriptions of both forests can be found in Chapters II and VII.

Breeding parameters

Data on breeding traits were gathered during 2005-2007. Nest boxes were visited once a week. Active nests were visited with a pattern which allowed us to assess important breeding traits for the present study such as laying date (assuming that one egg was laid per day; 1 = 1 April), clutch size, hatching date and fledging success (proportion of hatched eggs producing fledglings).

Adults were caught and weighed (using an electronic balance ± 0.1 g) whilst they were feeding 11-15 day-old chicks. Weight and tarsus length (using a digital calliper ± 0.01 mm) of nestlings were measured when they were 14 days-old. For the present study we only used first clutches, defined as the first breeding attempt of the year: 164 nests in the pine and 132 nests in the Holm Oak forest.

Food availability

Caterpillar phenology data were obtained by measuring caterpillar's droppings (also named frass-fall; e.g. Visser et al. 2006) from late March to early July during 2005-2007. This measure is well correlated with caterpillar density obtained from the trees (Fischbacher et al. 1998, Seki and Takano 1998). We placed five funnels (commonly named frass-collectors; 34-cm diameter) randomly erected under a developed and homogeneous canopy in each area (e.g. Dias and Blondel 1996b). They were placed 1-1.5 m away from the stem to collect droppings falling from the foliage (Zandt 1994, Fischbacher et al. 1998). A piece of filter paper was attached to the lower narrow end of the funnel, into which frass droppings rolled (Fischbacher et al. 1998). Filters were replaced weekly and then preserved in a freezer until the content was analyzed. Later, in the laboratory, samples were dried in an oven at 60 ºC during 24 h (e.g. Sanz 2001a, Visser et al. 2006). Gypsy Moth *Lymantria dispar* droppings could be identified by their very distinctive large size, egg-shape and sharply ridged surface (Dias and Blondel 1996b, Iglesias 1996, pers. obs.). Since Gypsy Moth caterpillars are not eaten by tits (Blondel et al. 1991, Iglesias 1996, pers. obs.), its droppings were removed from the samples, along with leaves and debris. Clean samples were weighed on an electronic balance to the nearest 0.1 mg. Frass-fall production was expressed as $\mathrm{mg \cdot day^{-1} \cdot m^{-2}}$. For each sampling day and forest, we calculated the average frass-fall production of the five funnels and used this value in the analyses. Some samples were lost mostly because of heavy rain. In total, 39 frass-fall samples were gathered from the pine forest and 35 from the Holm Oak forest during the 3 years.

Caterpillar peak date (CPD) was defined as the day when the average value of caterpillar frass-fall production was highest (Dias and Blondel 1996b). Because samples were collected once a week, CPD for each forest was considered as the day between two samplings. With it, we reduced the possible bias to 3 days. The date of maximum food demand by the nestlings (MFD) was calculated for each nest by adding 10 days to the hatching day. Then, for each nest we calculated the difference between MFD and CPD, and the mean of these differences was taken as a measure of synchronization for this year.

Temperature data

Maximum, minimum and average ambient temperatures were gathered from the Meteorological Station of "Bocairente" (Instituto Nacional de Meteorología) at 880 m a.s.l., close (c.a. 4 Km) to the pine forest. The meteorological station established in the Holm Oak forest by MEDSPAI started working from 29 May 2007. We correlated data from then to 30 November 2007 with those registered in "Bocairente" during the same period. Data for all temperatures were closely correlated (T_{max}: $r = 0.98$, $P < 0.001$; T_{min}: $r = 0.94$, $P < 0.001$; T_{med}: $r = 0.98$; $P < 0.001$; $n = 186$ days), being, on average, 3.5 ºC colder in the Holm Oak forest. Therefore, we used temperatures from "Bocairente" for both study areas, though being aware of the differences in absolute temperatures. Correlation between spring temperatures and laying date has been shown in a variety of ways. Here, we checked the suitability of the two most commonly used values. First, we took the average temperature of 30 days before the start of laying, since it has been shown to be the best predictor of laying date in evergreen forests in northern Europe and in montane Mediterranean deciduous forests (Slagsvold 1976, Fargallo and Johnston 1997). In such analyses, we used maximum, minimum and average temperatures. Relationships found were always stronger with minimum temperatures, so we only present these results. Secondly, we took the sum of maximum temperatures ("warmth sum") for three periods: 1 January-25 February, 1 February-25 March, and 1 March-25 April (Perrins and McCleery 1989). Linear Mixed Models were run to assess the relationship between mean laying date and ambient temperature (covariate) using forest type as fixed factor, and the relationship between laying date and clutch size for each forest type using year as fixed factor.

Fitness consequences of mistiming over fledgling weight and tarsus length, adult weight and fledging success were analyzed using GLM. For each year, we divided the nests into two groups: those where the MFD was within the period of maximum caterpillar abundance (one or two weeks depending on the year and forest; "synchronized nests") and those where the MFD was outside this maximum ("unsynchronized nests"). Year and timing were considered as fixed factors, and brood size as covariate when needed. All analyses were carried out using SPSS 15.0 statistical package.

RESULTS

Caterpillar phenology and abundance

Total mean frass-fall production was higher in the Holm Oak (mean of 3 yearly means = 29.72 ± 2.14 mg/day·m^2) than in the pine forest (11.38 ± 1.89 mg/day·m^2; t_4 = 6.43, P = 0.003). There were no significant differences in mean CPD between the Holm Oak (mean of 3 yearly means = 29 May ± 11 days) and the pine forest (24 May ± 5 days; $F_{1,4}$ = 0.49, P = 0.524). However, the shape of caterpillar phenology varied between forests (Fig. IV.1). In the Holm Oak forest there was only a pulse (1 week) when food was abundant, whilst in the pine forest the period of maximum food abundance usually lasted two weeks (except in 2007). The mean frass-fall production during the pulse registered in the Holm Oak forest was, on average, around six-fold (mean of 3 yearly means = 185.34 ± 58.19 mg/day·m^2) higher than that registered in the pine forest (30.67 ± 11.49 mg/day·m^2, t_4 = 2.44, $P < 0.05$). The food was exceptionally abundant during the peak in both forests in 2007 (pine: 53.16 mg/day·m^2; Holm Oak: 300.10 mg/day·m^2).

Mean frass-fall production outside the peaks was quite similar between forests (pine: mean of 3 yearly means = 9.84 ± 2.74 mg/day·m^2; Holm Oak forest 15.90 ± 3.49 mg/day·m^2; t_4 = -2.37, P =

0.077). The amount of food in the Holm Oak forest outside the pulse was similar to that registered during the pulse in the pine forest for the two first years. Food range outside the peak in the pine forest was 0.75-18.95 mg/day·m^2 (means of the 5 funnels; Fig. IV.1a). For the Holm Oak, the range varied from 0.60 to 38.74 mg/day·m^2, although it reached up to 65 mg/day·m^2 in a few instances (Fig. IV.1b).

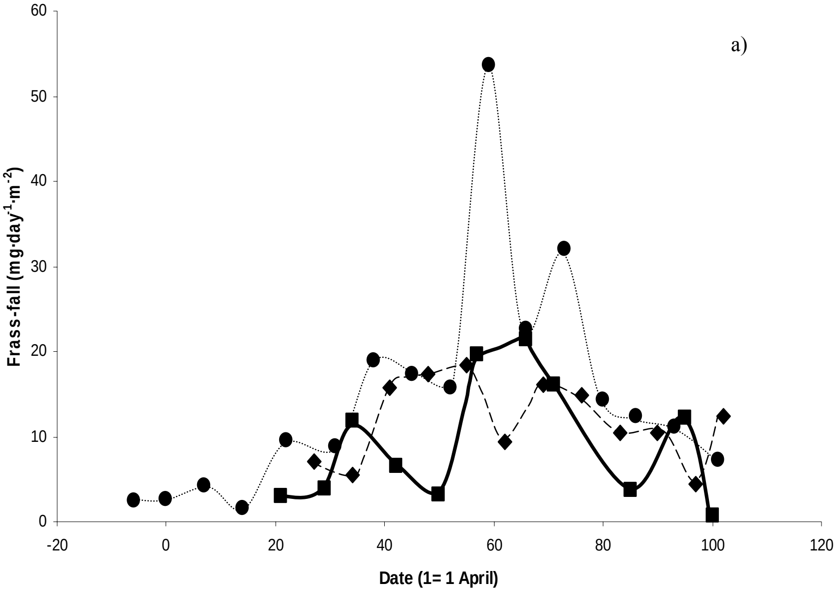


Figure IV.1. Seasonal variation in the frass-fall production for a) pine forest and b) Holm Oak throughout years: 2005 (solid line), 2006 (dashed line) and 2007 (dotted line).

Figura IV.1. *Variació estacional en la producció de biomasa d'orugues per a) bosc de pi, i b) bosc de Carrasca al llarg dels anys: 2005 (línia contínua), 2006 (línia discontínua) i 2007 (línia a punts).*

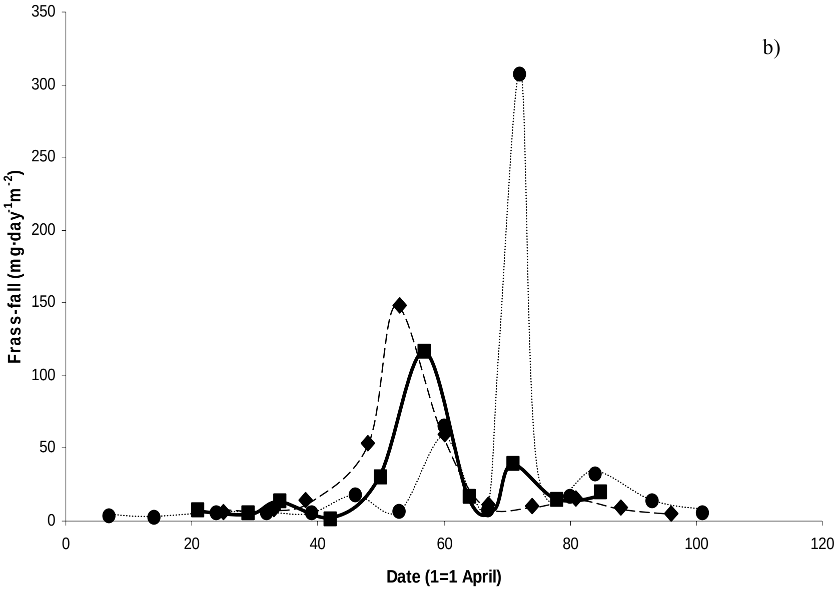


Figure IV.1. Continue.

Figura IV.1. *Continuació.*

Environmental cues for reproduction: prelaying temperatures and food peak date

Great Tits started laying earlier in warm years in both forests, and earlier in the pine than in the Holm Oak forest. The relationship between temperature and laying date was significant when using the warmth sum for the period 1st March to 25th April ($F_{1,3}$ = 19.29, P = 0.002, forest type: $F_{1,3}$ = 14.96, P = 0.031, Fig. IV.2), and almost so when using minimum temperature 30 days before laying ($F_{1,3}$ = 9.26, B = -0.53, P = 0.056; forest type: $F_{1,3}$ = 12.28, P = 0.039).

In the pine forest, mean clutch size decreased as the mean laying date was delayed ($F_{1,133} = 3.93$, $B = -0.82$, $P = 0.049$, year: $F_{1,133} = 19.40$, $P < 0.001$), and mean clutch size was larger in years with higher mean frass-fall production ($F_{1,1} = 274.41$, $B = 0.998$, $P = 0.038$). Those trends did not appear in the Holm Oak forest ($P > 0.05$).

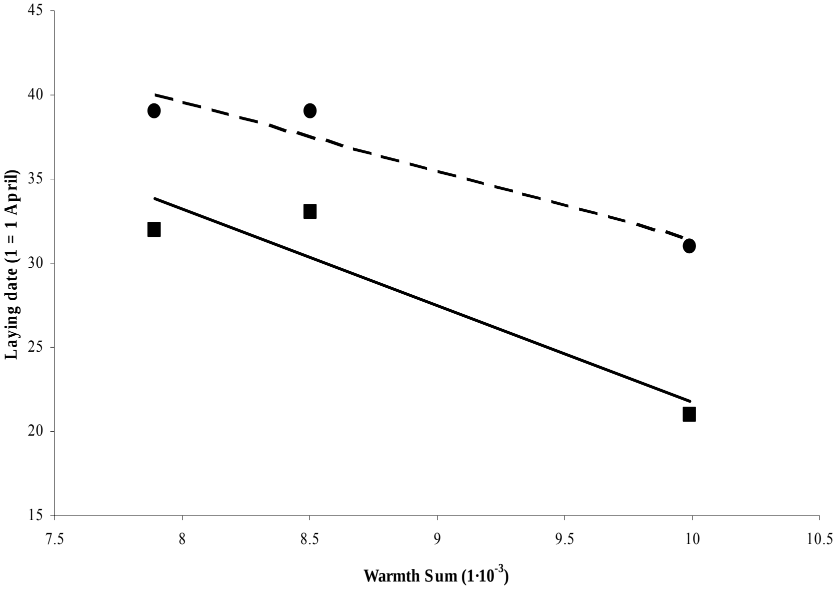


Figure IV.2. Correlationships between the sum of the daily maximum temperatures from 1st March to 25th April and the mean laying dates for Great Tits in the Hom Oak forest (dashed line) and in the pine forest (solid line).

Figura IV.2. *Correl.lacions entre la suma de les temperatures màximes diàries des de l'1 de Març fins al 25 d'Abril i la data promig de posta en la Mallerenga Carbonera al bosc de Carrasca (línia discontínua) i al de pi (línia contínua).*

Birds having chicks during the pulse of food abundance in the pine forest had laid larger clutches (6.23 ± 0.11 eggs, $n = 83$) than those out of the pulse (5.89 ± 0.13 eggs, $F_{1,131} = 6.27$, $n = 54$, $P =$

0.013; year: $F_{2,131} = 2.51$, $P = 0.085$). Instead, no statistical differences in clutch size between synchronized (7.19 ± 1.25 eggs, $n = 21$) and unsynchronized nests (6.76 ± 1.10 eggs, $F_{1,90} = 1.09$, $n = 74$, $P = 0.299$; year: $F_{2,90} = 1.09$, $P = 0.299$) were found in the Holm Oak forest.

In the pine forest, the peak of MFD by the nestlings was positively related to the CPD ($F_{1,2} = 306.70$, $r = 0.99$, $P = 0.036$, Fig. IV.3, see also Table IV.1). Indeed, more pairs were raising chicks during the pulse of food ($\chi^2_2 = 13.15$, $P = 0.001$). This relationship was not significant in the Holm Oak forest ($F_{1,2} = 0.75$, $r = 0.66$, $P =$

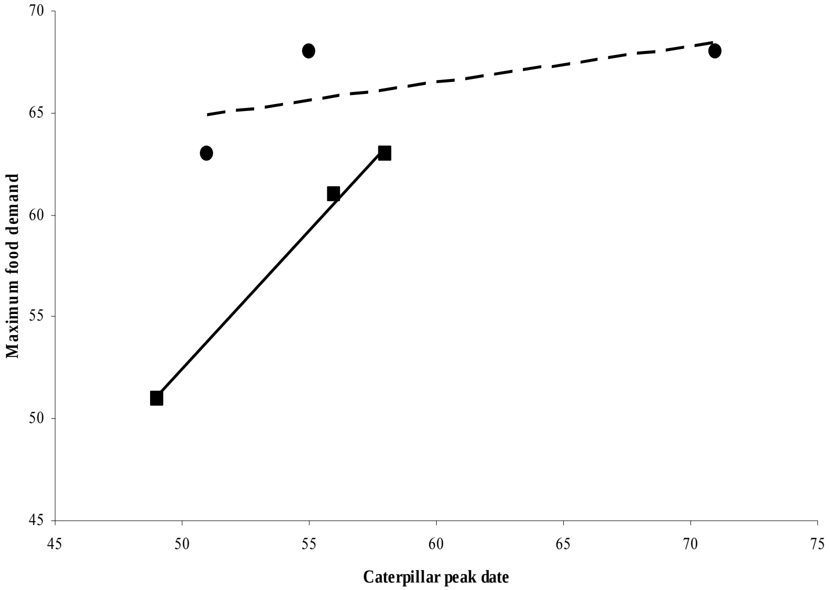


Figure IV.3. Regressions between the caterpillar peak date and maximum food demand by chicks in the Hom Oak forest (dashed line) and in the pine forest (solid line).

Figura IV.3. *Regressions entre la data del pic d'abundància d'orugues i la demanda màxima d'aliment per part dels polls al bosc de Carrasca (línia discontínua) i al bosc de pi (línia contínua).*

0.546) where, surprisingly, more pairs were raising chicks outside the pulse of food ($\chi^2_2 = 33.82$, $P < 0.001$).

Table IV.1. Mean laying dates, dates of maximum food demand by nestlings (10 days-old), dates of peak caterpillar abundance, and the number of days between MFD and CPD during 2005, 2006 and 2007. April dates are showed into brackets. For the caterpillar peak date, mean value for the interval is given into brackets. MFD = Maximum food nestling demand, CPD = caterpillar peak date. FR = Holm Oak forest, SM = pine forest.

Taula IV.1. *Data promig de posta, data de màxima demanda d'aliment pels polls (10 dies d'edat), data del pic d'abundància d'orugues, i el nombre de dies entre MFD i CPD durant 2005, 2006 i 2007. Entre corxets es mostra la data tenint en compte que 1 = 1 Abril, així com, el valor promig per al interval de la data del pic d'abundància d'orugues. MFD = Màxima demanda d'aliment pels polls, CPD = data del pic d'abundància d'orugues. FR = bosc de Carrasca, SM = bosc de pi.*

	Forest	2005	2006	2007
Laying date	FR	9 May (39)	1 May (31)	9 May (39)
	SM	3 May (33)	21 April (21)	2 May (32)
Maximum food demand	FR	7 June (68)	2 June (63)	7 June (68)
	SM	2 June (63)	21 May (51)	31 May (61)
Caterpillar peak date	FR	21 May-27 May (55)	19 May-23 May (51)	7 June-12 June (71)
	SM	21 May-5 June (58)	12 May-25 May (49)	23 May-29 May (56)
Nº days between MFD and CPD	FR	13	12	3
	SM	4	2	4

Fitness consequences of mistiming

There was an effect of timing over fledgling weight, finding heavier chicks during the pulse of food abundance in both forests (see Fig. IV.4, Table IV.2). Neither fledgling tarsus length, nor female weight were affected by mistiming in none of the forests (Table IV.2). A significant interaction was found for male weight between timing and forest type. Males from synchronized nests weighed slightly more (17.23 ± 0.10 g) than those from unsynchronized nests (16.87 ± 0.21 g, $n = 79$, $F_{1,72} = 3.32$, $P = 0.073$) in the pine forest. But, male weight was not affected by mistiming in the Holm Oak forest. Finally, fledging success was similar among synchronized (0.78) and unsynchronized nests in both forests (0.82, *P* > 0.05).

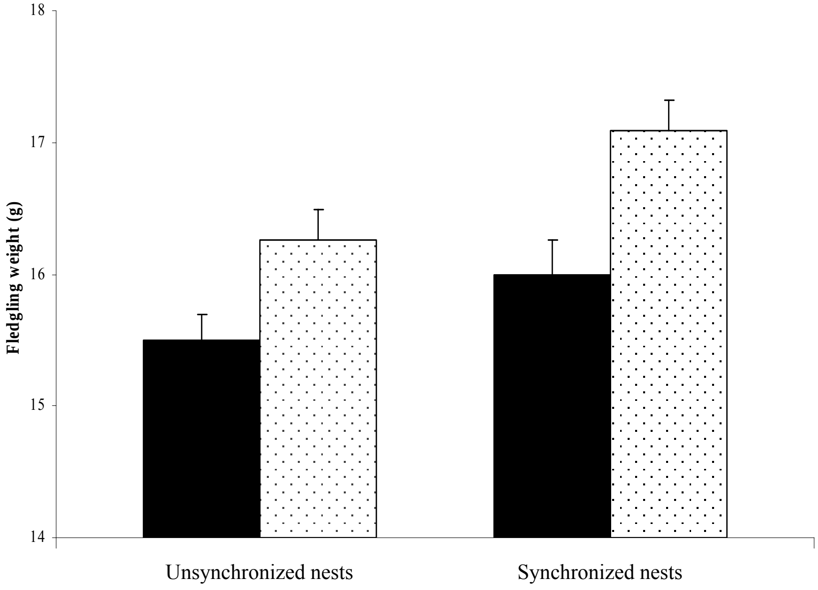


Figure IV.4. Mean fledgling weight (± *SE*) in unsynchronized and synchronized nests in the pine forest (black bar) and in the Holm Oak forest (dotted bar).

Figura IV.4. *Pes promig dels polls volantons (± ES) en nius sincronitzats i no sincronitzats al bosc de pi (barra negra) i al bosc de Carrasca (barra a punts).*

Table IV.2. Effects of timing over some breeding traits for both forests.

Taula IV.2. *Efectes de l'ajust entre la reproducció i la fenologia de l'aliment sobre alguns paràmetres reproductors als dos boscos.*

	F	*df*	*n*	*P*
Fledgling weight				
Timing	4.19	120	132	0.043
Forest type	9.70	120	132	0.002
Year	1.24	120	132	0.292
Brood size	2.79	120	132	0.098
Fledgling tarsus length				
Timing	0.64	120	132	0.426
Forest type	0.55	120	132	0.460
Year	2.00	120	132	0.140
Brood size	1.16	120	132	0.283
Female weight				
Timing	0.89	147	159	0.347
Forest type	11.70	147	159	0.001
Year	0.45	147	159	0.636
Brood size	0.30	147	159	0.584
Male weight				
Timing	0.09	128	140	0.760
Forest type	1.80	128	140	0.182
Timing x Forest type	4.04	128	140	0.047
Year	1.04	128	140	0.356
Brood size	0.004	128	140	0.953
Fledging success				
Timing	0.54	123	135	0.462
Forest type	1.03	123	135	0.311
Year	0.39	123	135	0.681
Brood size	3.92	123	135	0.050

DISCUSSION

Caterpillar phenology and abundance

Little is known about food phenology in forests of the Mediterranean region (Holm Oak forests: Dias and Blondel 1996b, Iglesias 1996; Downy Oak *Quercus pubescens* forests: Dias and Blondel 1996b). The shape of food phenology described by these authors in Holm Oak forests was similar to that described here, showing a sharp peak. Moreover, this peak occurred on average the 29 May in the Holm Oak forest, a date which was within the range found in other studies for the same forest type (30 May-6 June; Dias and Blondel 1996b, Iglesias 1996). Our data fit well with the general pattern of food being available later in Holm Oaks than in deciduous forests (range: 30 April-22 May; van Balen 1973, Blondel et al. 1992, Belda 1996). Blondel et al. (1992) pointed out that this was due to the later start of leaf growth in Holm Oaks.

To our knowledge, no studies on food phenology in Mediterranean pine forests are available. The pattern described above for Holm Oak forests contrasted with that found in pine forests, where food abundance increased slowly during the season, showing many fluctuations (see also van Balen 1973). The peak date of food abundance was much earlier than in other pine forest for which this information is available (26 June; van Balen 1973). In contrast, differences with the Holm Oak forests, including the one studied here, were very low. And, as it was the case for the Holm Oak forest, the peak of food abundance was later than in deciduous forests. Thus, in spite of differences in latitude among study areas, and on the wide range of years for which studies are available, it seems that food is available earlier in deciduous forests, and later in Mediterranean pine and Holm Oak forests, with small differences between pine and Holm Oak forests. Food seems to peak much later in central European pine forests.

Differences in mean food availability between forests are considered to be related to the dominant tree species. Deciduous forests renew the whole foliage annually, while only 30% is renewed in evergreen forests, being therefore deciduous forests richer in caterpillar biomass (Dias and Blondel 1996b, Tremblay et al. 2003). Within evergreen forests, food availability in Holm Oak forests in southern France and in Corsica was six-fold greater than in temperate pine forests (see Table 1 in Tremblay et al. 2003). We did not find previous information on food availability in Mediterranean pine forests. We found that mean frass-fall production values during the pulse of food abundance obtained were within the normal range from higher latitudes, pine forest (18-29 $mg/day \cdot m^2$) and Holm Oak forest (92-147 $mg/day \cdot m^2$). The length of the pulse of food abundance is difficult to guess from previous studies. It seems to be about two weeks long in Holm Oak forests (Figures 4.3, 1 and 3, in Belda 1996, Dias and Blondel 1996b, Iglesias 1996, respectively), while it is not clear the length of the pulse in pine forests (see Fig. 1 in van Balen 1973). In the present study, we have shown that this pulse lasted only one week in the Holm Oak and two weeks in the pine forest. Birds breeding in Mediterranean forests clearly experienced more feeding restrictions than those from deciduous forests where the pulse lasted around three weeks (Visser et al. 2006). Food in Mediterranean evergreen forests was, therefore, less abundant, and was available later and for a shorter time than in deciduous forests.

Environmental cues and breeding traits

Many cues could influence the start of reproduction in birds (Sanz 1998). Ambient temperature is, among environmental cues, one of the potential factors influencing the start of reproduction. Indeed, Great Tits breeding in the temperate forests start laying earlier in warm springs (Kluijver 1951, van Balen 1973, Slagsvold 1976, Visser et al. 2006). Some studies have shown that females start laying only after they have experienced a 'certain amount' of temperature, calculated as the sum of mean air temperatures from a fixed date, usually 1 March (Perrins and McCleery 1989, Perrins 1991). Presumably, tits lay earlier in warm springs because caterpillars emerge earlier. This highlights the importance for birds to use the ambient temperature as cue for triggering reproduction. Only one study performed in Mediterranean deciduous forests has tried to relate ambient temperatures and timing of reproduction in Great Tits (Belda 1996). This relationship has been analyzed more often in Blue Tits (Blondel 1985, Fargallo and Johnston 1997), which laid earlier in warmer years, although the general trend found elsewhere was not shown in Corsican populations (see Blondel 1985). Here, there was no relationship between temperature and laying date. Such relationship was very clear in our two Mediterranean bird populations, birds delayed the timing of reproduction in colder years. The following question is whether the cue used by the birds is relevant in these systems – i.e. whether the observed response to temperature makes the birds to synchronize the peaks of food demand and food availability.

Effects of mistiming in Mediterranean forests

Generally, tits have fine-tuned the reproduction in such way that chicks are raised when their caterpillar food is more abundant (Kluijver 1951, van Balen 1973, Perrins 1991, Blondel et al. 1993, Dias and Blondel 1996b, Tremblay et al. 2003, Visser et al. 2006). Examples of weak synchronization have been also found for tits (Blondel et al. 1987, Visser et al. 2006) and other passerines (Pied Flycatchers *Ficedula hypoleuca* and Redstarts *Phoenicurus phoenicurus* in Eeva et al. 2000). But little is known about the synchronization between MFD and CPD in the Mediterranean region for Great Tits (deciduous forests in Belda 1996, Holm Oak forests in Iglesias 1996). In these studies, conclusions were based only on graph interpretations (see Fig. 4.3 in Belda 1996, and Fig. 14 in Iglesias 1996), without proper statistical analyses, so conclusions are difficult to draw. In the present study, we found that reproduction was clearly timed so that chicks were at the nest when caterpillar biomass was plentiful in the pine forest, but not in the Holm Oak forest.

Van Balen (1973) found that Great Tits breeding in pine forests raised heavier chicks when they timed reproduction with food phenology. Our results for the pine forest agreed with this conclusion, and chicks raised out of the food pulse weighed less than those raised when food was abundant. Fledglings with low weight might have lower survival prospects (Greño et al. 2008), therefore reducing parental fitness. On the other hand, we did not find previous studies on the possible consequences of mistiming in Great Tits breeding in Holm Oak forests. Here, we have found that mistimed birds showed also fitness consequences, with fledglings from mistimed (unsynchronized) nests weighing less. Therefore, it seems that there is a pressure for synchronizing MFD and CPD in both forests, but only birds breeding in the pine forest achieved such synchronization.

What we have found in the Holm Oak forest was likely an apparent maladaptation to local conditions resulted from a source-sink population structure (Pulliam 1988). This would involve asymmetrical dispersal from the commoner habitat (pine forest, c.a. 12805 ha), where birds are adapted to the local timing of food availability, to the less common habitat, the Holm Oak forest (506 ha; Terrones et al. 2006, B. Terrones, unpubl. data) being this supported by two facts. First, Great Tits, as well as other tit species (e.g. Coal Tits *Periparus ater*) were ringed 1 Km far and out of the Holm Oak forest during a ringing program, and later recovered breeding in the nest boxes placed within the Holm Oak forest (J.L. Cantó, pers. com.). Second, the higher rate of nest box occupation by hole-nesters in pine forests (83% vs. 68% in the Holm Oak forest, unpubl. data) would indicate that this forest may be saturated first, so many individuals may redistribute themselves among other less common habitats (Dias and Blondel 1996a). Therefore, the possible flow prevented birds to adapt to local conditions.

V

FACTORS AFFECTING NESTLING FOOD PROVISIONING IN GREAT TITS

SUMMARY

The rate at which parents deliver food to dependent offspring is critical to understand a wide range of behavioural questions. Their patterns of variation might reveal important information on the effort of the parents and which factors are really affecting them. Mechanical counters were used to determine food provisioning patterns in 229 Great Tits *Parus major* nests during 4 years. Feeding frequency per chick showed a linear increase with nestling age and total feeding frequency stabilized towards the end of the nestling period. The number of visits per nest increased linearly, while those per nestling decreased linearly with brood size. Feeding rates per nest declined throughout the season parallel to the seasonal brood size decline; feeding frequencies per nestling did not vary seasonally. Adult effort was almost constant throughout the day, independently of variations in brood size, ambient temperature and date. Previous studies of nestling provisioning patterns were either contradictory or poorly supported by low sample sizes. The present study involved a much larger sample and clarifies nestling provisioning patterns and the factors with which they are associated.

RESUM

La taxa a la qual els adults d'aus nidícoles duen menjar a la seua descendència és important per entendre l'ampli abanic de preguntes comportamentals que hi puguen surgir. Els patrons de variació podrien donar important informació sobre l'esforç dels adults i dels factors que realment estan afectant-los. Vam emprar contadors mecànics per tal de determinar els patrons d'aprovisionament d'aliment en 229 nius de Mallerenga Carbonera Parus major *durant 4 anys. El nombre total de visites que va rebre cada poll va augmentar linialment amb l'edat dels mateixos i, el nombre total de visites s'estabilitzà cap al final del període d'estància dels polls al niu. Per altra banda, el nombre total de visites augmentà linialment amb el tamany de la posta però, en canvi, va disminuir el nombre de visites que cada poll va rebre. Els adults disminuïren l'esforç cap al final de l'estació reproductora; això no va afectar al nombre de visites que cada poll va rebre. Els adults no van variar en el nombre de visites al niu al llarg del dia tenint en compte les variacions en tamany de posta, temperatura ambiental i data. Estudis previs sobre els patrons d'aprovisionament en la Mallerenga Carbonera foren contradictoris o es sostenien a base d'un tamany mostral reduït. En aquest treball el nombre de mostres ha sigut molt major que en treballs anteriors aclarint els patrons d'aprovisionament d'aliment i els factors amb els què estaven associats.*

INTRODUCTION

The rate of food provisioning to young is a basic aspect of the study of the foraging behaviour in wild animals, which has been primarily studied in birds (e.g. Gibb and Betts 1963, Biermann and Sealy 1982, Blondel et al. 1991, Barba and Monrós 1999). The number of provisioning visits made by adults during the nestling period lead to a greater understanding of the foraging strategies (Tremblay et al. 2005, Kryštofková et al. 2006) and of the effort made to raise their young (e.g. Moreno et al. 1995, Stauss et al. 2005), as well as to a better identification of the environmental factors which might affect provisioning effort (e.g. Rytkönen et al. 1996, Naef-Daenzer and Keller 1999, Freitag et al. 2001).

In species where adults normally bring one prey item per visit (single-prey loaders; Orians and Pearson 1979), it is possible to estimate the number of prey items brought based on the number of visits made by the adults to the nest (e.g. Kluijver 1950, Stienen et al. 2000). Therefore, the study of feeding frequencies, and their patterns of variation should reveal important information on the effort that parents are making and the result of this effort from the nestlings' point of view, i.e. how many prey items they actually receive.

An important factor which might affect the rate of food provisioning is nestling age. Older nestlings are bigger and may therefore require more food. On the other hand, growth rates are not constant, and nestlings may need more energy when growth rates are higher. A usual pattern is an increase in feeding rates with age during the first part of the nestling period, when nestlings are growing faster, and a levelling off when they are close to their final weight (Grundel 1987, Blondel et al. 1991). In some studies feeding rates have been showed to decrease in the days previous to fledging (Blondel et al. 1991, Rytkönen et al. 1996). A complicating factor could be the changes in either prey size or prey type brought by the parents as the nestlings grow, since parents might shift to more energy and/or larger prey (e.g. Rytkönen et al. 1996, Stienen et al. 2000), or even change the degree of preparation of the prey brought (Barba et al. 1996, Ponz et al. 1999).

Furthermore, feeding frequencies could increase with the number of nestlings present in the nest. This has been found in some studies (Gibb 1950, Rauter et al. 2000, Stauss et al. 2005). On the other hand, this increase in frequency is not always proportional to the increasing needs, so each nestling receives fewer visits as brood size increases (Royama 1966, Rytkönen et al. 1996, Naef-Daenzer and Keller 1999, MacColl and Hatchwell 2003). Interacting with this, the energy requirements of the chicks change with brood size, and greater heat loss in a small brood could be compensated for by the chicks being supplied with more food (Royama 1966).

Ambient temperatures might affect feeding rates (Rauter et al. 2000). Low temperatures might make the parents spend more time brooding at the nest, therefore decreasing the feeding frequency (e.g.

Wiebe and Elchuk 2003). On the other hand, low temperatures increase thermoregulation costs of the nestlings, which might require more food, which in turn might result in increased feeding rates by the parents. Moreover, temperature might affect prey availability (Wiebe and Elchuk 2003). Therefore, the effect of temperature would very much depend on the actual ambient temperature, on the ability of nestlings to thermoregulate (i.e. their age), on the prey types consumed and the effects of temperatures on prey availability.

Most studies have found a decline in feeding frequencies during the breeding season (e.g. Naef-Daenzer et al. 2000), although both an increase (Smith et al. 1988) and a lack of seasonal variation have also been reported (Johnson and Best 1982, MacColl and Hatchwell 2003). A number of reasons could be behind these patterns, including variation in mean brood size, the value of the current nestlings to the parents in terms of inclusive fitness (Winkler 1987), and the availability and size of prey items available (Royama 1966, Naef-Daenzer and Keller 1999).

Finally, parents might schedule their foraging activities considering those periods of the day when food demand by the nestlings is more intense (Freitag et al. 2001), food more easily available (Stienen et al. 2000) or foraging costs lower (Rastogi et al. 2006). Foraging should also be traded-off against other activities, such as brooding small nestlings (Wiebe and Elchuk 2003). Therefore, feeding frequencies would be expected to vary throughout the day (see

Knapton 1984), and this pattern of variation could change with factors such as nestling age, number of nestlings and ambient temperatures (food demand, need of brooding), and throughout the season (food availability, temperature patterns, etc.).

The Great Tit *Parus major* is a good model species to study patterns in feeding frequencies. Their tendency to occupy nest boxes allows detailed measurement of many breeding parameters (e.g. Gibb 1955, Royama 1966, Eguchi 1980, Smith et al. 1988, Tinbergen and Verhulst 2000). Great Tits typically behave as single-prey loaders (Gibb and Betts 1963, Naef-Daenzer et al. 2000), and most visits to the nest are for feeding young (Kluijver 1950, Eguchi 1980). Therefore, the number of visits made by the parents can be translated into the number of prey received by the nestlings. Not suprisingly, several studies have been published either directly addressing the patterns of feeding rates of this species (Kluijver 1950, Gibb 1955, Gibb and Betts 1963, Royama 1966, van Balen 1973, Eguchi 1979, Cowie and Hinsley 1988, Naef-Daenzer et al. 2000), or including feeding rates as a measure of parental effort in wider contexts (Smith et al. 1988, Verhulst and Tinbergen 1997, Naef-Daenzer and Keller 1999, Sanz and Tinbergen 1999, Tinbergen and Verhulst 2000).

In spite of this large number of reports, studies trying to describe feeding patterns in detail (e.g. Gibb and Betts 1963, Royama 1966, Eguchi 1980) have been done with relatively small sample sizes and lack statistical treatments. More recent studies, though including more adequate statistical treatments, have not included exhaustive analyses of the feeding patterns (see Cowie and Hinsley 1988 for an exception). Our main aim here was to describe the feeding patterns of Great Tits in detail. We explored the effect of nestling age, brood size, time of season, time of day and temperature on this feeding behaviour.

METHODS

The study area was located in Sagunto (eastern Spain, 39º 42' N, 0º 15' W, 30 m a.s.l.) and it was completely occupied by orange plantations (Andreu and Barba 2006). Nest boxes were distributed over the area, and checked periodically to determine the basic breeding parameters (laying date, clutch size, number of hatchlings and fledglings produced, etc.) of Great Tits occupying them (e.g. Barba et al. 1995). Most parents were trapped at the nest and individually ringed (e.g. Monrós et al. 2002). Data for this study were collected in 1996, 1998, 1999 and 2000 in 46, 7, 74 and 102 clutches (198 first, 5 second and 26 replacement clutches). Experimental nests used in the Chapter VI were not used for this descriptive study. First clutches were defined as the first breeding attempt of the year; second clutches were those laid after a successful first breeding attempt (i.e. at least one chick fledged) and replacement clutches were those laid after a breeding failure.

To estimate feeding rates, we used mechanical counters placed at the nest box entrance. These consisted in a switch activated by a wire crossed at about two thirds of the bottom of the entrance hole, so the bird pushed it down when entering or leaving the nest box. These counters were not able to distinguish among the visits made by each member of the pair, so total number of visits is considered throughout. The counters were moved among available nests in our population, to maximize the sample size and distribute them among different nestling ages, brood sizes and throughout the season.

We defined "sample" as a continuous registration of feeding rates during at least two hours in a nest. Recording times varied between two hours and one day. In cases where a counter was operating overnight, we computed the number of hours of daylight, using official sunset and sunrise times. When feeding nestlings, parents usually start their visits by sunrise and finish close to sunset (e.g. Kluijver 1950; pers. obs.). The feeding rates recorded in these cases were assigned to the day in which the counter was operating more useful time.

Maximum, minimum and average ambient temperatures were gathered from a meteorological station placed close to the study area (c.a. 4 Km) and were available for each of the sampling days. The three temperatures were closely related. We repeated the analyses with the all of them, and relationships were always stronger with minimum temperatures, so we only present these results.

We could not analyze the data in full models, with all the independent factors considered and their interactions contributing to explain variations in feeding rates. The main reason was that, for some analyses (e.g. effects of nestling age or time of day), we needed repeated measurements of the same nests, so a limited set of nests fulfilled the requirements. These nests were randomly selected among available ones each year. Therefore, our approach was asking specific questions and using the best set of data available to answer them.

To analyze the effect of nestling age on feeding rates, we used four age categories: 4-6, 7-9, 10-12 and 13-15 days. Data outside this range were too scarce and were removed from these analyses. We only used nests for which samples were available for each of the four age categories. In cases where more than one sample per nest and age category was available, we used the average frequency of the available samples. We ended up with data from 20, 20 and 12 successful first clutches collected in 1996, 1999 and 2000, and 6 replacement clutches (one from 1996, 5 from 1999). No second clutches fulfilled the above criteria to be included in the analyses.

We tested how the number of nestlings present at the time of sampling affected the effort made by the adults using data from 229 clutches, including first, replacement and second clutches of all years. We performed both linear and quadratic regression analyses choosing the one which best fitted to the data. When we had data for several days on a nest, we randomly selected one day.

To test for seasonal variation in feeding rates we used all the nests available in 1996, 1999 and 2000, including first, replacement and second clutches, and selected one sample per nest to remove the effect of nestling age. For each nest, we selected the sample closest to day 10, the day where food demand by the nestlings is more intense; 76% of the nests had samples between days 8 and 12, the rest between days 4 and 15. Then, we calculated the residuals of regressing feeding frequency against age of the nestlings, and explored the seasonal trend of these residuals. Data covered the period from 27 April to 26 June. To explore the effect of temperatures on seasonal variation, we also selected for each nest the minimum temperature when the nestlings were 10 days-old.

Finally, data on diurnal variation were collected in 1996, 1998 and 1999. Each day was divided into six periods from sunrise to sunset. The first period from sunrise to 10:00 and the last one from 18:00 to sunset, all other periods were 2 hours long. We included into the analyses 40 nests (successful first clutches) for which we had data on feeding rates for each one of the six periods, as well as exact information on the age of the nestlings (mean 8.6 ± 0.5 days, range: 4-15) and brood size (mean of 5.5 ± 0.29 chicks, range: 2-9) on the date of sampling. In nests where we had data for more than one day, one of the days was randomly selected for the analyses.

We next explored whether any of the potential factors considered affected diurnal variation in feeding rates. Each year, half of the nests were classified as "early" and the other half as "late", based on the date of laying of their first egg. Based on the minimum temperature, days were classified as either "hot" ($T_{min} > 12$ ºC) or "cool" ($T_{min} \leq 12$ ºC). Other factors included in the analyses were nestling age, brood size and year.

Repeated measures analyses of variance (RMANOVAs) were used when the feeding frequency (dependent variable) of the same nest was measured at different times, i.e. in testing for the effects of the age of the nestlings or time of day (within-subject factors). In these cases, the assumption of sphericity was tested (Mauchly test), and Huynh-Feldt corrected degrees of freedom used if this assumption was not held. When between-subject factors where included in the models, we also tested for homogeneity of variances and covariances (M-Box test). Dunn-Sidak *post hoc* tests were used to test for differences among categories in within-subject factors. The effect size was calculated through the strength of relationship (r_s) when both variables were continuous, and through the size of difference (d) when the response variable was continuous while the predictor was categorical (Nakagawa et al. 2007). In both cases, statistics are showed with their respective confidence intervals (CI).

Values are presented as mean ± *SE*. Statistical analyses were carried out using SPSS (version 15.0, SPSS Inc., Chicago).

RESULTS

Nestling age

Considering all the available clutches (*n* = 58), feeding rates varied with the age of the nestlings (Huynh-Feldt test, $F_{2.5,140.4} = 4.20$, $P = 0.012$; Fig. V.1). However, Dunn-Sidak *post hoc* tests did not reveal, in general, statistical differences among ages, though the increase from the first (4-6 days) to the third (10-12) age class was close to statistical

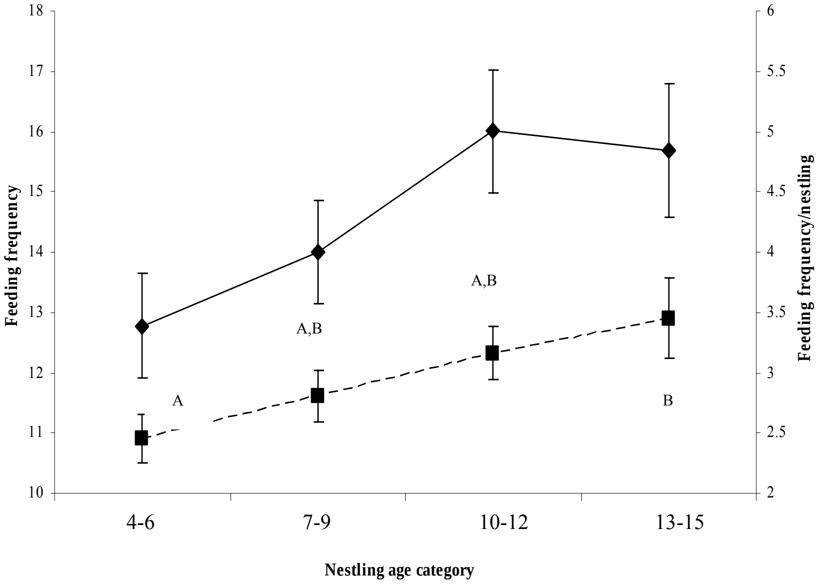


Figure V.1. Variation of total feeding frequency (number of visits per hour, solid line) and feeding frequency per nestling (number of visits per nestling per hour, dashed line; *n* = 58 nests in both cases) throughout the nesting period. Nestling age categories (days) with the same letter were not significantly different. Means ± *SE* are shown.

Figura V.1. *Variació de la freqüència d'aprovisionament d'aliment (nombre de visites per hora, línia contínua) i freqüència d'aprovisionament d'aliment per poll (línia discontínua; n = 58 en ambdúes casos) durant el període d'estància dels polls al niu. Categories d'edat (dies) amb la mateixa lletra no foren significativament diferents. Es mostren les mitges ± ES.*

significance (*d* = 0.25 with 95% CI = -6.5 to 0.0, $P = 0.050$), levelling off later on.

A potential factor affecting this pattern might be the reduction of the number of nestlings throughout the nesting period by death of some nestlings. In fact, brood size differed slightly between age categories (Huynh-Feldt test, $F_{2.0,100.0} = 6.71$, $P = 0.002$) being highest (6.0 chicks ± 0.27) for the youngest, and lowest (5.7 chicks ± 0.30) for the oldest age class (Dunn-Sidak *post hoc* tests, $P = 0.016$; no significant differences were detected among other age classes). We therefore explored how the number of visits per nestling varied with their age, and significant differences among age classes were found (Huynh-Feldt test, $F_{2.5,140.0} = 6.06$, $P = 0.001$; Fig. V.1). The pattern of increase with age was almost linear until the oldest age class, i.e. the final levelling was not observed. Significant differences (Dunn-Sidak *post hoc* tests) were detected between the first and the fourth age classes (*d* = 0.28 with 95% CI = -1.7 to -0.3, $P = 0.002$), and marginally significant differences between the first and the third (*d* = 0.20 with 95% CI = -1.4 to 0.0, $P = 0.062$) and the second and the fourth age classes (*d* = 0.18 with 95% CI = -1.3 to 0.0, $P = 0.054$). Therefore, the parents increased their effort per nestling as they grew older, at least within the range of ages explored, though the total number of visits they performed stabilized by the end of the nesting period when they had to feed fewer nestlings.

Another question addressed was whether the pattern of variation of feeding rates with age changed through the season. To check this possibility we used only first broods (n = 52), and divided them into "early" and "late", allocating half of the broods of each year into each category. The interaction term between nestling age and seasonal period was not significant either considering feeding rates per nest (Huynh-Feldt test, $F_{2.4,121.7}$ = 1.42, P = 0.236) or per nestling (Huynh-Feldt test, $F_{2.5,126.2}$ = 1.03, P = 0.400). Therefore, the pattern of variation of feeding rates with age did not differ throughout the season among first clutches.

Brood size

Considering all the clutches available (n = 229), the number of visits made by the parents increased linearly with brood size (r_S = 0.25 with 95% CI = 0.5 to 1.5, $F_{1,227}$ = 14.74, P < 0.001; Fig. V.2). However, the number of feeding visits per nestling declined linearly as brood size increased (r_S = -0.41 with 95% CI = -0.4 to -0.2, $F_{1,227}$ = 46.02, P < 0.001; Fig. V.2). Quadratic terms did not improve significantly the fitting in any case. This means that parents with more nestlings made more effort, but that increase was not proportional to the increment in brood size, and each particular nestling received fewer prey items in larger broods.

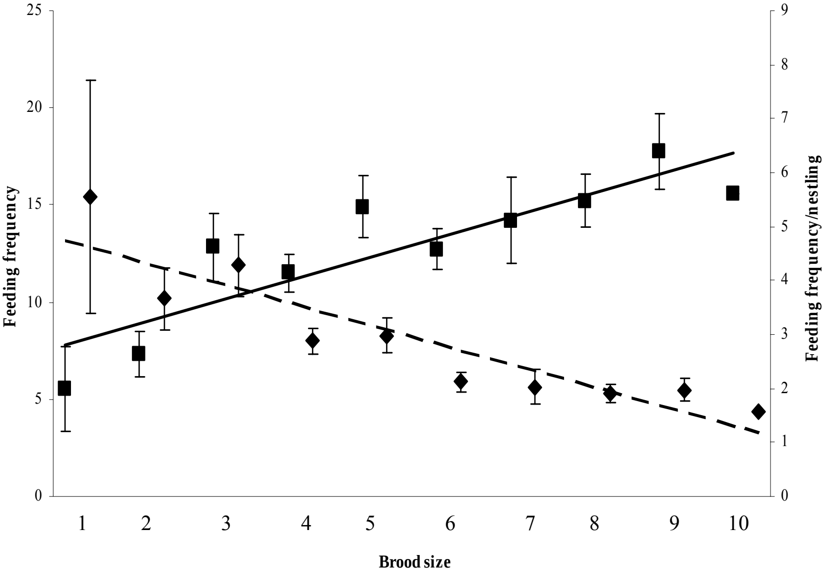


Figure V.2. Brood size effect on parental effort (solid line) for first (*n* = 198 nests), second (*n* = 5 nests) and replacement (*n* = 26 nests) clutches. Feeding frequency (number of visits per hour): 7.6 + 1.0·brood size, $R^2 = 0.061$, $F_{1,222} = 14.32$, $P < 0.001$. Linear regression among brood size and parental effort per nestling (dashed line) for the same above sample size. Feeding frequency per nestling (number of visits per nestling per hour): 4.5 - 0.3·brood size, $R^2 = 0.150$, $F_{1,222} = 39.09$, $P < 0.001$.

Figura V.2. *Efecte del tamany de la posta sobre l'esforç parental (línia contínua) per a primeres (n = 198 nius) i segones postes (n = 5 nius) i, reposicions (n = 26 nius). La freqüència d'aprovisionament (nombre de visites per hora): 7.6 + 1.0·tamany de posta,* $R^2 = 0.061$, $F_{1,222} = 14.32$, $P < 0.001$. *Regressió lineal entre el tamany de posta i l'esforç parental per poll (línia discontínua) per al mateix tamany mostral que a dalt. Freqüència d'aprovisionament per poll (nombre de visites per poll i per hora): 4.5 - 0.3· tamany de posta,* $R^2 = 0.150$, $F_{1,222} = 39.09$, $P < 0.001$.

Seasonal variation

Seasonal variation was explored using one data point per nest and removing the effects of the nestling age at the time of sampling (see Methods). The general pattern for the total feeding frequency was a decline during the breeding season (r_S = -0.13 with 95% CI = -3.4 to -0.01, $F_{2,221}$ = 4.02, P = 0.048). However, more detailed analysis showed that the seasonal pattern differed between years (ANCOVA, $F_{2,218}$ = 7.05, P = 0.001, with date as a covariate). Only in 1999 was the seasonal decline significant (Fig. V.3).

Two of the studied factors might affect seasonal variation in feeding rates: brood size and temperature. Brood size decreased throughout the season in all three years (ANCOVA, date (covariate): $F_{1,218}$ = 47.73, P < 0.001; year: $F_{2,218}$ = 6.01, P = 0.003), and ambient temperatures, when nestlings were 10 days-old, varied during the season (ANCOVA, date (covariate): $F_{1,218}$ = 83.02, P < 0.001; year: $F_{2,218}$ = 12.00, P < 0.001) increasing in all the three years. We therefore built a regression model for each year with date, brood size and temperature as independent variables and feeding frequency as response variable, using a stepwise selection of variables. In all the three years, brood size was the only variable included into the regression model (1996: R^2 = 0.102, r_S = 0.33 with 95% CI = 0.2 to 3.0, $F_{1,45}$ = 5.04, P = 0.031; 1999: R^2 = 0.211, r_S = 0.46 with 95% CI = 1.1 to 3.0, $F_{1,73}$ = 19.22, P < 0.001; 2000: R^2 = 0.076, r_S = 0.27 with 95% CI = 0.4 to 2.0, $F_{2,101}$ = 8.23, P = 0.005). Therefore, the seasonal decrease in feeding rates was mostly explained by the seasonal decrease in brood size. On the other hand, and agreeing with the above pattern, each nestling received the same number of visits during the season. Although the adult effort per nestling was different in different years, there was no seasonal variation in feeding rates per nestling within each year (ANCOVA, date (covariate): $F_{1,218} = 2.51$, $P = 0.115$; year: $F_{2,218} = 12.71$, $P < 0.001$).

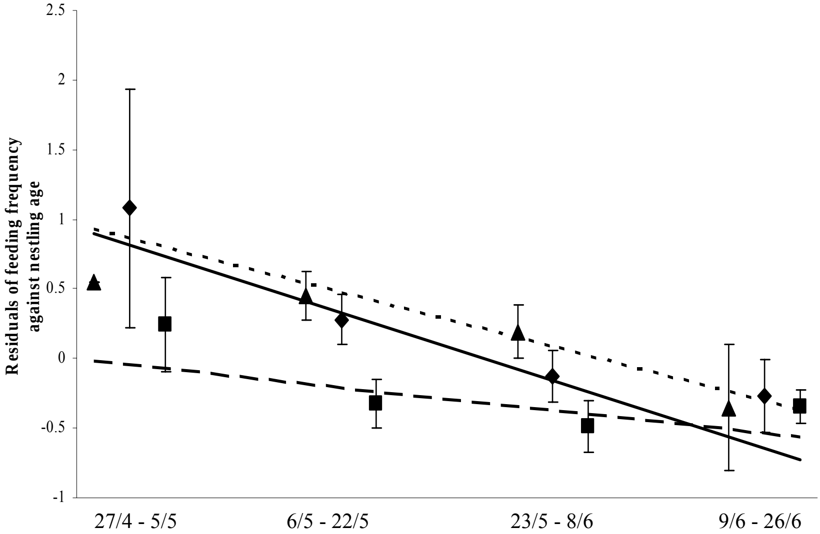


Figure V.3. Seasonal variation in feeding rates for the 3 study years. Residual feeding rates, after removing the effect of nestling age, were used. To simplify the presentation, mean (± *SE*) values are presented for arbitrary periods: 27 April-5 May, 6 May-22 May, 23 May-8 June and 9 June-26 June. However, regression analyses were performed using all data points: 1996 (solid line, triangles): 1.3 - 0.02·date, $R^2 = 0.050$, $r_S = -0.22$ with 95% CI = -6.0 to 0.8, $F_{1,44} = 2.31$, $P = 0.068$, data points from 46 nests; 1999 (dotted line, rhombi): 1.4 - 0.02·date, $R^2 = 0.069$, $r_S = -0.26$ with 95% CI = -5.5 to -0.4, $F_{1,72} = 5.33$, $P = 0.012$, n = data points from 74 nests; 2000 (dashed line, squares): 0.1 - 0.008·date, $R^2 = 0.013$, $r_S = -0.12$, $d = 41.33$, $F_{1,100} = 1.35$, $P = 0.124$, data points from 102 nests.

Figura V.3. *Variació estacional en la freqüència d'aprovisionament al llarg dels tres anys d'estudi. Vam emprar els residus de la freqüencia d'aprovisionament després de corregir per l'efecte de l'edat. Per simplificar la presentació, la mitja (± ES) es mostra per a períodes arbitraris: 27 Abril-5 Maig, 6 Maig-22 Maig, 23 Maig-8 Juny i 9 Juny-26 Juny. Malgrat això, als anàl.lisis de regressió s'utilitzaren totes les dades: 1996 (línia contínua, triangles): 1.3 - 0.02·data,* $R^2 = 0.050$, $r_S = -0.22$ *amb 95% IC = -6.0 fins 0.8,* $F_{1,44} = 2.31$, $P = 0.068$, $n = 46$ *nius; 1999 (línia de punts, rombes): 1.4 - 0.02·data,* $R^2 = 0.069$, $r_S = -0.26$ *amb 95% IC = -5.5 fins -0.4,* $F_{1,72} = 5.33$, $P = 0.012$, $n = 74$ *nius; 2000 (línia discontínua, quadrats): 0.1 - 0.008·data,* $R^2 = 0.013$, $r_S = -0.12$, $d = 41.33$, $F_{1,100} = 1.35$, $P = 0.124$, $n = 102$ *nius.*

Diurnal variation

Over the 40 nests included in the sample, feeding rates did not vary significantly throughout the day ($F_{5,195} = 2.12$, $P = 0.062$). Mean values ranged between 12.1 and 14.7 visits per hour at the different periods considered (Fig. V.4). Since differences among diurnal periods were, however, close to statistical significance, we also looked for the underlying factors associated with them (laying date, temperature,

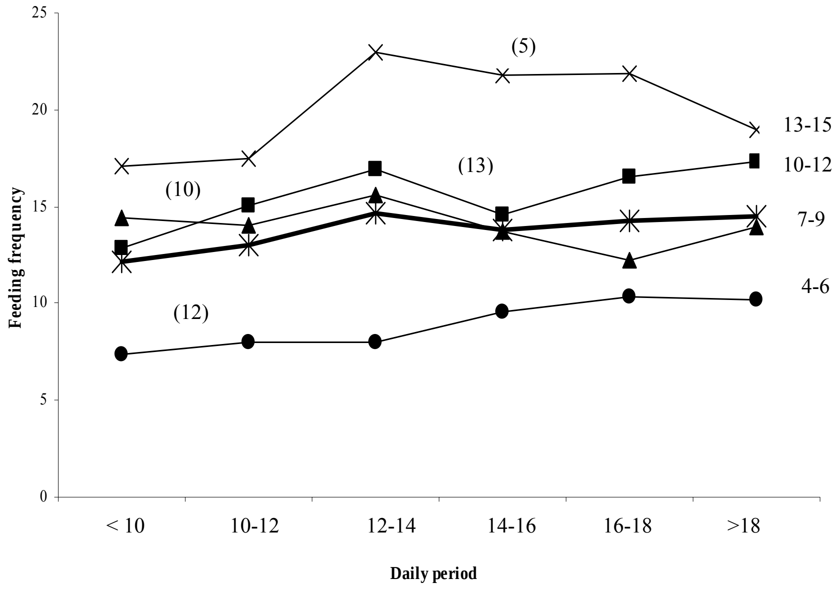


Figure V.4. Effects of nestling age on diurnal patterns of variation in feeding frequencies. There is a thin line for each age category; age-ranges are shown at the end of the lines on the right; sample sizes for each line are in brackets. Mean values are joined by the thickest line.

Figura V.4. *Efectes de l'edat dels polls sobre els patrons diürns de variació en les freqüencies d'aprovisonament. Per a cada categoria d'edat s'ha emprat una línia estreta: els rangs d'edat es mostren a la part final dreta de cada una de les línies; els tamanys mostrals per cada una de les línies es mostren entre parèntesi. El valor mitjà es representa amb una línia més grossa.*

nestling age, brood size and year). A full model, including all variables mentioned above as between-subject factors, was not significant ($F_{5,110} = 0.32$, $P > 0.05$). However, when we only included the age of the nestlings as between-subject factor, significant differences in feeding frequencies between periods were obtained ($F_{5,180} = 2.32$, $P = 0.045$). Dunn-Sidak *post hoc* tests showed that feeding rates increased significantly from the first to the third period ($d = 0.40$ with 95% CI = -5.8 to -0.1, $P = 0.036$), while inspection of Fig. V.4 suggests that most of this difference was probably caused by the oldest nestlings. When other factors where individually included into different models, no significant differences in feeding rates throughout the day were detected ($P > 0.05$ in all cases).

DISCUSSION

Nestling age

Total feeding rates usually increase linearly with the age of the nestlings, levelling off towards the end of the nestling period, and even decreasing before fledging (Johnson and Best 1982, Grundel 1987, Blondel et al. 1991, Karlsson 1994, MacColl and Hatchwell 2003). However, some studies failed to detect changes in feeding rates with nestling age, and changes in prey size and/or quality were suggested to compensate for this lack of increase (e.g. Knapton 1984, Laiolo et al. 1998, Stienen et al. 2000), though this is not always so (e.g. Schadd and Ritchison 1998). Other authors argued that the lack of effect was due to the absence of samples from very young nestlings (Schadd and Ritchison 1998, Kryštofková et al. 2006).

Among the studies on Great Tits that have examined this pattern, Verhulst and Tinbergen (1997) found a linear increase of feeding rates with age up to 14 days. Data presented by Gibb (1955) suggested a more or less linear increase up to 10-13 days (see also Eguchi 1980), levelling off afterwards, and even decreasing by the end of the nestling period in late broods. Some authors have suggested that this lack of increase of feeding rates at older ages was due to fatigue of the parents (e.g. Gibb 1955), or to changes in prey size with nestling age (Royama 1966, Knapton 1984), whilst the decrease was attributed by Kluijver (1950) to the fact that adults were preparing for a second brood.

Our results clearly showed that parents increased the number of feeding trips per nestling at least from 4 to 15 days. When considering the total number of visits, it seems to level off after day 12. These results strongly suggest that the lack of increase in parental effort towards the end of the nestling phase is mostly a consequence of a brood reduction due to nestling mortality throughout the nesting period, and not to fatigue of adults. On the other hand, while parents could bring smaller prey to very young nestlings (e.g. Slagsvold and Wiebe 2007, for Pied Flycatchers *Ficedula hypoleuca*), it is unlikely that changes in prey size occurred during the last part of the nestling period (e.g. Kabisch 1965). We have no data after day 15, so it would be possible that feeding rates per nestling actually levelled off after this age, as suggested in previous studies (Gibb 1955, Grundel 1987, Blondel et al. 1991).

Brood size

Probably the most commonly reported pattern is that parents feeding large broods make an effort to increase their feeding rate in order to fulfil the greater requirements of the brood (e.g. Gibb 1950, Nur 1984a, Robinson and Hamer 2000). However, it is also usual that the increased feeding rates do not fully compensate for the increase in brood size, resulting in fewer visits per nestling in larger broods (e.g. Royama 1966, Nur 1984a). In a number of studies, however, feeding rates per nest were reported to be independent of brood size (see e.g. Bengtsson and Rydén 1983, Knapton 1984, Schadd and Ritchison 1998 and references therein) while, at the other extreme, Naef-Daenzer et al. (2000) suggested that Great Tits could maintain constant the number of visits per nestling, therefore proportionally increasing the number of visits as brood size increased. Agreeing with the general pattern, our results showed that adults worked harder when provisioning larger broods, but not enough to compensate for the increase in brood size, so nestlings received fewer visits when they were more numerous.

Four different hypotheses could contribute to explain the patterns of feeding frequencies per nest and per nestling. First, larger broods would have thermal benefits, the chicks conserving their heat more efficiently than those in small broods (Royama 1966), and needing therefore less energy. For example, Schadd and Ritchison (1998) did not find differences in feeding rates between small (2 chicks) and large (3-4 chicks) broods of Yellow-breasted Chats *Icteria virens*, and they used the thermal benefits of larger broods to explain this. Royama (1966) restricted this effect to relatively small broods (up to five nestlings; see also O'Connor 1975), so that thermal benefits would not be significant for larger broods. This would predict that, above five chicks, per-nestling feeding rates would keep more or less constant (i.e. not decreasing any further with increasing brood size). What we have observed is that feeding rates decreased linearly also among large brood sizes, so the "Royama effect" seemed to be unimportant to explain the patterns found in our population. Perhaps hotter temperatures in our study area (see Greño et al. 2008) as compared with those in England, where Royama (1966) performed his study on Great Tits, could explain this, but this effect has not been found in colder environments either (see Rytkönen et al. 1996).

Second, the Gibb-Lack hypothesis (Nur 1984a) suggests that there might be an upper limit to the effort that parents could make, so that broods above the modal size would receive less feeding trips per nestling. This predicts that total feeding rates would increase up to the modal brood size and then level off, while rates per nestling should remain constant up to the modal brood size and decline thereafter (see

Nur 1984a for a graphical interpretation). This is clearly not occurring at our population.

Third, Pettifor et al. (1988) suggested that each particular pair optimizes its brood size, so all the pairs are making the same relative effort independently of their actual brood size. Taking this into account, the pattern that should be observed is an increase of feeding rates proportional to the increase in brood size, so that feeding rates per nestling would be kept constant. This did not occur in our studied Great Tit population.

Finally, parents might be optimizing costs and benefits of feeding nestlings in the long term (Nur 1984a). This implies that parents would not be prone to increase their investment in the current brood above a certain level, even though they potentially could. This trade-off model predicts a continuous increase in per-brood and a continuous decrease in per-nestling effort with increasing brood size, perhaps levelling off at very large brood sizes (see also Rytkönen et al. 1996). Thus, our data seems to be consistent with Nur's (1984a) hypothesis. However, we did not detect the levelling off of the feeding frequency per nestling at large brood sizes, but the results presented by Nur (1984a) included experimentally enlarged broods, and perhaps this levelling off is harder to find in unmanipulated clutches. Nevertheless, experimental studies (e.g. Smith et al. 1988, Moreno et al. 1995, Rytkönen et al. 1996, Tinbergen and Verhulst 2000) would be needed to determine whether particular individuals would be willing to increase parental effort in response to brood size enlargement in our population (see Chapter VI).

Seasonal variation

Most studies to date have found a seasonal decline of feeding rates by Great Tits (Kluijver 1950, Gibb and Betts 1963, Royama 1966, Naef-Daenzer et al. 2000). We also found this general pattern, although the trend was only significant in one out of the three years studied.

We investigated potential causes of this seasonal pattern, and its variation among years, by considering whether other seasonally-related variables could produce it (brood size and temperature). It is obvious that changes in brood size could affect total feeding rates (see above), while an increase in ambient temperature could reduce energy needs. When considering these two variables, we found that the seasonal pattern in feeding rates was mostly explained by seasonal changes in brood size, i.e. total feeding rates decrease during the season because parents have fewer nestlings to feed as the season progresses. This is also consistent with our finding that feeding rates per nestling were constant throughout the season in our population.

Another potential cause of a seasonal decline in feeding rates is that, from the parental point of view, the fitness value of fledglings decrease during the season, so parents would be less likely to invest in them (e.g. Winkler 1987). However, this would clearly predict a seasonal decrease in per-nestling feeding rate, something that does not occur in our population. It should be considered that Monrós et al. (2002) found that late fledglings had good survival prospects in some years in our study site, so parents could keep constant their investment per nestling due to the uncertainties of the outcome in this habitat.

Finally, seasonal changes in prey type, abundance and size could affect feeding rates (Gibb 1950, Kluijver 1950). Gibb and Betts (1963) and Royama (1966) reported that the low feeding frequency in late broods resulted from an increase in the availability of large prey, mainly caterpillars (see Johnson and Best 1982). Naef-Daenzer and Keller (1999) made a more detailed analysis of how feeding rates in Great Tits varied seasonally with seasonal changes in caterpillar abundance and size. Nestling diet in our population was quite particular for Great Tits, since moths, and not caterpillars, form the bulk of the diet (Barba and Gil-Delgado 1990b, Barba et al. 2004). These authors found that the size of the moth species found in the nestling diet was smaller late in the season. Therefore, if changes in prey size were determining the seasonal pattern in feeding rates, we should expect a seasonal increase in per nestling feeding rates, which was not the case.

Diurnal variation

With 40 nests followed during a whole day, this is the most extensive study to date that deals with diurnal variation in feeding frequencies in Great Tits. The first attempts to describe diurnal variation in feeding frequencies in Great Tits produced very different results. Gibb (1955), for example, stated that "When all stages of all broods were lumped together, no rhythm was apparent …" (p. 54). However, when the early and late phases of the nesting period were analysed separately, he found that parents fed more often in the afternoon when nestlings were young, while the pattern later on was more variable, even feeding more frequently early in the morning in large broods. He thus identified two factors, nestling age and brood size, which might affect the diurnal rhythm of feeding visits (see also Gibb 1950). Other diurnal patterns might be found in old studies (e.g. Kluijver 1950, Eguchi 1980), but they also based their conclusions on few nests and they did not apply statistical analyses to their data. More recent studies including proper statistical tests (Cowie and Hinsley 1988, Moreno et al. 1995, Verhulst and Tinbergen 1997) have failed to find significant diurnal variation in the feeding rates. The same lack of diurnal variation has been found in Blue Tits *Cyanistes caeruleus* (Parejo and Danchin 2006) as well as in other species (e.g. Black-throated Blue Warblers *Dendroica caerulescens*; Goodbred and Holmes 1996). This constancy contrasts with what would be theoretically expected since several factors could cause diurnal variation in feeding rates (e.g. Gibb 1955, Stienen et al. 2000, Freitag et al. 2001, Rastogi et al. 2006; see Introduction).

Our first analysis aimed at detecting diurnal variation in feeding rate approached significance, especially when nestling age was considered. Differences seem to be caused by the increase of feeding rates from the first hours of the morning to mid-day in nests with the oldest nestlings. This result does not fit with any of the theoretical patterns presented above, and we have no explanation for it. We therefore conclude that in our study area Great Tits fed their nestlings at a constant rhythm throughout the day, independently, at least within the range of conditions explored, of variations in such factors as laying date, temperature, brood size and year. The potential effect of nestling age on diurnal patterns of feeding rates should be explored further.

As a final note, results presented here have been collected in a southern European population, and the patterns obtained have been compared with those of central and north European populations. It is not conclusive whether the differences found are related to the small sample sizes and/or lack of statistical tests of previous studies, or to actual differences between populations. Both temperatures and nestling diet are different in Sagunto compared with northern Great Tit populations. If parents could adjust their feeding patterns to these local conditions they might differ with location. Clearly to understand fully the provisioning patterns of Great Tits and other single prey loaders, studies similar to those described here should be conducted in central and north European populations and appropriate comparisons made.

VI

EVIDENCES FOR INDIVIDUAL OPTIMIZATION OF CLUTCH SIZE IN MEDITERRANEAN GREAT TITS

SUMMARY

Two main hypotheses have been formulated to explain the observed variation in clutch size among individuals, the Individual Optimization Hypothesis (IOH) and the Trade-Off Hypothesis (TOH). Most experimental brood size manipulation studies have supported the TOH. Based on life history theory, individuals from populations where adult survival is high would be expected to be less prone to incur in reproductive costs. We increased or decreased original brood sizes in a Mediterranean Great Tit (*Parus major*) population, where adult survival was known to be higher than in other populations, and analyzed its effects on several parameters. Adults did not increase their feeding effort in enlarged broods, but decreased it proportionally in reduced ones. Each nestling received fewer visits in enlarged than in control broods, and similar number of visits in reduced and control broods. Chicks from enlarged broods weighed marginally less than those from the other treatments. Males attending reduced broods were in better condition by the end of the nestling period than those from control or enlarged broods. Fledging success was similar among treatments, so more chicks fledged in enlarged broods. Estimated post-fledging survival probability was lower for enlarged broods. Finally, the estimated number of chicks to be recruited in the following season was slightly higher in control broods. Our results globally support IOH predictions, i.e. Mediterranean Great Tits seemed to be laying that clutch size which maximized the number of recruits. Adults were not prone to increase their effort beyond the necessary to feed brood sizes naturally produced.

RESUM

S'han formulat dos hipòtesis principals per tal d'explicar la variació observada en el tamany de posta entre individus, la Hipòtesi d'Optimització Individual (HOI) i la Hipòtesi del Trade-Off (HTO). La majoria d'estudis experimentals de manipulació del tamany de posta han recolzat la HTO. En base a la teoria de la història de vida, els individus de poblacions on la supervivència adulta es elevada, s'esperaria que foren menys predispostos a incòrrer en costos reproductius. Al present estudi, augmentàrem i reduïrem el tamany original de posta en una població Mediterrània de Mallerenga Carbonera Parus major, *on la supervivència adulta es sap que és major que la d'altres poblacions, analitzant els efectes de dita manipulació sobre diversos paràmetres. Els adults no augmentaren el seu esforç en*

postes augmentades, però ho disminuïren proporcionalment quan la posta fou reduïda. Cada poll de postes augmentades va rebre menys visites que aquells de postes control, mentre que en reduïdes i control, els polls reberen un nombre de visites semblant. Els polls de postes augmentades pesaren marginalment menys respecte a la resta de grups experimentals. Els mascles que atengueren postes reduïdes estigueren en millor condició que aquells de postes control o augmentades. L'èxit de vol fou semblant entre grups experimentals, volant més polls en postes augmentades. A més, la probabilitat de supervivència dels polls al eixir del niu fou menor en postes augmentades. Finalment, el nombre estimat de polls reclutats al següent període reproductor fou lleugerament major en postes control. Els nostres resultats recolzen globalment les prediccions de la HOI, és a dir, les Mallerengues Comunes al Mediterrani pareixien estar ponent un nombre d'ous en tal de maximitzar el nombre de polls reclutats. Els adults no estigueren predispostos a augmentar el seu esforç més del necessari a l'hora d'alimentar postes produïdes de manera natural.

INTRODUCTION

Clutch size varies between species as well as among individuals within species (Klomp 1970). Generally, those females naturally laying large clutches tend to be more successful, in terms of the number of offspring that survive to breed (recruits), than those laying smaller ones. Hence, why all the individuals of the same population do not lay large clutches? Two, not necessarily mutually exclusive hypotheses have been put forward to explain the observed variation in clutch size among individuals.

The Individual Optimization Hypothesis (IOH) of clutch size was derived from Lack's (1947) ideas by Perrins and Moss (1975). This hypothesis suggests that altricial birds lay the number of eggs that correspond to the maximum number of young they are able to feed adequately (Both 1998, Pettifor et al. 1988). Thus, females producing larger clutches than the average do so because their individual circumstances allow them to raise more young. On the other hand, the Trade-Off Hypothesis (TOH) states that parents might be optimizing the relationship between costs (reduction in parental survival and/or fecundity) and benefits (enhancing offspring survival) of feeding nestlings in the long term (Nur 1984a). The TOH predicts, unlike the IOH, that individuals would produce more recruits if they would have laid slightly more eggs than they actually do, though at the cost of reductions in future survival and/or fecundity of the parents.

Because of the covariance between clutch size and aspects of individual quality (Tinbergen and Verhulst 2000, and references therein), to test such hypotheses is essential to carry out brood size manipulations. These experiments allow seeing whether birds of the same "quality" (measured by their original clutch size), but then given different brood sizes to rear, experience differences in, for example, future fecundity or survival (Tinbergen 1987, Pettifor 1993) or ability to meet the food demands of their young (Pettifor 1993).

Predictions derived from brood size manipulations differ depending on the hypothesis. The IOH predicts that birds exposed to larger brood sizes than those naturally produced, independently of their size, would be unable to increase their total provisioning effort, i.e. enlarged and control broods would receive a similar amount of visits. Instead, parents would proportionally decrease their total provisioning effort in reduced broods. As a consequence, the amount of visits per nestling would be similar in reduced and control broods, and lower in enlarged broods (Fig. 6 in Nur 1984a), so mean fledgling weight would be lower in enlarged than in control or reduced broods. Thus, though an increase in the number of fledglings from reduced to enlarged broods would be expected, post-fledging survival probabilities would be expected to be lower in enlarged than in control or reduced broods. At the end, experimental addition or removal of chicks from nests would not result in the parents recruiting any more offspring than if they had reared their own original brood size (Pettifor et al. 2001). Finally, body condition of adults by the end of the nesting period would be expected to be similar in control and enlarged broods, and better in reduced broods.

On the other hand, the TOH predicts that total deliveries to the nest should increase in enlarged broods, since parents are not working at their maximum capacity. If this increase is enough to compensate for additional nestlings, feeding rate per nestling would be expected to keep constant from control to enlarged broods (Nur 1984a). If this is so, the TOH would predict similar nestling weight from reduced to enlarged broods, an increase in the number of fledglings from reduced to enlarged broods, and more recruits in enlarged broods. Finally, adults attending enlarged broods would be expected to end up the nesting period in a worse condition than controls.

Great Tits *Parus major* have been used as model species in several brood size experiments to test the above hypotheses (see Table VI.1 present study, Pettifor et al. 2001). Most studies found a cost over adults (e.g. weight loss, reduction of second clutches), or benefits (increment of recruitment rate in enlarged broods; see more in Tinbergen and Sanz 2004), thus supporting the TOH. In other studies, the lack of costs or benefits in reproduction supported the IOH (Both 1998, Pettifor et al. 2001). Other experimental studies, also shown in Table VI.1, were not explicitly designed to test these hypotheses so, though providing relevant information for some of the items dealt with here, no clear support for any hypothesis could be drawn. For instance, Verhulst and Tinbergen (1997) carried out brood size experiments, but only using two treatments, reduced and control broods.

How to allocate adult resources between themselves and their offspring may depend on the life-history strategy of the species or population (Stearns 1976). Individuals from populations whose survival to the next breeding season is high, would be expected to invest relatively less in the current breeding attempt. This, in the context of brood size manipulations, leads to avoid increases in adult investment in artificially enlarged broods (Stearns 1976). On the other hand, increments of investment by adults rearing enlarged broods would be expected if inter-annual adult survival was relatively low.

Our aim here was testing the IOH and the TOH in a Mediterranean Great Tit population where adult survival was relatively high compared with that of populations previously studied in central and northern Europe (Belda and Orell 2003). We predict that adults would be less prone to increase their investment in the current reproductive attempt, so we expect to find more evidences towards the IOH.

Table VI.1. An overview of the results in brood manipulation experiments in Great Tits. R = reduced, C = control and E = enlarged; m = male, f = female, 0 = not analyzed, Y = significant differences among treatments, N = non significant differences among treatments in the feeding frequency, nestling and adult weight. In the last column we shown which hypothesis (IOH: Individual Optimization Hypothesis or TOH: Trade-Off Hypothesis) is supported by the results of each study.

Taula VI.1. *Resum dels resultats en experiments fets a la Mallerenga Carbonera en els que el tamany de pollada ha sigut manipulat. R = reduït, C = control i E = augmentat; m = mascle, f = femella, 0 = no analitzat, Y = diferències significatives entre tipus de manipulació, N = sense diferències entre tipus de manipulació en la freqüència d'aprovisionament, pes dels polls i dels adults. A l'última columna es mostren les hipòtesi que recolzen cadascú dels estudis (HOI: Hipòtesi d'Optimització Individual o HTO: Hipòtesi del Trade-Off).*

	Feeding frequency		**Nestling weight**		**Adult weight**			
Authors	**R vs C**	**C vs E**	**R vs C**	**C vs E**	**R vs C**	**C vs E**	**Remarks**	**IOH, TOH**
Tinbergen 1987			Y	Y	N	N	Reduction second clutches	TOH
Smith et al. 1988	Y	N	0	0	Y	Y		TOH
Richner et al. 1995	N	Y (m)	0	0	0	0		?
	N	N (f)	0	0	0	0		
Verhulst and Tinbergen 1997	Y	0	0	0	N	0		?
Both 1998			N	N				IOH
Sanz and Tinbergen 1999	Y?	Y (C < E)	N	N	0	0	Recruitment rate positive to brood size	TOH
Tinbergen and Verhulst 2000	Y	N	Y?	Y	N	Y (m)	Reduction second clutches	TOH
	Y	N			Y	N (f)		
Rytkönen and Orell 2001	Y	Y (C > E)	Y	N	?	N		?
Neuenschwander et al. 2003	Y	N	N	Y	0	0		IOH

METHODS

Data used in the present study were collected during 1996 in a Mediterranean Great Tit population located in an extensive orange plantation in Sagunto, eastern Spain (39º 42’ N, 0º 15’ W, 30 m a.s.l.). Nest boxes were visited regularly from nest building to fledging to determine laying date, clutch size, hatching date and number of fledglings (more details in Barba et al. 1993, 2009).

For the experiments, nests were randomly selected to become reduced, control or enlarged, with similar initial clutch size (maximum difference of one egg) and hatching date (maximum difference of one day; Table VI.2). The day after hatching we took two newly hatched chicks from some nests (reduced group, n = 11 nests) and added them to other nests (enlarged group, n = 11 nests), while leaving a third group as control (n = 11 nests). Some nests failed by desertion or predation along the nesting period, so sample size could vary in different analyses. The number of fledglings was squared-root transformed for the analyses.

Nestlings were weighed (using a Pesola spring balance), and their tarsus length measured (using a calliper: ± 0.01 mm), when they were 15 days-old. As a simple estimate of body condition at day 15, the ratio of body weight to tarsus length was used. Within the same nest, measurements over chicks were averaged to obtain one measure per trait per nest. Adults were trapped whilst they were feeding 12-14 day-old nestlings, weighed, their tarsus length measured, and their body condition calculated.

Firstly, we analyzed the probabilities of survival for both adults (reduced *n* = 12 [4 recaptured], control *n* = 19 [12 recaptured] and enlarged *n* = 18 [10 recaptured]) and nestlings (reduced *n* = 34 [3 recaptured], control *n* = 63 [1 recaptured] and enlarged *n* = 54 [2 recaptured]). These data were analysed using capture-recapture methods derived from the CJS model (e.g. Lebreton et al. 1992). The best model that fitted the data in both cases (adults and fledglings) was a model without differences among treatments. These results are probably due to the low sample size. Therefore, we decided not to show these results. Secondly, Greño et al. (2008) found that nestling weight and temperatures during the nestling period affected post-fledging survival probability in this Great Tit population. Hence, we estimated the survival probability of each fledgling taking into account these two variables and using the formula: $\text{logit}\ \Phi = 1.96 - 0.38 \cdot T_{min} + 0.25 \cdot \text{weight}$. Daily temperatures were obtained from the Meteorological Station "El Pontazgo", close to the study area. For each nest, average minimum ambient temperature was calculated during the first 15 d after hatching. To estimate the number of chicks recruited by each pair in the following season, we multiplied mean post-fledging survival probability by the number of chicks fledged.

Total feeding frequency (total number of visits per hour) was assessed using mechanical counters placed at the nest box entrance

(Gibb 1955, Barba et al. 2009) when chicks were 11-15 days-old. In nests where the feeding frequency was measured more than once within this range, we used the mean for analyses (Barba et al. 2009). We defined a sample as the record of the feeding frequency during at least 2 hours (mean number of hours per nest: 10.17 ± 0.24 h; range 2.05 to 29.35 h; only daylight hours considered). In cases where a counter was operating overnight, we computed as "valid" the number of hours of daylight, using official sunset and sunrise times, and feeding frequency was assigned to the day with more working hours. In a previous study (Barba et al. 2009), we found that the feeding frequency did not vary significantly with time of day, so this variable was not taken into account.

GLMs were carried out throughout study to look for possible effects of brood manipulations over some traits measured. Tukey HSD *post hoc* tests were used to test for differences among categories in within-subject factors. Mean ± *SE* are shown when needed. Analyses were carried out using SPSS 15.0 (SPSS Inc. 2006).

Table VI.2. Mean brood size before and after manipulation, and hatching date among reduced, control, and enlarged broods (*n* = 11 in each case). Mean ± *SE* is showed.

Taula VI.2. *Tamany promig de pollada abans i després de la manipulació i, data d'eclosió dels ous entre pollades reduïdes, control i augmentades (n = 11 per a cada cas). Es mostren les mitges ± ES.*

Factor	Reduced	Control	Enlarged	P-value
Initial brood size	7.00 ± 0.44	6.70 ± 0.47	7.00 ± 0.33	0.841
Final brood size	5.00 ± 0.44	6.70 ± 0.47	9.00 ± 0.33	< 0.001
Hatching date	34.71 ± 1.41	34.50 ± 1.33	35.00 ± 1.58	0.969

RESULTS

Both hatching date and brood size were similar among treatments before manipulation (Table VI.2). Switching of newly hatched nestlings produced the desired effect of reduced broods having fewer nestlings, and enlarged broods more nestlings than controls (Tukey *post hoc* tests, $P < 0.05$ in all cases).

Feeding frequency when nestlings had 11-15 days-old varied among treatments ($F_{2,22} = 6.00$, $P = 0.008$). Parents feeding reduced broods showed lower feeding rates than controls (Tukey *post hoc* test, P

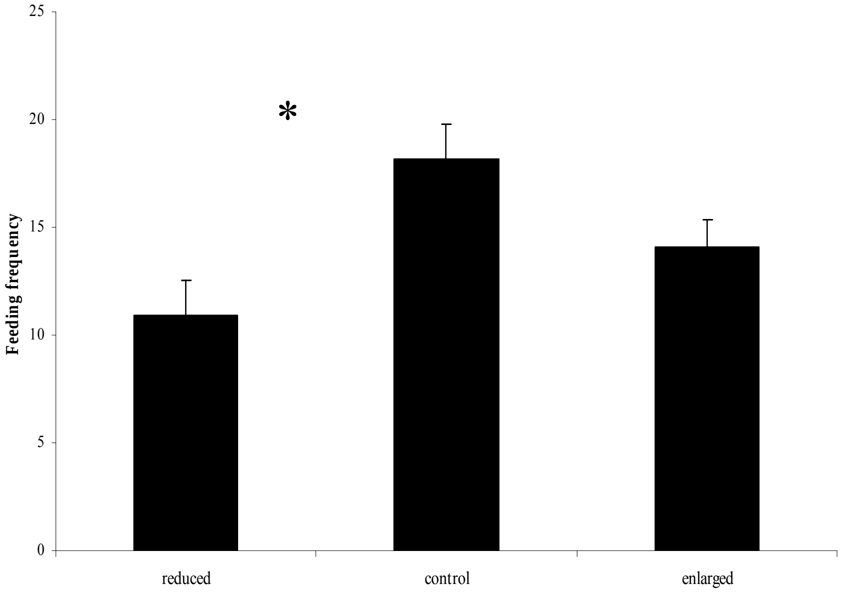


Figure VI.1. Mean feeding frequency (± *SE*, number of visits per hour) in relation to brood size manipulation treatment. The asterisk indicates differences among treatments.

Figura VI.1. *Freqüència d'aprovisionament promig (± ES, nombre de visites per hora) en relació al tipus de manipulació del tamany de pollada. L'asterisc assenyala les diferències entre tipus de manipulació.*

= 0.007), while parents from enlarged broods did not increase their feeding rates relative to controls (Tukey *post hoc* test, P = 0.135, Fig. VI.1).

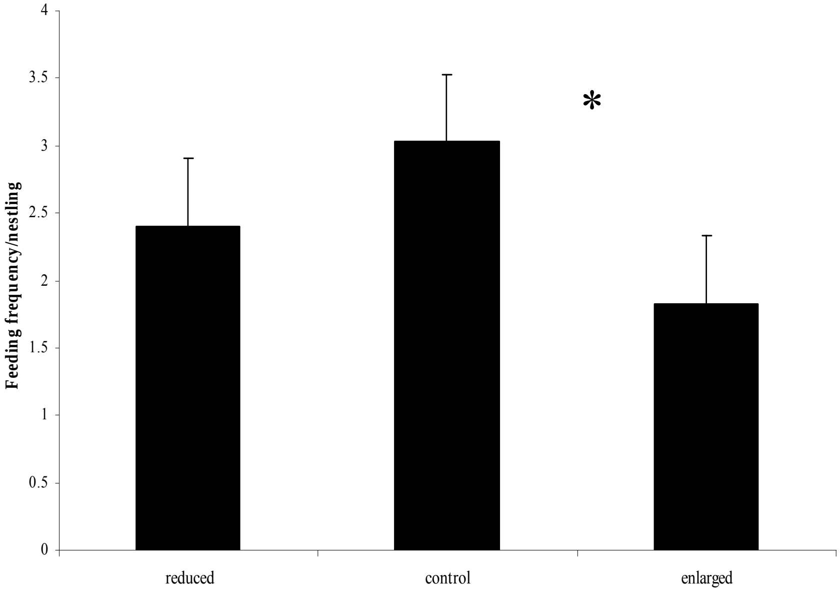


Figure VI.2. Mean feeding frequency per nestling (± *SE*, number of visits per hour per chick) in relation to brood size manipulation treatment. The asterisk indicates differences among treatments.

Figura VI.2. *Freqüència d'aprovisionament per poll promig (± ES, nombre de visites per hora per poll) en relació al tipus de manipulació del tamany de pollada. L'asterisc indica les diferències entre tipus de manipulació.*

This different response was mirrored on the number of visits each nestling received ($F_{2,22}$ = 3.51, P = 0.047). Each nestling belonging to enlarged broods received fewer visits than control broods (Tukey *post hoc* test, P = 0.038; Fig. VI.2). On the other hand, parents from reduced broods seemed to decrease their total effort proportionally to brood size: we did not find statistical differences in the amount of visits received by nestlings in control and reduced broods (Tukey *post hoc* test, $P = 0.399$).

Nestling weight at day 15 was affected by the treatment ($F_{2,22} = 3.73$, $P = 0.041$). *A posteriori* tests showed that chicks from enlarged broods were lighter (14.57 ± 0.83 g) than those of control broods (16.53 ± 0.36 g), though differences were only marginally significant (Tukey *post hoc* test, $P = 0.053$). There were no differences between reduced (16.52 ± 0.55 g) and control broods (Tukey *post hoc* test, $P = 0.999$). On the other hand, nestling body condition did not differ significantly among treatments ($F_{2,22} = 3.20$, $P = 0.062$), although it was poorer for nestlings of enlarged broods (0.76 ± 0.04) than for nestlings from control (0.83 ± 0.02) or reduced broods (0.84 ± 0.02).

Fledging success (ratio between fledglings and hatchlings) was similar among treatments (0.89-0.96; $F_{2,22} = 1.08$, $P = 0.358$). Therefore, the number of chicks fledged successfully increased from reduced to enlarged broods (reduced 4.86 ± 0.40, control 6.40 ± 0.48, enlarged 8.13 ± 0.40, $F_{2,22} = 12.61$, $P < 0.001$). Differences among treatments were all significant (Tukey *post hoc* tests, $P < 0.001$). There were differences in the estimated post-fledging survival probability among treatments ($F_{2,22} = 4.84$, $P = 0.018$, Fig. VI.3). Survival probability was lower for fledglings from enlarged broods than those from controls (Tukey *post hoc* tests, $P = 0.028$), while there were no differences in the estimated post-fledging survival probability between control and reduced broods (Tukey *post hoc* tests, P = 0.997). Finally, the estimated number of chicks to be recruited in the following season was higher in control (0.73 ± 0.06) than in reduced (0.55 ± 0.08) and enlarged broods (0.65 ± 0.23), although these differences were not significant ($F_{2,22}$ = 1.55, P = 0.234).

No effects of treatments were observed on female condition or weight (P > 0.05). Instead, differences in male body condition were detected ($F_{2,17}$ = 4.34, P = 0.030), males rearing reduced broods ending

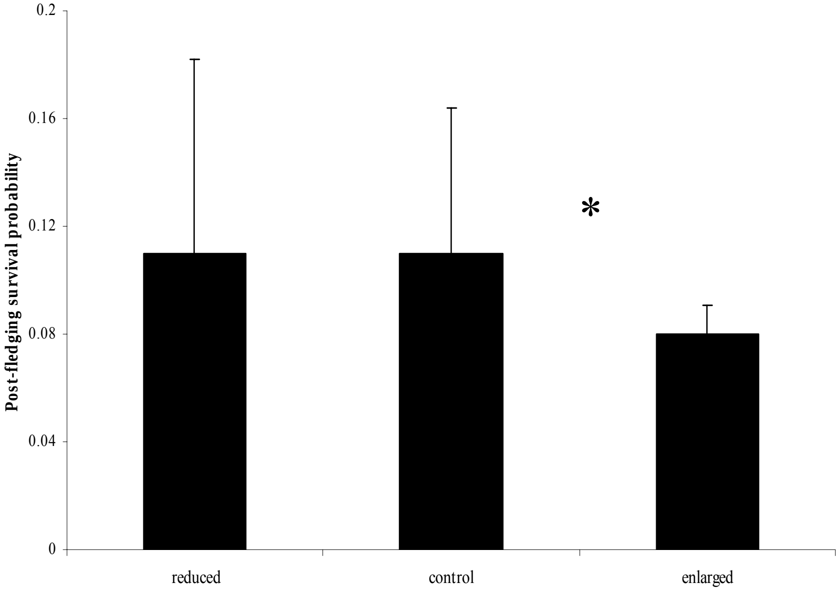


Figure VI.3. Post-fledging survival probability in relation to the brood size manipulation. The asterisk indicates differences among treatments.

Figura VI.3. *Probabilitat de supervivència dels polls al abandonar el niu en relació al tipus de manipulació del tamany de pollada. L'asterisc indica les diferències entre tipus de manipulació.*

up in better condition than those rearing control broods (Tukey *post hoc* tests, *P* = 0.025; Fig. VI.4). Males from control and enlarged broods showed similar body condition (Tukey *post hoc* tests, *P* = 0.779). Males showed similar weight among treatments (*P* > 0.05).

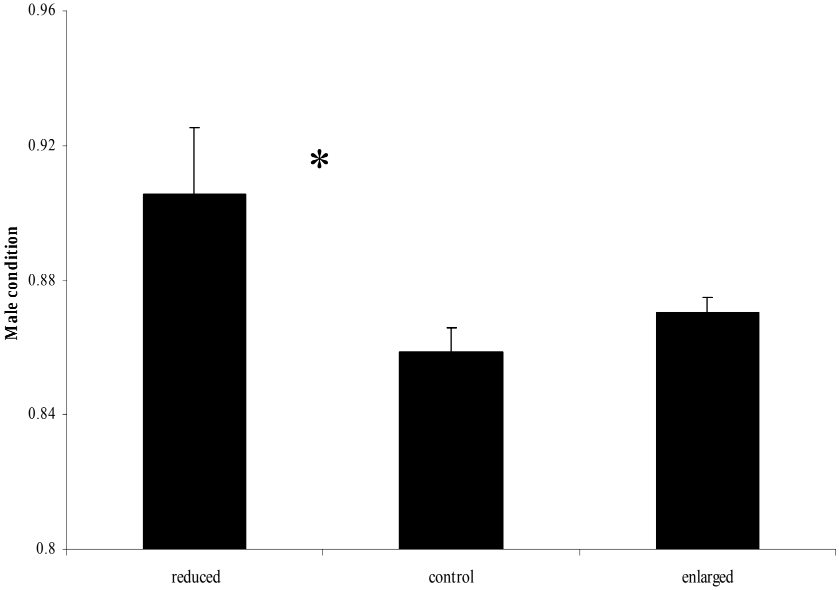


Figure VI.4. Male body condition in relation to brood size manipulation. The asterisk indicates differences among treatments.

Figura VI.4. *Condició corporal dels mascles en relació al tipus de manipulació del tamany de pollada. L'asterisc indica les diferències entre tipus de manipulació.*

DISCUSSION

Here, we analyzed whether Mediterranean Great Tits were optimizing clutch size. Adults seemed to be laying a clutch size that corresponded with the largest number of young that parents could feed successfully, maximizing the number of offspring recruited: adding or removing young did not increase parental fitness. Findings showed in the present study supported the IOH predictions.

Feeding frequency

In natural brood sizes, feeding frequency is in general positively related to brood size (Nur 1984a, Barba et al. 2009). In experimentally altered broods, the general pattern found in Great Tits (see Table VI.1) and in other species (Tree Swallow *Tachycineta bicolor* in Leffelaar and Robertson 1986, Pied Flycatcher *Ficedula hypoleuca* in Sanz 2001b) was a decrease of feeding frequency in reduced broods and a lack of increase in enlarged ones. This is what we found in our studied population. A possibility explaining such pattern is that adults changed to more profitable prey when feeding enlarged broods (Wright and Cuthill 1990, Moreno et al. 1995), so chicks would receive more food without increments in the feeding rates. However, Arteaga et al. (2000) showed that prey types did not vary among control and artificially altered brood sizes in this population, so we think that changes in prey type were unlikely. On the other hand, adults have been also found to respond to brood manipulation in other ways. For example, when brood size has been experimentally enlarged, adults have been found to increase (Sanz and Tinbergen 1999) or decrease their feeding rates (Rytkönen and Orell 2001). Such results suggest that different populations of the same species responded in a different way to a similar brood size manipulation.

Only two studies have analyzed the effects of brood size manipulations from the nestlings' point of view in Great Tits (Sanz and Tinbergen 1999, Neuenschwander et al. 2003). Both of them concluded that the amount of visits that each nestling received was independent of the treatment (see also Moreno et al. 1995 in Pied Flycatchers, Parejo and Danchin 2006 in Blue Tits *Cyanistes caeruleus*). This agreed with the significant increase in feeding rates for enlarged broods (Sanz and Tinbergen 1999). This was also argued by Neuenschwander et al. (2003), who said that adults compensated for the increase in brood size. But in this case, this was very weakly supported by the data (see their Table 3), since there was not a significant increase of total feeding rates in enlarged broods compared to controls. In the present study, each nestling from enlarged broods received fewer visits than those from control broods, i.e. adults did not respond to the enlargement of brood size. This result has been also found in other species [Starlings *Sturnus vulgaris* (Wright and Cuthill 1990), Eastern Kingbirds *Tyrannus tyrannus* (Maigret and Murphy 1997)]. On the other hand, parents rearing reduced broods decreased their feeding frequency proportionally, so each nestling received a similar number of visits than nestlings reared in control nests [see Smith et al. (1988) for similar results in other Great Tit population].

Effects of brood size manipulations on offspring and on parents

Mean fledgling weight has been found to be lower in enlarged broods in Great Tits (Pettifor et al. 2001, see Table VI.1) and in other species as Blue Tits (Nur 1984b), Starlings (Wright and Cuthill 1990), Barn Owls (*Tyto alba*, Roulin et al. 1999) and Tree Swallows (Burnes et al. 2000). This was also the result obtained here, which presumably is a direct consequence of each nestling receiving less food. Neuenschwander et al. (2003) suggested that the lower nestling condition in enlarged broods could be a consequence of the increased energetic costs of begging and food solicitation behaviour in such broods, and this might contribute to make the nestling condition worse. In other cases, there was no effect over nestling weight in enlarged broods. The ability of adults to increase their effort in such broods in comparison to control broods may explain those results (Sanz and Tinbergen 1999).

The effects of brood size over nestling weight may be translated into survival prospects (Perrins 1965, Both 1998, Greño et al. 2008), and therefore, to recruitment rates (average number of offspring recruited per nest, Pettifor et al. 1988). Few experimental brood size studies have measured or even estimated the number of young subsequently recruited into the breeding population. The main finding was a similar recruitment rate between control and enlarged broods (Both 1998, Tinbergen and Both 1999, Hõrak 2003, Parejo and Dachin 2006), and less often an increase (Sanz and Tinbergen 1999) or a decrease in recruitment rate (Pettifor et al. 1988, 2001). The weight of the nestlings when leaving the nest was usually assumed to be the major cause of differences in survival. Thus, recruitment rate would be higher in enlarged broods if chicks from enlarged and control broods had similar fledging weight (Nur 1984b, Sanz and Tinbergen 1999), while lower recruitment in enlarged broods would be found if fledging weight in enlarged broods was lower (Pettifor et al. 2001). Based on fledging weight and conditions (temperature) during growth, we estimated that fledglings from enlarged broods had lower survival prospects than those from reduced or control broods. Based on both the number of fledglings and post-fledging survival prospects, the estimated recruitment per nest would tend to be maximized by those birds rearing control broods.

Artificial changes in brood sizes may also affect adult condition (see Table VI.1). Although studies in which the consequences of brood manipulations on adult body mass have been performed, their results were not conclusive, since either adults from reduced or from enlarged broods showed similar weight [Barn Swallows *Hirundo rustica* (Jones 1987), Great Tits (Tinbergen 1987), Barn Owls (Roulin et al. 1999)]. The loss of adult weight is known to be proportional to the feeding frequency (Smith et al. 1988). Hence, the lack of variation in adult weight found here among treatments is consistent with the lack of increment in feeding frequency in enlarged broods. Also, it would be expected that adults from reduced broods weighed more than those from controls (see Smith et al. 1988), but we did not find such a difference (see also Verhulst and Tinbergen 1997). However, males ended up in better condition rearing reduced broods. Although with the methodology used for the present study we were unable to distinguish between male and female feeding rates, results on male body condition suggest that males tended to reduce proportionally more than females their contribution when feeding reduced broods.

Optimization of reproductive effort?

Two hypotheses have been proposed to explain the observed variation in clutch size among individuals, the IOH and the TOH. Since they were put forward, substantial debate exists over the extent to which parental behaviour and reproductive effort are or not individually optimized (Maigret and Murphy 1997, Pettifor et al. 2001). According to this, studies have, sometimes, supported the TOH based on the effects of brood size manipulation on the production of second clutches or on recruitment rate (see Table VI.1 and references above), despite some other results were contradictory to predictions from the TOH (e.g. lack of loss of adult weight and increase in feeding frequency for enlarged broods; Tinbergen 1981, Tinbergen and Verhulst 2000). In other cases, studies did not test several predictions (e.g. responses related to feeding effort, feeding effort per chick, nestling and adult weight) simultaneously or, if they did, results were not conclusive (see Maigret and Murphy 1997) or they were inadequate tests to support any hypotheses (see review in Pettifor et al. 2001).

The IOH predicts a parental inability to feed larger broods than naturally produced, and therefore a reduction in the survival of offspring in such broods. Instead, the TOH predicts no upper bound to the ability of parents to successfully rear broods larger than naturally produced. Thus, it would be expected an increase in the recruitment rate. What we found here was an inability of parents to increase their effort in experimentally enlarged broods, and higher post-fledging survival prospects in control broods. Therefore, it seems that, in the studied population, adults would be laying a clutch size that corresponded with the largest number of young for which parents can provide enough food, maximizing the number of chicks recruited. Our results would be in accordance with the life-history of our studied tit population – a higher inter-annual adult survival probability would select for individuals which limit current reproductive investment. Evidences showed would be globally in accordance with the IOH predictions, though we are aware that actual recruitment rate was not measured (see Pettifor et al. 2001). Instead, we were unable to establish an intra-generational cost of reproduction (e.g. adult weight) as predicted by TOH (see Introduction).

At least two reasons may be behind our results. First, the willingness to increase the investment in the current reproductive attempt might vary with the particular ecological circumstances, and especially with adult survival prospects found in our studied population. High adult survival would make adults to be more reluctant to increase their investment in enlarged broods. Second, adults may be already feeding at their maximum capacity, with no further resources left for any extra effort (Tinbergen and Verhulst 2000). Nevertheless, parental effort includes resources allocated to other forms of parental care such as brooding or nest defence. One approach to this problem is quantifying parental effort in terms of parental energy expenditure (Sanz and Tinbergen 1999). We did not measure it, so we can not distinguish whether the lack of increase in feeding frequency was a "strategic decision" (i.e. benefits of investing more would be lower than costs), or simply a physiological inability to do it (i.e. an "energetic ceiling" *sensu* Tinbergen and Verhulst 2000).

VII

EFFECTS OF HABITAT STRUCTURE AND COMPOSITION OVER GREAT TIT BREEDING TRAITS

SUMMARY

Forest type and habitat structure can have profound effects on different aspects of avian life-histories. These effects may, however, strongly differ across and within forests that vary in vegetation composition and/or structure, especially when the ancient forest has been replaced by a different one. To test for these differences in effect, we studied Great Tit *Parus major* life-history traits (280 first clutches) during 2005-2007 in two Mediterranean evergreen forests, an ancient Holm Oak *Quercus ilex* and a reforested pine forest. A comparison between forests revealed that, females breeding in the Holm Oak started laying one week later, and produced larger clutches and broods both at hatching and fledging. Chicks raised in the Holm Oak forest fledged in better condition than in the pine forest. Within forests, however, the reproductive success of pairs breeding in nest boxes surrounded by Holm Oaks within the pine forest was not higher than that of pairs breeding in nest boxes surrounded by pine trees in the Holm Oak forest and *vice versa*. Instead, the maturity of the vegetation patch, rather than tree species composition, affected hatching success, which was, surprisingly, higher in patches with immature vegetation. This may be due to a lower nest predation. Different factors seem to be operating across forests (food availability) and within a forest (nest predation), explaining part of the variation in breeding success in Mediterranean Great Tits.

RESUM

Tant el tipus de bosc com l'estructura de la vegetació del mateix poden tindre efectes importants sobre diferents aspectes del cicle vital de les aus. Dits efectes podrien, en canvi, diferir entre boscos així com dins d'un mateix bosc que varien en la composició i/o estructura de la vegetació, especialment quan el bosc original ha sigut substituït per uno diferent. Per testar dites diferències, nosaltres vàrem estudiar aspectes del cilce vital de la Mallerenga Carbonera Parus major *(280 primeres postes) durant 2005-2007 en dos boscos mediterranis perennifolis, un Carrascar* Quercus ilex *(bosc original) i un bosc repoblat de pins. La comparació entre boscos va revelar que, les femelles que es reproduïren al Carrascar començaren a pondre ous una setmana més tard, el tamany de posta i el nombre d'ous eclosionats així com el nombre de polls que abandonaren el niu fou major. Els polls nascuts al Carrascar isqueren del niu en millors condicions que aquells nascuts al pinar. Dins*

de cada bosc, en canvi, l'èxit reproductor no fou major per aquelles parelles de mallerenga que es reproduiren en caixes niu envoltades per Carrasques dins del bosc de pins o viceversa. *Per altra banda, la maduresa de la vegetació del territori més que el tipus d'espècie d'arbre, afectà a l'èxit d'eclosió, que fou sorprenentment major en territoris amb vegetació inmadura. Això fou degut a una menor taxa de predació de nius en dits territoris. Pareix que diferents factors estan actuant entre boscos (disponibilitat d'aliment) i dins d'un mateix bosc (predació de nius), explicant part de l'èxit reproductor en Mallerengues Comunes al Mediterrani.*

INTRODUCTION

Many environmental and anthropogenic factors contribute to habitat heterogeneity in the Mediterranean region, among which are altitude, slope, forest management of the forests and land-use practises (Blondel and Aronson 1999). A clear example comes from reforestations of *Pinus* sp. plantations, which represent a new habitat in south-eastern Iberian Peninsula (Maícas and Fernández 2004). These plantations have replaced most of the ancient Holm Oak *Quercus ilex* forests (Tremblay et al. 2003), and this transformation of the native forest may have had evolutionary consequences for forest bird populations (Smith et al. 2008). Because tree species composition has been regarded as the main parameter influencing forest bird life-histories, comparing breeding traits among different types of forests may provide insight into how birds would respond to local conditions (e.g. in remnant Holm Oak patches within the pine forests), and what factors (e.g. differences in food availability) might affect to breeding traits (see Blondel et al. 1993, Lambrechts et al. 2004).

Vegetation structure (e.g. variation in density and age of the trees, presence and development of the shrub layer, etc.), on the other hand, promotes small-scale heterogeneity, which is sometimes enhanced by human activities (e.g. silvicultural practices for preventing forest fires; Baeza et al. 2003). Differences in vegetation structure might cause differences in breeding parameters among individuals nesting relatively close to each other (Dhondt et al. 1992, Enoksson et al. 1995, Arriero et al. 2006) or in the efficiency of predators searching for nests (Davis 2005). For example, among forest birds, those breeding in areas with mature vegetation within a forest usually show higher reproductive output than those nesting in young vegetation patches, so mature vegetation patches are considered of higher quality for birds (Riddington and Gosler 1995, Hinsley et al. 2002, Arriero et al. 2006).

Therefore, the analyses of both tree composition and vegetation structure are important to understand the processes underlying how birds behave in a structured landscape, especially when floristic composition is not homogeneous and the ancient forest has been replaced by a different one. Habitat structure takes on greater importance in managed forests, where management practices may accentuate variation among nearby areas with similar natural characteristics, enhancing, for instance, predation risk (Thompson 2007) or reducing food availability (Arriero et al. 2006). Hence, knowledge of the influence of tree composition and habitat structure on life-history traits in birds must be considered by managers to design effective conservation, management and reforestation plans (Lusk et al. 2003, Quevedo et al. 2006).

The Great Tit *Parus major* is a generalist species that readily accepts artificial nest boxes and breeds in many forest types (Cramp and Perrins 1993). Different reproductive traits have been shown to vary among forest types (e.g. van Balen 1973, Riddington and Gosler

1995, Sanz 1998). Moreover, it is also known that, among tits (*Paridae*), small changes in habitat structure can have profound effects on reproduction and condition (Otter et al. 2007, Wilkin et al. 2007), making this species a good model for evaluating the extent to which reproductive traits are affected by habitat features (e.g. Sánchez et al. 2007, Wilkin et al. 2007). The effects of forest type on breeding traits are known since a long time for this species. However, most of these studies have compared deciduous (food-rich forests) and evergreen forests (poor-food forests). Additionally, studies that combine forest type and vegetation structure appear to be less common in the literature (but see Tarvin and Garvin 2002, Fort and Otter 2004, Díaz 2006).

We aimed to study the effect of habitat on Great Tit reproductive parameters at two levels, across forests (different forest types) and within a forest (considering habitat structure and tree composition around nest boxes). Thus, we selected two forests representing two different forest types: a Holm Oak forest, an example of the ancient forest of the Mediterranean region, and a pine forest, an example of relatively new reforested areas, both located at the same latitude.

METHODS

Study area

The study was conducted in two natural parks, Sierra Mariola (38º 44’ N, 0º 33’ W, 900 m a.s.l.) and Font Roja (38º 39’ N, 0º 32’ W, 1090 m a.s.l.) in eastern Spain. The distance between these areas is about 8 km. Despite the short distance, vegetation composition and climatic conditions are different because of differences in altitude, orography and mountain orientation. For instance, based on available temperatures gathered from a meteorological station located within Font Roja and, from another meteorological station 4 km far from Sierra Mariola, mean maximum temperature during June was 3.5 ºC lower in Font Roja.

In both forests, human activity has created a vegetation structure mainly characterized by regeneration of stands of even age. From March to July during three breeding seasons (2005 to 2007), a total of 110-121 nest boxes in Sierra Mariola and 118-140 in Font Roja were checked. All nest boxes were located using a geographic positioning system (Garmin 12).

Habitat features

Sierra Mariola is a pine forest product of the replacement of the former vegetation (scrub vegetation and Holm Oak forests). This forest and surroundings have been profoundly modified by shepherding and forest fires, being human clearing practises going on to date. Young trees and open areas are quite common. The tree layer around nest boxes was composed almost exclusively of Aleppo (the most abundant species), Umbrella and Maritime Pines (*Pinus halepensis*, *P. pinea* and *P. pinaster* respectively). Isolated patches of Holm Oaks are also present. Up to 20 different species were identified in the shrub layer (up to 3 m in height) with young Aleppo Pine stands being the most abundant species. Other abundant shrub species were Prickly Junipers *Juniperus oxycedrus* and Kermes Oaks *Quercus coccifera*. Shrubs were included in our study because many birds were observed foraging on them (pers. obs.) and thus can be considered as a secondary habitat for tits (Díaz et al. 1998).

Font Roja is an evergreen Holm Oak forest, a remnant of the ancient forest which covered vast extensions in the south-eastern Iberian Peninsula. In particular, this forest has been exploited for centuries to extract firewood and charcoal. The Holm Oak is the most abundant species followed by the far less common Aleppo Pine at the altitude where nest boxes were placed. Deciduous trees, the most representative being Flowering Ashes *Fraxinus ornus* and Portuguese Oaks *Quercus faginea*, are also found, though they are quite isolated and thus do not form clear "deciduous patches". Understorey was mainly composed by Laurustinus *Viburnum tinus*.

Vegetation cover and species composition were quantified by performing three 50-m line intercept transects starting from each nest box. For each transect, we measured the cover of both trees (more than 3 m in height) and shrubs (range 0.5-3 meters) for those that intercepted the line (see Elzinga et al. 2001, Hill et al. 2005 for further information). Vegetation under 0.5 m was not considered. The direction of transects from the nest box was chosen at random, though we did require that each transect differ by at least 45º from the adjacent one; angles were measured with a compass. Transects were performed throughout the year (2006-2007), but in the Holm Oak forest the sampling was done in spring and summer to allow easy identification of deciduous species. We considered that vegetation structure did not differ appreciably during the study period.

Additionally, sampling plots of 25-m radius centered at each nest box were established to measure the average diameter of the five thickest trunks measured at breast height (dbh; using a 1-m metric tape), and the number of young (5-10 cm dbh) and old trees (> 30 cm dbh; Arriero and Fargallo 2006) classified by eye after previous training. To increase the accuracy of the count of the trees, the 25-m radius circle created around each nest box was split into four sections.

Vegetation was sampled from all nest boxes in the pine forest but only from 116 (83% of the maximum number present) in the Holm Oak forest; the remaining boxes were excluded because the slope was too steep to safely sample vegetation. These amount of nest boxes were also used in the Chapters VIII and IX. All vegetation measurements were made by F. Atiénzar.

GIS-procedure and vegetation gradient

We used ARCGIS spatial analyst version 9.1 for processing vegetation data. Transect data were georeferenced in a Transverse Mercator Complex WG1984, Complex UTM-Zone 30 N coordinate system. From each transect, we calculated the spatial distribution of several tree species and shrubs with Inverse Distance Weighted (IDW) interpolation techniques (Wilkin et al. 2007). This method estimates cell values by averaging the values of sample data points in the vicinity of each cell. The closer a point is to the center of the cell being estimated, the more influence, or weight, it has in the averaging process. Thus, a complete vegetation map of each forest was generated.

Finally, after creating three different buffers around each nest box (25, 50 and 75-m radius), we estimated different vegetation parameters (tree species, tree and shrub cover) for each one with a specially written program that uses an overlapping zonal statistical technique (see Appendix). This method examines environmental variation within search buffers formed with fixed and predetermined radii around each breeding location. A clear advantage of this approach is the ability to examine environmental variation over a range of spatial scales by altering the radius of the search buffers (see Wilkin et al. 2007). The maximum distance around each nest box (75 m) was selected to be biologically meaningful for breeding traits such as laying date (Wilkin et al. 2007) and because it is within the range of the foraging area for Great Tits (Naef-Daenzer 2000).

As variables describing habitat structure were highly correlated, principal component analyses (PCA) were run to obtain a single factor that summarized habitat structure (see González 2003) for each buffer (25, 50 and 75 m). The first principal component (PC1) defined a gradient of vegetation maturity (or age) patch around nest boxes (Table VII.1). PC1 correlated significantly with all variables (except for the percentage of tree cover in the 25-m radius).

Table VII.1. Results of principal component analyses with the variables measured at 25, 50 and 75 m. Variables measured within 75 m for PC1 and correlated negatively they did positively for 25 and 50 m instead. Significant correlations among the variables describing habitat structure and the factor are shown in bold.

Taula VII.1. *Resultats de l'anàlisi de components principals amb les variables mesurades als 25, 50 i 75 m. Dites variables dins dels 75 m per al CP1 i correl.lacionades negativament, ho feren en canvi positivament per a 25 i 50 m. Els valors significatius per a cadascú dels dos primers components es mostren en negreta.*

	25 m		50 m		75 m	
	PC1	PC2	PC1	PC2	PC1	PC2
Nº trunks 5-10 cm	**-0.64**	-0.06	**-0.67**	**0.12**	**0.68**	**0.47**
Nº trunks > 30 cm	**0.84**	**0.24**	**0.83**	**0.18**	**-0.81**	**0.44**
Mean diameter 5 thickest trees	**0.87**	**0.16**	**0.86**	**0.14**	**-0.84**	**0.39**
Shrub cover (%)	**-0.59**	**0.57**	**-0.64**	**0.54**	**0.65**	**0.22**
Tree cover (%)	0.04	**-0.89**	**-0.18**	**-0.86**	**0.38**	**0.59**
Eigenvalue	2.21	1.19	2.30	1.09	2.40	1.03
% variance accounted for	44.30	23.90	46.10	21.80	47.90	19.20

Mature vegetation in breeding territories were characterized by a greater number of large trunks (diameter larger than 30 cm), while immature vegetation in breeding territories were characterized by high number of young trees with a well developed tree and shrub cover. Positive loadings values of PC1 corresponded to more mature habitat for 25 and 50-m radii, while lower loadings values of PC1 corresponded to more mature vegetation in breeding territories within a 75-m radius around nest boxes. Based on a broken stick analysis (Jackson 1993), PC2 should be also considered here. This variable was mainly related with tree and shrub cover (see Table VII.1). All the analyses performed with PC1 were repeated with PC2, but none of the results for PC2 were significant and are not presented here.

Breeding parameters

Nest boxes were visited once per week, and active nests were visited with a pattern that allowed us to assess laying date (assuming that one egg was laid per day; 1 = 1 April), clutch size, and hatching date (with visits every day or every other day around the expected hatching date). As many adults as possible were trapped whilst feeding 11-15 day-old nestlings (hatching date = day 0) using door traps and/or mistnets. Adults caught were sexed, aged (classifying them into yearlings or older birds using plumage characteristics; Svensson 1992), weighed (using an electronic balance; ± 0.1 g), and their tarsus length measured (using a digital calliper; ± 0.01 mm). As a simple estimate of body condition, the ratio of body weight to tarsus length was used, because body mass scaled linearly to tarsus length ($r = 0.18$, $F_{1,156} = 5.66$, $P = 0.019$). Each adult bird was marked with an individually numbered aluminium ring and colour rings. Some adults that could not be trapped in a particular year could be identified at their nests by reading previously fitted colour rings using binoculars.

For nestlings, tarsus length and weight were measured, and body condition estimated, at day 14. To avoid pseudoreplication, measurements of nestlings from the same nest were averaged to obtain a single value per trait per nest (Eddison 2000), so the statistical unit is the brood. Male characteristics were initially considered in the analyses but, as no explored relationship was significant, results concerning them are not presented.

Failed nests were those in which at least one egg was laid but no chicks fledged. Two measures of breeding success were used: hatching success – the ratio of the number of hatchlings over clutch size; and fledging success – the ratio of the number of fledglings over the number of hatchlings. Hatching success was estimated over nests where at least one egg hatched, and fledging success in nests where at least one chick fledged.

Statistical analyses

A total of 280 first clutches (pine 164 clutches, Holm Oak = 116 clutches), for which we measured the surrounding environment, was used for analyses.

Across-forest analyses were conducted with linear mixed models (LMM). We included year and forest type as fixed factors; female identity as a random effect; and laying date, clutch size, and nestling parameters as dependent variables.

We first focused on the effect of tree species composition surrounding nest boxes. Thus, we considered that a certain tree species or group of tree species (e.g. mixed, evergreen) was dominant around a particular nest box when it amounted to a minimum of 10% of the total cover, being for other species or group of species lower than 10%. In cases when two or more species or group of species amounted to 10% or more, no single species was considered dominant and these data points were excluded from this particular analysis.

Secondly, to study the effects of habitat structure, we considered shrub and tree species separately. For both cases (composition and structure within forest), LMM were run using laying date and clutch size as dependent variables. To analyze the effects on hatching and fledging success, we ran LMM with binominal error using R statistical software 2.6.1. For habitat structure analyses, the gradient of vegetation maturity (PC1 for 25, 50 and 75 m) and female condition were included as covariates, year, forest type and female age as fixed factors and female identity as random factor. We included forest type to take into account possible differences in habitat structure owing to the dominant tree species around each nest box. Statistics were calculated for each of the three buffer distances. When the same pattern was reached for more than one distance for any of the breeding traits analyzed, only the plot for the lowest distance is shown.

Nominal regressions were used to assess the probability of a nest being deserted or predated, including year and forest type as fixed factors and vegetation gradient as a covariate. SPSS 15.0 statistical package was used for statistical analyses unless otherwise indicated.

RESULTS

Breeding traits and tree composition across and within forests

Great Tits started breeding, on average, one week later in the Holm Oak forest than in the pine forest (Table VII.2). Despite this, clutch size, number of hatchlings and number of fledglings were larger in the Holm Oak forest. Also, chicks and females were heavier and in better condition in the Holm Oak forest, while mean tarsus length was similar in both forests. A year effect was found in most life-history traits ($P < 0.001$, see Table VII.2), but those effects varied in parallel in both forests and no interaction between forest type and year was significant.

Table VII.2. Effects of forest type (pine [SM] versus Holm Oak [FR]) and year (2005-2007) on life-history, chick and female traits in Great Tits using linear mixed models. Mean values ± *SE* are shown.

Taula VII.2. *Efecte del tipus de bosc (pi [SM] versus Carrasca [FR]) i any (2005-2007) sobre alguns paràmetres de vida dels polls i de les femelles en la Mallerenga Comuna emprant models linials mixtes. Es mostra la mitja ± ES.*

Life-history traits	*F*	*df*	*P*	Mean SM	Mean FR
Timing of reproduction (1 = 1 April)					
Forest type	55.40	255	<0.001	31.23±2.72	38.58±1.23
Year	36.41	262	<0.001		
Forest type x Year	1.09	270	0.338		
Clutch size					
Forest type	29.61	254	<0.001	6.16±0.36	6.93±0.16
Year	10.09	256	<0.001		
Forest type x Year	0.66	257	0.517		
Nº hatchlings					
Forest type	20.98	205	<0.001	5.82±0.52	6.28±0.23
Year	4.41	205	0.013		
Forest type x Year	1.18	206	0.311		
Nº fledglings					
Forest type	19.20	129	<0.001	5.09±0.73	5.71±0.32
Year	1.65	129	0.195		
Forest type x Year	1.37	129	0.257		

In within-forest comparisons, for the pine forest we first compared breeding traits between nests where the dominant tree species were Aleppo Pines (31% on average vs. < 1% of Umbrella Pine cover) with those where Umbrella Pines were dominant (29%) over Aleppo Pines (<1%). Laying date and clutch size were similar at all distances considered ($P > 0.05$). Hatching success was higher in Aleppo Pine patches (89.93 ± 2.41) than in Umbrella Pine patches (82.78 ± 3.87; $t_{118} = 1.70$, $P = 0.037$) only when considering 50-m radius. Second, when comparing breeding traits between nests placed in pine- (38% vs. 3% of Holm Oak) versus Holm Oak-dominated patches (26% vs. 5% of all pine species), no differences in any of the breeding traits were found at any of the three distances explored ($P > 0.05$ in all cases).

For the Holm Oak forest, two comparisons were also done, firstly between patches dominated by Holm Oaks (43% vs. 2% of Aleppo Pines) and those by Aleppo Pines (21% vs. 3% of Holm Oaks), and second between mixed (56% vs. 6% evergreen) and evergreen patches (42% vs. 3% deciduous). Mixed breeding territories were characterized by an average of 21% of cover of deciduous trees, and an average of 35% of cover of evergreen trees (pines, Holm Oaks). We did not do a comparison with only deciduous trees because they were too scarce to be considered as dominant around nest boxes (cover less than 10%). None of the breeding traits studied differed between any of the vegetation types at any of the three distances considered ($P > 0.05$ in all cases).

Table VII.2. Continue.

Taula VII.2. *Continuació*

Chick traits	*F*	*df*	*P*	Mean SM	Mean FR
Tarsus length (mm)					
Forest type	0.33	112	0.570	18.99±0.26	19.24±0.11
Year	1.30	112	0.277		
Forest type x Year	2.54	117	0.083		
Body mass (g)					
Forest type	11.52	118	0.001	15.47±0.55	16.76±0.24
Year	0.59	110	0.556		
Forest type x Year	2.33	114	0.102		
Body condition					
Forest type	13.45	122	<0.001	0.81±0.02	0.87±0.01
Year	0.24	117	0.785		
Forest type x Year	1.45	120	0.239		
Female traits					
Tarsus length (mm)					
Forest type	0.56	136	0.457	19.27±0.30	19.23±0.13
Year	4.45	50	0.017		
Forest type x Year	0.64	50	0.530		
Body mass (g)					
Forest type	10.17	130	0.002	16.54±0.40	17.25±0.18
Year	0.52	110	0.517		
Forest type x Year	1.11	110	0.335		
Body condition					
Forest type	8.83	122	0.004	0.85±0.02	0.89±0.01
Year	3.94	83	0.023		
Forest type x Year	0.14	83	0.867		

Description of vegetation structure and their effects on breeding traits within forests

In the Holm Oak forest, the percentage of shrub cover around nest boxes was higher (27.59 ± 13.52%, $n = 116$) than in the pine forest (7.40 ± 7.11%, $n = 121$, $F_{1,235} = 36.45$, $P < 0.001$, data arcsin transformed). In the Holm Oak forest, the average tree diameter around nest boxes was smaller (27.97 ± 5.04 cm, $n = 116$) than in the pine forest (32.37 ± 6.10 cm, $n = 121$, $F_{1,235} = 245.98$, $P < 0.001$) because of both a higher young to old trees ratio ($\chi^2_1 = 2664.11$; $P < 0.001$) and a higher number of young trees (mean number of young trees: Holm Oak forest = 27.53 ± 16.92, $n = 116$; pine forest = 13.04 ± 9.12, $n = 121$, $F_{1,235} = 81.49$, $P < 0.001$, data squared-root transformed). In both forests gaps and overlapping in the tree canopy were common.

Laying date was not significantly related to the maturity of the vegetation (Table VII.3). Since female quality might simultaneously affect laying date and nest site selection, we explored whether female characteristics varied along the vegetation maturity gradient, and their relationships with breeding traits. Laying date was not related to female condition, but old females laid a mean of 2.4 days earlier than young ones (Table VII.3). Mean values of vegetation maturity did not differ between nests of females of different age ($F_{1,145} = 0.40$; $F_{1,139} = 0.05$ and $F_{1,144} = 0.22$, $P > 0.05$ for 25, 50 and 75-m buffers respectively), and female body condition was not affected by the maturity of the vegetation patch ($F_{1,156}$ = 0.33; $F_{1,155}$ = 0.19 and $F_{1,156}$ = 0.02 for 25, 50 and 75-m radii respectively).

Clutch size varied between years and forests, but it was not related to vegetation maturity (all distances $P > 0.05$) nor to laying date ($F_{1,260}$ = 2.55, $P > 0.05$; Table VII.3). Clutch size was not related to female condition or age (Table VII.3).

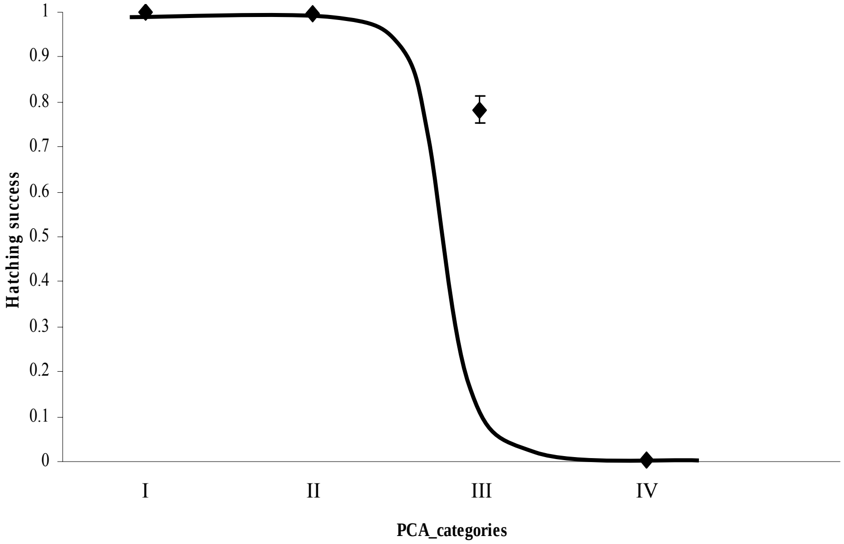


Figure VII.1. Mean hatching success (number of hatchlings over number of eggs laid) (± SE) in relation to the territory vegetation maturity within 25 m around the nest box. Hatching success = -5.28·(PC1_25m) + 4.43. For presentation purposes only (as the analysis was done on the individual data points) mean (± *SE*) hatching success values are presented for four PCA categories: I (PCA < -1.5), II (-1.5 < PCA ≤ 0), III (0 < PCA ≤ 1.5) and IV (PCA > 1.5). The line is the regression line from a statistical model with binominal errors.

Figura VII.1. *Èxit d'eclosió promig (nombre d'ous eclosionats en relació al nombre d'ous posats) (± ES) en relació a la maduresa de la vegetació del territori dins dels 25 m al voltant de la caixa niu. L'èxit d'eclosió = -5.28·(PC1_25m) + 4.43. Sols per raons de presentació (tenint en compte que els anàlisi s'han fet amb totes les dades), es mostra la mitja (± ES) de l'èxit d'eclosió per a les quatre categories de l'ACP: I (ACP < -1.5), II (-1.5 < ACP ≤ 0), III (0 < ACP ≤ 1.5) i IV (ACP > 1.5).*

Table VII.3. Results of linear mixed models on laying date and clutch size within a forest. Female identity was included as a random effect.

Taula VII.3. *Resultats dels models linials mixtes sobre la data i tamany de posta dins del mateix bosc. La identitat de la femella fou inclosa com a efecte aleatori.*

	25 m			50 m			75 m		
	F	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*
Laying date									
PC1 (Territory vegetation maturity)	0.14	148	0.710	0.05	147	0.816	0.04	149	0.844
Year	56.76	85	<0.001	57.03	85	<0.001	57.06	85	<0.001
Forest type	17.22	138	<0.001	16.03	138	<0.001	15.95	138	<0.001
Female age	7.87	123	0.006	7.91	124	0.006	7.93	124	0.006
Female condition	0.73	152	0.394	0.72	153	0.399	0.71	152	0.402
Clutch size									
PC1 (Territory vegetation maturity)	0.33	152	0.565	0.60	152	0.441	0.97	152	0.325
Year	9.14	152	<0.001	9.16	152	<0.001	9.14	152	<0.001
Forest type	18.61	152	<0.001	16.83	152	<0.001	15.96	152	<0.001
Female age	0.004	152	0.953	0.004	152	0.952	0.003	152	0.955
Female condition	0.005	152	0.943	0.006	152	0.94	0.005	152	0.943

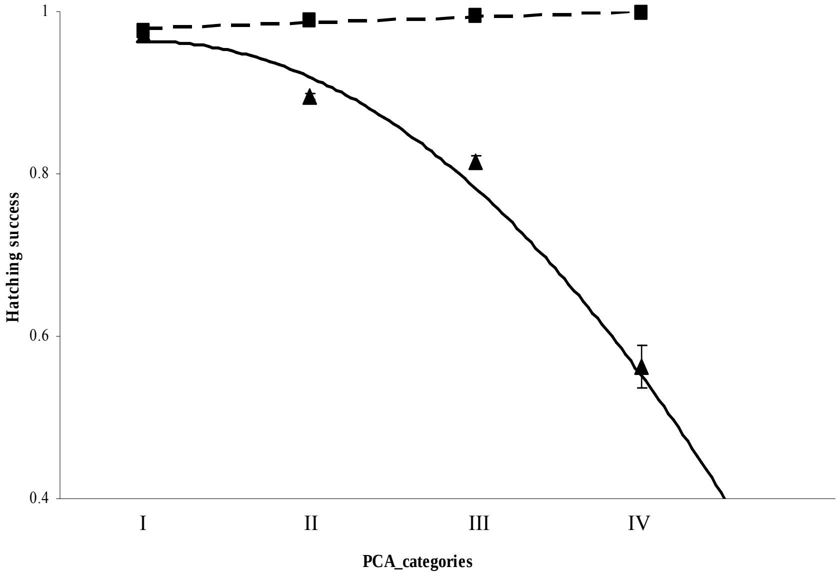


Figure VII.2. Effects of female condition on hatching success in interaction with the territory vegetation maturity in a 25-m radius around the nest box. As a measure of female condition we used the ratio of body mass to tarsus length. For presentation purposes only, we classified females whose values for condition were equal to or less than 0.88 as poor condition (solid line) and females with values higher than 0.88 (dashed line) as good condition. For presentation purposes only (as the analysis was done on the individual data points) mean (± *SE*) hatching success values are presented for four PCA categories: I (PCA < -1.5), II (-1.5 < PVA ≤ 0), III (0 < PCA ≤ 1.5) and IV (PCA > 1.5). The lines are the regression lines, only for the low quality females the relationship is significant.

Figura VII.2. *Efectes de l'estat de condició de les femelles sobre l'èxit d'eclosió interactuant amb la maduresa de la vegetació del territori dins d'un radi de 25 m al voltant de la caixa niu. Com a mesura de l'estat de condició de les femelles vam emprar el qüocient entre el pes corporal i la llargària del tars. Sols per raons de presentació, vam classificar les femelles en ambdúes categories, les femelles de mala condició foren aquelles amb un valor de condició igual o menor a 0.88 (línia contínua) i, les femelles amb valors majors a 0.88 (línia discontínua) foren les que presentaven un bon estat de condició. Sols per raons de presentació (tenint en compte que els anàlisi s'han fet amb totes les dades) es mostra la mitja (± ES) de l'èxit d'eclosió per a les quatre categories de l'ACP: I (ACP < -1.5), II (-1.5 < ACP ≤ 0), III (0 < ACP ≤ 1.5) i IV (ACP > 1.5). Les línies són les línies de les regressions, sols per a les femelles de baixa qualitat, la relació fou significativa.*

Table VII.4. Results of linear mixed models on hatching and fledging success. Female identity was included as a random effect in the models.

Taula VII.4. *Resultats dels models linials mixtes sobre l'èxit d'eclosió i de vol. La identitat de la femella fou inclosa com a efecte aleatori.*

	25 m			50 m			75 m	
	t	*df*	*P*	*t*	*df*	*P*	*t*	*df*
Hatching success								
PC1 (Territory vegetation maturity)	-2.98	151	<0.001	-2.98	151	<0.001	2.8	151
Forest type	0.3	151	0.657	0.12	151	0.646	0.12	151
Female age	-0.5	151	0.614	-0.49	151	0.625	-0.51	151
Female condition	-0.54	151	0.588	-0.53	151	0.597	-0.54	151
Female condition x PC1	2.88	151	<0.001	2.67	151	<0.001	-2.68	151
Fledging success								
PC1 (Territory vegetation maturity)	-0.39	120	0.695	-0.32	120	0.746	0.22	120
Forest type	1.22	120	0.73	1.22	120	0.719	1.29	120
Female age	-0.21	120	0.834	-0.22	120	0.823	-0.23	120
Female condition	-0.14	120	0.893	-0.15	120	0.798	-0.16	120

Hatching success was higher in young and dense vegetation patches than in mature and open patches for all the three radii considered (Fig. VII.1, Table VII.4), whilst it was not significantly affected by female age or condition (Table VII.4). However, there was a significant interaction between the age (maturity) of vegetation for all three radii and female condition (Table VII.4). To explore this interaction further, we split female condition into two groups: poor (values of body condition lower or equal to 0.88) and good condition (values higher than 0.88), classifying approximately half of the females in each category (Fig. VII.2). For good condition females (mean condition index = 0.92 ± 0.11), hatching success did not vary along the vegetation gradient, while that for poor condition females (0.84 ± 0.01) decreased along the gradient from young to mature vegetation territories for all three radii.

Finally, neither fledging success, nor nestling tarsus length or body mass, were related to vegetation structure at any of the distances around the nests explored ($P > 0.05$ in all cases).

Lower hatching success in mature areas: potential underlying causes

We found that hatching success was lower in mature vegetation patches, at least for females in poor condition. Therefore, we explored some of the potential causes that might underlie this pattern.

Death of embryos might occur if incubation pattern is not adequate, and this could happen if females have to spend more time foraging away from nests to satisfy energy demands or to avoid predation. We therefore explored how vegetation structure was related to the proportion of nests containing unhatched eggs, deserted, or affected by predation. The likelihood of a nest containing unhatched eggs was not related to the surrounding environment at any of the three distances considered ($P > 0.05$ in all cases). However, the probability of nest desertion during incubation increased (Wald's $\chi^2 = 5.49$, $B = -5.07$, $P = 0.019$), and that of nest predation decreased (Wald's $\chi^2 = 4.85$, $B = 4.24$, $P = 0.028$) with the age of vegetation for a 75-m radius. On the other hand, when considering a 50-m radius, predation during incubation increased with vegetation maturity (Wald's $\chi^2 = 4.75$, $B = 6.99$, $P = 0.029$, Fig. VII.3). Nest desertion during the nestling phase was not related to the maturity of the vegetation for 25 m or 50 m, but it increased with increasing such maturity for 75-m radius around nest boxes (Wald's $\chi^2 = 4.28$, $B = -3.04$, $P = 0.039$). Finally, there were no significant differences in predation pressure among forest types (64% of nests lost to predators in the Holm Oak forest, 54% in the pine forest, $\chi^2_1 = 1.84$, $P = 0.175$). Therefore, most results pointed out that both nest desertion and predation increase with the degree of maturity of the vegetation in these two forests.

Despite the risk of predation, occupation rate of the available nest boxes by Great Tits was not affected by the maturity of the vegetation (*P* > 0.1 for all distances), although it tended to be slightly higher in environments with lower nest predation.

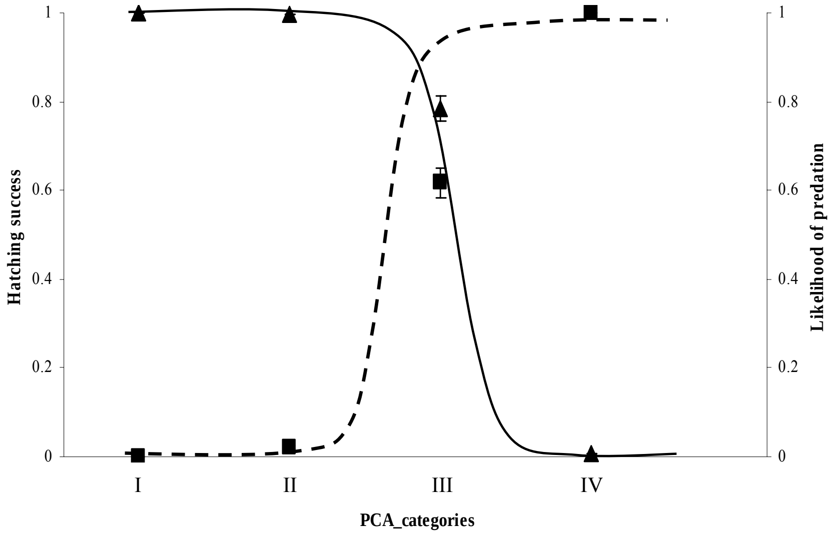


Figure VII.3. Relationship between mean hatching success (proportion of eggs hatched, solid line) and mean predation level (proportion of nests predated, dashed line) during the incubation period through the territory vegetation maturity in a 50-m radius around the nest box. For presentation purposes only (as the analysis was done on the individual data points) mean (± SE) hatching success/predation level values are presented for four PCA categories: I (PCA < -1.5), II (-1.5 < PCA ≤ 0), III (0 < PCA ≤ 1.5) and IV (PCA > 1.5). The lines are the regression lines from statistical models with binominal errors.

Figura VII.3. *Relació entre l'èxit d'eclosió promig (proporció d'ous eclosionats, línia contínua) i el nivell promig de predació (proporció de nius predats, línia contínua) durant el període d'incubació al llarg del gradient de maduresa de la vegetació del territori en un radi de 50 m al voltant de la caixa niu. Sols per raons de presentació (tenint en compte que els anàlisi s'han fet amb totes les dades) es mostra la mitja (± ES) de l'èxit d'eclosió per a les quatre categories de l'ACP: I (ACP < -1.5), II (-1.5 < ACP ≤ 0), III (0 < ACP ≤ 1.5) i IV (ACP > 1.5). Les línies són les línies de les regressions dels models estadístics amb errors binomials.*

DISCUSSION

Laying date

Several studies have pointed out that mean laying date differs among forest types (van Balen 1973, Dhondt et al. 1984, Blondel et al. 1987, Maícas and Fernández 1996, Belda et al. 1998). Based on two facts, (1) ambient temperature affects the timing of breeding (low temperatures delay the timing) through its effects on vegetation phenology and on the development rate of insects (van Balen 1973, Blondel et al. 1991, Belda et al. 1998, Sanz 1998); (2) ambient temperature decreases as altitude increases, laying date would be expected to be delayed for high altitudes (Fargallo and Johnston 1997, present study). Therefore, differences in mean laying date among habitats may be owing to differences in altitudes. Indeed, the effect of the forest type on laying dates disappeared after controlling for differences in altitude and latitude (e.g. Sanz 1998; see also Chabi and Isenmann 1997). Examples addressing the effect of altitude over laying dates come from Chabi and Isenmann (1997) and, Belda et al. (1998) who compared laying dates of Blue *Cyanistes caeruleus* and Great Tits respectively at different altitudes within the same forest and latitude. Based on the results extracted from these two studies, and having account that the Holm Oak and the pine forest differ 200 m in altitude, we would expect a delay of 4-5 days in the mean laying date for these birds breeding in the Holm Oak regards to these breeding in the pine forest. Also, Hopkins (1938 in Wilkin et al. 2007) concluded that spring is often delayed by 1 day for every 30 m rise in altitude, which might imply a delay of 6.7 days in the Holm Oak in relation to the pine forest. Therefore, we may then conclude that most of the difference in laying dates between the two studied forests were likely caused by differences associated with altitude.

To date, detailed studies relating Great Tit breeding traits to tree composition within a forest are scarce. For example, Wilkin et al. (2007) found that laying date was earlier as the number of oaks around Great Tit nests increased, arguing that food availability was the underlaying factor. Also, to the best of our knowledge, the only study relating breeding traits to habitat structure in Great Tits was published by Sánchez et al. (2007), who found that nestlings tended to be in better condition in mature vegetation patches. Van Noordvijk et al. (1981) concluded that neither differences in microhabitat nor in temperature among nest boxes explained laying date variability among individuals within a population. Because most nest boxes within each forest were placed at similar altitude (at different altitude between forests), a possible effect of temperature on vegetation phenology and therefore on food availability would be negligible. In the present study, neither the degree of vegetation maturity nor differences in tree composition among nest boxes within any of the forests were cues for the starting of reproduction in the Great Tit populations studied.

Clutch size

Clutch size in Great Tits is typically larger in forests containing more food (Kluijver 1951, van Balen 1973), and it has been shown to decrease with increasing altitude in Great Tits and other species (Klomp 1970, Järvinen 1989, Sanz 1998). Belda et al. (1998) found that clutch size of Great Tits was larger in a Holm Oak than in a pine forest placed at the same altitude and latitude. Caterpillars are more abundant in Holm Oaks than in pine trees (Illera and Atienza 1995, Tremblay et al. 2003, see also Chapter IV), and this may explain the differences in mean clutch size found in these two forest types. The Holm Oak forest was located at higher altitude than the pine forest, while differences in clutch size were opposite to what would be expected by differences in altitude. Therefore, this allows us to conclude a clear effect of forest type (i.e. food availability), which overrides the effect of altitude.

Within forests, clutch size would be expected to decrease along a food gradient from richer mixed forests (deciduous plus evergreen trees, Tremblay et al. 2003), to Holm Oak, to pine-dominated areas (Illera and Atienza 1995, Tremblay et al. 2003), and to be larger in young and dense vegetation, which probably holds more food (Cody 1981, Martin 1993) than in mature and sparse vegetation areas (Arriero et al. 2006). However, neither tree composition nor the age of vegetation around nest boxes affected clutch size. A possible explanation is that neither monospecific tree patches, nor pure "young" or "mature" patches are present. Rather the whole area was a mixture of tree species, without clear dominant species around the nest boxes in many cases, and the index of maturity did not differ by much among nest boxes. It seems that differences in these two factors were not enough to generate differences in clutch size.

Therefore, our results suggest that differences in clutch size between forests are mainly related to the forest type, probably through differences in food availability between forests (Chapter IV). However, within the forests studied, the features of the breeding territory seem to have low importance in clutch size determination.

Hatching success

Hatching success decreased with vegetation maturity for females in poor condition, while it was independent for females in good condition. This suggests that females in poor condition have more problems during the incubation process in mature areas, where probably food is scarcer, and they have to allocate more time to foraging (Hinsley et al. 2008). Arriero et al. (2006) found higher hatching success in mature areas in a deciduous forest for Blue Tits. Perhaps the relationship between food availability and forest maturity is dependent on the type of forest, and mature areas hold more food in deciduous forests. Given that nestling diet is similar for Blue and Great Tits (Perrins 1979), it seems unlikely that the divergence in the results was caused by the bird species considered.

At the same time, we found that nest predation was significantly lower in immature and dense vegetation patches, so reduced hatching success in mature vegetation patches may be also mediated by a higher nest predation (see Powell and Steidl 2000, Huhta et al. 2003a). In our study, predators which could mediate in the hatching decline in mature areas of vegetation were mostly Montpellier Snakes *Malpolon monspessulanus* (in the pine forest) and Beech Martens *Martes foina* (in the Holm Oak forest). In these predators with diurnal activity (Posillico et al. 1995, Blázquez and Pleguezuelos 2002), vision plays an important role in prey detection (see Barbadillo et al. 1999 for the Montpellier Snake), both snakes and martens locating nests by responding to specific search images (movements) of provisioning birds (Mullin and Cooper 1998). Thus, in immature vegetation patches with dense canopy and shrub layer, nests were likely more difficult to locate (high nest concealment), reducing the searching efficiency of visual predators (Davis 2005). Reducing the time allocated to nest defense would allow females to invest more in the incubation, therefore increasing hatching success (Martin 1987, Nilsson and Smith 1988, Devereux et al. 2006).

Female and nestling traits

Females were in better condition, and produced more and heavier fledglings in the Holm Oak forest. The probable higher food abundance in the Holm Oak forest may have had positive effects on breeding performance both directly, more food for parents and nestlings, and indirectly, stimulating greater reproductive investment in parents (Riddington and Gosler 1995, Huhta et al. 1998), which may in turn accentuate the forest type effect on chick quality. Nest predation rate was similar in both forest types, so differences in breeding performance could not be generated by parents investing more in lower predation risk territories (see Fontaine and Martin 2006).

Within forest, our results showed that nestlings raised in nest boxes located in patches with immature vegetation differed little in size and weight from those raised in patches with mature vegetation, confirming results of Arriero et al. (2006 in Blue Tits), and of Sánchez et al. (2007 in Great Tits). Therefore, it seems that possible differences in food availability among mature and immature vegetation territories (Arriero et al. 2006) were not a limiting factor for raising nestlings in these forests.

Conclusion

Summing up, different factors seem to be operating explaining the breeding success in Mediterranean Great Tits. Firstly, differences in food availability across forests. Secondly, nest predation is playing an important role in determining nest success through the maturity of the vegetation. Considering both habitat attributes (forest type and habitat structure), as well as conditions that might constrain the habitat use (e.g. nest predation, Johnson 2007), we could conclude that immature vegetation patches located in the Holm Oak forest are the ones providing the better conditions for the reproduction of Great Tits among the range of forest conditions considered here.

VIII

MATE CHOICE IN GREAT TIT FEMALES

SUMMARY

Mate choice is an integral part of sexual selection in animals. In birds, males are usually brighter in plumage and have a more active role in courtship, while females are usually less colourful but are responsible for mate choice. Female mate choice is often for colourful males, where colour is an honest signal of male vigour and pairing with such males is associated with an increase in female fitness. However, if male vigour and habitat safety are uncoupled, and there is a high risk for females and nests to be predated, females may choose habitat safety rather than male characteristics. We examine the choice by female Great Tits *Parus major* of colourful males or habitat safety. Males were brighter than females, but there was no assortative mating based on any of the colour and morphological characteristics analyzed (brightness, chroma, tarsus length, weight). Coloured males were uncoupled with habitat safety. In nests reared by bright males, nest productivity and feeding frequency did not differ from those reared by dull males. On the other hand, bright females raised more nestlings per brood than dull females, when nests were sited in dense and young vegetation. Such nests had a low likelihood of experiencing a predation event. Although both bright and dull females made similar numbers of visits to the nest, bright females brought larger caterpillars. The probability of nest occupancy by a bright female increased in dense and young vegetation surrounding nest boxes. Bright females appear to reduce the costs of predation (likelihood of being detected and so revealing their nests to predators) by choosing concealed sites for breeding. Dull females breed in more risky habitats. Thus, where female and nest predation is high, female Great Tits choose habitat safety over male characteristics.

RESUM

L'elecció de parella forma part de la selecció sexual en animals. A les aus, els mascles són normalment els més brillants en plomatge adquirint un paper important durant el corteig. Per altra banda, les femelles són les qui elegixen la seua parella. En aquest cas, les femelles elegixen principalment mascles colorits degut a què emparellar-se amb dits mascles li'ls proporciona un increment de l'èxit reproductiu. Mentre que si no hi ha relació entre la coloració del mascle i la seguretat de l'hàbitat, i a més hi ha un elevat risc de predació per a les femelles i nius (veure Capítol VII), aquestes podrien elegir la seguretat de l'hàbitat més que les característiques del mascle. Vàrem examinar l'elecció per part de femelles de Mallerenga Carbonera Parus major *de mascles colorits o de la seguretat de l'hàbitat. Obtinguérem que els mascles foren més colorits que les femelles, però no*

trobàrem un aparellament selectiu basat en les característiques analitzades (lluminositat, saturació, longitut del tars i pes). Mascles colorits no es relacionaren amb la seguretat de l'hàbitat. La coloració/lluminositat dels mascles no es va relacionar ni en la productivitat al niu ni en la seua taxa d'aprovisionament d'aliment. Per altra banda, la productivitat fou major en femelles colorides que niuaren en territoris amb vegetació jove i densa. Dits nius tingueren una baixa probabilitat d'experimentar un fenomen de predació. Malgrat els dos tipus anteriors de femelles feren un mateix nombre de visites al niu duent aliment, les més colorides dugueren orugues més llargues. La probabilitat de què un niu fora ocupat per una femella colorida augmentà amb la inmaduresa de la vegetació al voltant del niu. Els nostres resultats sugerixen que les femelles colorides reduiren el cost (probabilitat de ser detectades i per tant, la detecció dels seus nius pels predadors) seleccionant llocs ocults per reproduir-se. Les femelles menys colorides es reproduiren en llocs de més risc de predació. Per tant, en un ambient on la predació de les femelles com de nius és elevada, les femelles de Mallerenga Carbonera donaren més importància a les característiques del hàbitat més que a les característiques del mascle.

INTRODUCTION

Bird plumage colouration has an important role in sexual selection (Saetre et al. 1994, McGraw and Hill 2000, Hadfield and Owens 2006). Males are usually the conspicuous sex in dimorphic species (Andersson 1994, Arriero and Fargallo 2006), and colourful plumage signals high quality individuals, which might be reflected, for instance, in a higher contribution to the feeding of nestlings (Saetre et al. 1995, Linville et al. 1998, Senar et al. 2002). Female choice is central to the theory of sexual selection (Andersson 1994). Indeed, by choosing colourful males, female fertility may be increased through raising more and better offspring (Bateson 1983, Norris 1990a, Linville et al. 1998). Such choice can be extended to other traits, such as tail length, black stripe size, body size or condition, (e.g. Jawor et al. 2003, MacDougall and Montgomeri 2003, Murphy 2008, Quesada and Senar 2009). Colourful plumage in females is associated with higher levels of female aggression, which generally implies dominance of colourful over dull females (Johnson 1988, Irwin 1994). Hence, the general pattern found in cases where male plumage colour is important in female decision, is that colourful dominant females preferentially mate with colourful males (Quesada 2007). This is known as assortative mating (Warkentin et al. 1992, Johnstone et al. 1996, Jawor et al. 2003).

However, females do not always choose male traits similar to their own, either because different forms of selection operate on these traits, or because ornaments do not function as sexually selected signals (Alatalo et al. 1986a, Linville et al. 1998, Murphy 2008). In fact, some cases have been described in which female reproductive success was mainly affected by the characteristics of the environment surrounding the nest, and not so much by those of the male (Björklund 1990). For example, Alatalo et al. (1986a) showed experimentally that Pied Flycatcher *Ficedula hypoleuca* females did not choose male characteristics, including a measure of colour. They suggested that females chose territories with low nest predation risk and not the male *per se*. Thus, if nest predation risk (on eggs, nestlings and incubating females) is high, females may choose territories with safer nesting sites, independently of male quality (see Björklund 1990, Andersson 1994).

Great Tits *Parus major* are monogamous, both sexes provide a similar amount of parental care (Perrins 1979), and assortative mating has been reported to occur (Norris 1990a, Ferns and Hinsley 2008, Quesada 2007, Quesada and Senar 2009). Our main target here was checking whether assortative mating also occurs in a scenario of high nest predation (see Chapter VII), where females might pay more attention to habitat (predation risk) than to male quality (chroma, tarsus length, weight). Natural selection should favour female choice for nesting characteristics if there is no relationship between male colouration and reproductive success, and if territories vary in their effects on female reproductive success.

METHODS

Study area

The study was performed in two natural parks, Sierra Mariola (38º 44’ N, 0º 33’ W, 900 m a.s.l.) and Font Roja (38º 39’ N, 0º 32’ W, 1090 m a.s.l.) in eastern Spain. For further information, see Chapters II and VII.

The main predators acting on nest boxes present in our study area were Montpellier Snakes *Malpolon monspessulanus* in the pine forest and Beech Martens *Martes foina* in the Holm Oak forest. In both cases, vision plays an important role in prey detection (see Mullin and Cooper 1998, Barbadillo et al. 1999). Both predators show diurnal activity (Posillico et al. 1995, Blázquez and Pleguezuelos 2002) locating nests by responding to specific search images (movements) of provisioning birds (Mullin and Cooper 1998). In our study, predation within the nest boxes affected to eggs, chicks and incubating or brooding females. In fact, we know that Beech Martens could prey on chicks and/or females inside the nest boxes, since we could identify their remains (pers. obs.). However, we have no direct evidence that snakes also prey on females (but see for instance, Stake 2001), since they do not leave remains (Sorace et al. 2000, pers. obs.).

GIS-procedure and vegetation gradient

Vegetation cover and species composition were quantified by using different methods (see Chapter VII). Such data were processed according to that described in the Chapter VII, using ARCGIS spatial analyst (Arcview) 9.1. Three different buffers around each nest box (25, 50 and 75-m radius) were created. The maximum distance around each nest box (75 m) was selected to be biologically meaningful, since it is within the range of the foraging area for Great Tits (Naef-Daenzer 2000). Analyses including vegetation structure at 25 m were either nonsignificant, or their results were generally redundant with those of the 50 and/or 75-m radius, so they are not showed. Those for 50 or 75-m radius were presented when significant: they were never contradictory, but in some analyses only one of them was significant.

To integrate the variety of factors that characterize complex habitats, we ran principal component analyses (PCA) to reduce the variables considered into a few axes which summarize vegetation characteristics (see Cody 1981, González 2003) for each buffer. The first principal component (PC1) defined a gradient of increasing vegetation age in a patch around nest boxes. Immature vegetation patches composed by young trees with well developed canopy and understorey (high tree and shrub cover). Mature patches composed by older trees with low tree and shrub cover, i.e. low dense vegetated patches. PC1 correlated significantly with most variables (see Table VIII.1). Large values of PC1 corresponded older vegetation within a

50-m radius, while lower values of PC1 did for 75-m radius. Although the total variance associated with PC2 was lower in comparison with PC1, based on broken stick analyses (Jackson 1993), this principal component should be taken into account. Hence, PC2 was initially considered in the analyses but, as no explored relationship was significant, results concerning PC2 are not presented.

Table VIII.1. Correlations among the variables describing habitat characteristics and the two first principal components for the three buffers performed. The percentage of variance explained for both components and for each buffer is also presented. Variables measured within 75 m and correlated negatively they did positively for 25 and 50 m instead for PC1. Significant correlations among the variables describing habitat structure and the factor are shown in bold.

Taula VIII.1. *Correl.lacions entre les variables que descriuen les característiques de l'hàbitat i els dos primers components principals per als tres radis creats. Es mostra el percentatge de la variança per als dos components principals i per a cadascú dels radis. Les variables dins dels 75 m per al CP1 i correl.lacionades negativament, ho feren en canvi positivament per a 25 i 50 m. Els valors significatius per a cadascú dels dos primers components es mostren en negreta.*

	25 m		50 m		75 m	
	PC1	PC2	PC1	PC2	PC1	PC2
Nº trunks 5-10 cm	**-0.67**	**0.25**	**-0.70**	**0.27**	**0.71**	**0.34**
Nº trunks > 30 cm	**0.84**	**-0.17**	**0.83**	0.04	**-0.82**	**0.26**
Mean diameter 5 thickest trees	**0.86**	-0.08	**0.85**	0.07	**-0.84**	**0.28**
Shrub cover (%)	**-0.63**	**-0.55**	**-0.65**	**-0.41**	**0.67**	**-0.20**
Tree cover (%)	0.03	**0.93**	**-0.18**	**0.94**	**0.39**	**0.85**
Eigenvalue	2.29	1.26	2.36	1.12	2.48	1.02
% variance accounted for	45.818	25.107	47.168	22.444	49.554	20.294

Breeding parameters and colour measurements

During the breeding season 2007, a total of 121 nest boxes in the pine and 140 in the holm Oak forest were checked. They were visited at least once a week, and active nests were visited with a pattern which allowed us to assess laying date (assuming that one egg was laid per day; 1 = 1 April), clutch size and hatching date (with visits every day or every other day around the expected hatching date). As many adults as possible were trapped whilst they were feeding 11-15 day-old nestlings (hatching date = day 0). Adults caught were sexed, aged (classifying them into yearlings or older birds using plumage characteristics; Svensson 1992), weighed (using an electronic balance ± 0.1 g), their tarsus length (using a digital calliper ± 0.01 mm) and the breast colour measured. We used as a measure of breeding success, nest productivity (brood size x mean brood weight).

Colour measurements were taken by the same author (F. Atiénzar) using an Ocean Optics USB2000 spectrophotometer (range 250-800 nm), holding the optic fibre at an angle of 90º from the breast surface (left breast side). We used a probe socket to ensure that readings were taken at a fixed short distance above the surface, minimizing also the possible effect of ambient light over the measures. Two measurements were taken from the same individual, moving the sensor at least 5 mm between readings. A total of 60 males (41 in pine, 19 in Holm Oak) and 66 females (44 in pine, 22 in Holm Oak) attending a total of 70 nests were measured.

Curves of reflectance for breast colour were determined by calculating the median of the percent reflectance in 10 nm intervals beginning at 300 nm and ending at 700 nm to cover the full spectra range that can be detected by birds (Hill and McGraw 2006b). However, since the reflectance of UV (300-400 nm) is highly correlated with the peak of the yellow-red spectrum (500-700 nm) in Great Tits, these two measurements are redundant (Quesada and Senar 2006). Hence, we did not take into account UV values for the analyses. We used the most common parameters to describe plumage colour (Hill and McGraw 2006b): brightness, chroma and hue (400-700 nm). Data were processed using OOIBase^{TM} software.

Plumage brightness is the total amount of light reflected, and is related to the structural properties of feathers and not to the physiological condition of the bird. On the other hand, plumage hue and chroma, which depend on the amount of carotenoids, are usually related to the nutritional condition of birds (Saks et al. 2003). Since all

Table VIII.2. Values of the repeatability (r) of the colour parameters, brightness, chroma and hue for males (pine forest [SM] *n* = 41, Holm Oak forest [FR] *n* = 19) and for females (*n* = 44 SM, *n* = 22 FR). Significant values are shown in bold.

Taula VIII.2. *Valors de la repetibilitat (r) dels paràmetres del color, brillantor, croma i saturació per als mascles (bosc de pi [SM] n = 41, bosc de Carrasca [FR] n = 19) i per a les femelles (n = 44 SM, n = 22 FR). Valors significatius es mostren en negreta.*

	Brightness		Chroma		Hue	
	SM	FR	SM	FR	SM	FR
Males	**0.72**	**0.77**	**0.83**	**0.80**	**0.76**	0.29
Females	**0.88**	**0.79**	**0.90**	**0.62**	0.33	0.27

the three colour parameters have been suggested to be involved in mate choice and in parental care, we initially considered all three, discarding afterwards the hue, since its repeatability was low (Table VIII.2; Saetre et al. 1994, Linville et al. 1998, Senar 1999, MacDougall and Montgomerie 2003, Quesada 2007, Ferns and Hinsley 2008). On the other hand, we used plumage brightness in analyses related to predation according to Huhta et al. (2003b) who analyzed it over 63 bird species, including Great Tits.

Diet sampling procedure and feeding frequency

Prey size and volume were obtained through video surveillance using digital video cameras (Sony DCR-DVD 203) working during one hour per nest when nestlings were 10 days-old. A total of 36 nests, in which both parents entered during the filming period, were used for analyses. DVDs were played and the number of visits by each sex was recorded. Only the most abundant prey, caterpillars and spiders, were considered in the present study. Prey body size (length and width, ignoring appendages) were measured over the computer screen by placing graph paper and comparing it with bill length (see Atiénzar et al. 2009, Chapter III). Measurements of bill length were obtained from trapped birds in both populations (pine forest: 11.68 ± 0.08 mm, n = 78; Holm Oak forest: 12.35 ± 0.06 mm, n = 46). Prey volume was calculated using $V = \pi/4 \cdot [L \cdot W^2]$ and $V = \pi/6 \cdot [L \cdot W^2]$ for caterpillars and spiders respectively, where L = length and W = width (Blondel et al. 1991).

Statistical analysis

Analyses regarding assortative mating within all pairs were conducted by correlating relevant parameters (brightness, chroma, tarsus length and weight) between males and females, with forest type as fixed factor. To study which factors affected nest productivity, feeding frequency (number of visits per hour), caterpillar length and total (caterpillar and spider) prey volume acted as dependent variables depending on the analysis, with forest type, male and female age as fixed factors, and brood size (this variable was not included when nest productivity was analyzed), vegetation maturity and male and female brightness as covariates. Linear mixed models (LMM) were used in these cases. Multinomial regressions were used to assess the probability of predation of a nest reared by bright females as well as the relationship between nest predation and the age of the vegetation patch. For this last analysis, we took into account all nests (first clutches) in which at least one egg was laid (i.e. not only those where adult colour was measured).

Birds were caught within a relatively short time window (maximum one month). We thus considered that possible seasonal changes in colour (reduction in brightness) should have been minimal (Figuerola and Senar 2005) and did not control for day of measurement. Interactions among response variables are shown when significant. Mean ± standard error are showed when required. SPSS 15.0 statistical package was used for the analyses.

RESULTS

Plumage brightness was similar among study sites but birds were more yellow in the pine (26.25 ± 0.26) than in Holm Oak forest (25.10 ± 0.29). Males were on average brighter, though equally yellow, than females (Table VIII.3). Neither brightness ($F_{1,53} = 2.61$, $P = 0.112$) nor chroma ($F_{1,53} = 0.03$, $P = 0.875$) were correlated within breeding pairs. Other traits used for assortative mating such as tarsus length and weight were also not significantly correlated between males and females (all $P > 0.05$). There was no effect of forest type in such analyses of correlation (all $P > 0.05$).

Table VIII.3. Sex differences (mean ± *SE*) in plumage colour characteristics.

Taula VIII.3. *Diferències entre sexes (mitja ± ES) en les característiques del color del plomatge.*

Parameters	*F*	*df*	*P*	Male	Female	SM	FR
Brightness							
Forest type	0.52	122	0.473				
Sex	5.71	122	0.018	24.45 ± 0.18	20.21 ± 0.50		
Chroma							
Forest type	7.25	122	0.008			26.25 ± 0.26	25.10 ± 0.29
Sex	0.09	122	0.983				

Nest productivity (brood size x mean brood weight) was not affected by male or female brightness or age, nor by the maturity of the vegetation patch (all $P > 0.05$), but it was higher in the Holm Oak (101.20 ± 8.76 g) than in the pine forest (84.31 ± 8.76 g; $F_{1,39} = 4.52$, $P = 0.040$). However, nest productivity was related to female brightness through the interaction with the maturity of the vegetation for 75 m ($F_{1,45} = 4.66$, $P = 0.036$). To explore this interaction further, females were randomly assigned to two groups by their brightness: dull (values of brightness lower than 25) and bright (values equal to or higher than 25), regressing nest productivity against the maturity of the vegetation patch within each group. For bright females, nest productivity was greater in young vegetation patches ($r = 0.65$, $P = 0.032$, Fig. VIII.1) whereas nest productivity in dull females was not affected by the vegetation structure ($r = 0.21$, $P = 0.200$). Bright females showed, on average, higher nest productivity than dull females (ANCOVA, $F_{1,44} =$

7.70, P = 0.008, bright 114.80 ± 39.75 g, dull 101.25 ± 13.44 g, with hatching date as covariate, $F_{1,44}$ = 0.59, P = 0.445).

Male and female feeding effort was similar (t_{35} = 1.946, P = 0.060), and was not related to the parameters considered here, except for that feeding rates in males increased with brood size (Table VIII.4). We re-analized feeding frequency for both sexes using chroma, and non significant results raised. Finally, caterpillar length and total prey volume brought by males were not related to their brightness. Instead, for females, total prey volume was greater in younger vegetation. Bright females brought larger caterpillars, and caterpillar length increased in those nests surrounded by more immature or younger vegetation at 50 m (Table VIII.4). We repeated this analysis controlling for female tarsus length with the same results, finding no relationship between caterpillar length and tarsus length ($F_{1,33}$ = 1.63, P = 0.220), so female body size was not mediating in the relationship between brightness and caterpillar size.

Nests reared by dull females were predated with higher probability than those reared by bright females (Wald statistic = 4.31, B = -0.13, P = 0.038). Additionally, nest predation increased with the maturity of the vegetation around the nest within 50 m (Wald statistic = 4.44, B = 0.53, P = 0.035). On the other hand, the likelihood of a nest being occupied by a bright female increased in these nests surrounded by low dense vegetation within 50 m (Wald statistic = 5.15, B = -5.88, P = 0.012, Fig. VIII.2). This relationship was not found for males (*P* > 0.05 for all three distances), i.e. males were distributed independently of the maturity of vegetation patch.

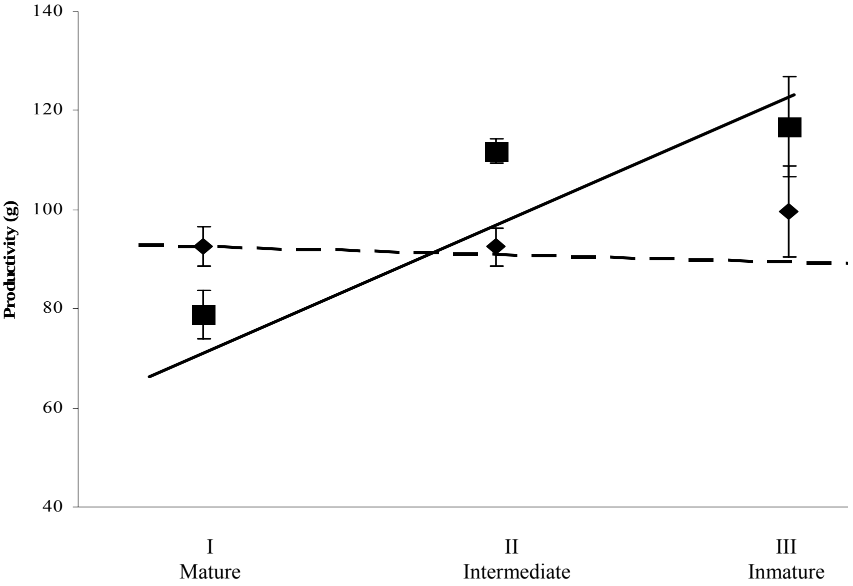


Figure VIII.1. Relationship between female brightness and nest productivity (total brood weight) in interaction with the gradient of decreasing vegetation age in a 75-m radius around the nest box. We classified females whose values for brightness were less than 25 as dull females (dashed line) and females with values higher or equal to 25 (solid line) as bright females. Such lines are based on individual data. For presentation purposes only (as the analysis was done on the individual data points) mean (± *SE*) nest productivity values are presented for three PCA categories: I (-0.4 ≥ PCA), II (-0.4 < PCA < 0.4) and III (PCA ≥ 0.4).

Figura VIII.1. *Relació entre la lluminositat del plomatge de la femella i la productivitat al niu (la suma del pes de tots els polls d'un mateix niu) interactuant amb la maduresa de la vegetació del territori dins d'un radi de 75 m al voltant de la caixa niu. Vam classificar a les femelles amb valors menors de 25 en relació a la lluminositat del plomatge com poc brillants (línia discontínua) mentre que les femelles amb valors superiors o iguals a 25 (línia continua) es classificaren com a brillants. Dites línies estan fetes en dades individuals. Sols per raons de presentació (tenint en compte que els anàlisis s'han fet amb totes les dades) es mostren els valors mitjans (± ES) de la productivitat al niu per a les tres categories de l'ACP: I (-0.4 ≥ PCA), II (-0.4 < PCA < 0.4) i III (PCA ≥ 0.4).*

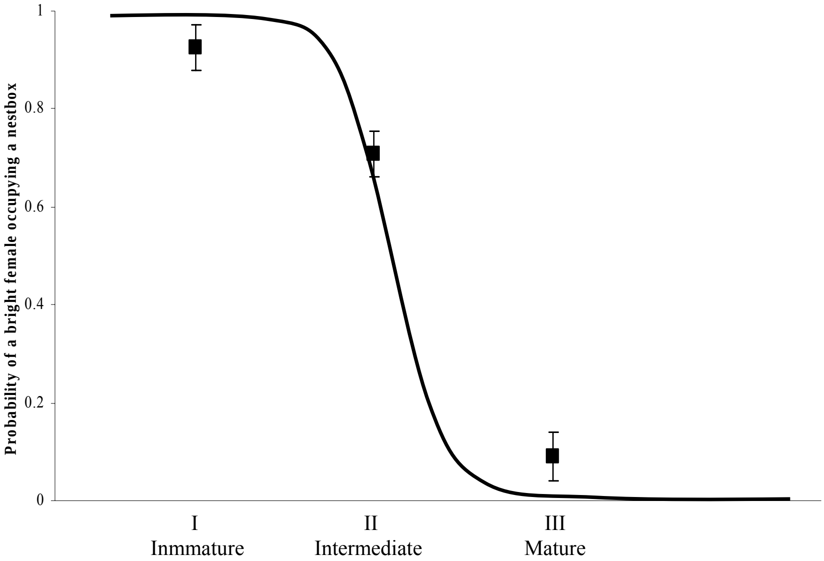


Figure VIII.2. Relationship between the gradient of territory vegetation maturity 50 m and the probability of a nest being occupied by bright females. The line is based on individual data. For presentation purposes only (as the analysis was done on the individual data points), mean (± *SE*) values of probability of occupancy are presented for three PCA categories: I (-0.4 ≥ PCA), II (-0.4 < PCA < 0.4) and III (PCA ≥ 0.4).

Figura VIII.2. *Relació entre el gradient de maduresa de la vegetació del territori en un radi de 50 m i la probabilitat de què un niu siga ocupat per una femella brillant. La línia està feta en dades individuals. Sols per raons de presentació (tenint en compte que els anàlisis s'han fet amb totes les dades) es mostren els valors mitjans (± ES) de la probabilitat d'ocupació per a les tres categories de l'ACP: I (-0.4 ≥ PCA), II (-0.4 < PCA < 0.4) i III (PCA ≥ 0.4).*

Table VIII.4. Relationship among feeding frequency, prey volume and caterpillar length with several parameters measured either for males or females. Here, only results concerning to 50 m are showed.

Taula VIII.4. *Relació entre la freqüència d'aprovisionament, volum de presa i llargària de les oruges amb varis paràmetres mesurats tant als mascles com a les femelles. Ací, sols es mostra els resultats que afecten al radi de 50 m.*

	Female			Male		
Feeding frequency	*F*	*df*	*P*	*F*	*df*	*P*
Forest type	0.76	28	0.390	0.04	28	0.953
Brightness	1.20	28	0.282	1.27	28	0.270
Age	1.27	28	0.269	0.06	28	0.814
Territory vegetation maturity	0.11	28	0.744	0.08	28	0.781
Brood size	0.10	28	0.768	6.92	28	0.014
Prey volume						
Forest type	0.875	35	0.356	6.58	38	0.014
Brightness	0.66	35	0.421	0.08	38	0.776
Age	0.15	35	0.704	3.41	38	0.072
Territory vegetation maturity	4.53	35	0.040	3.34	38	0.075
Brood size	1.00	35	0.324	0.16	38	0.696
Caterpillar length						
Forest type	1.171	33	0.287	5.49	38	0.024
Brightness	5.29	33	0.028	0.73	38	0.397
Age	2.33	33	0.137	10.05	38	0.003
Territory vegetation maturity	4.24	33	0.047	0.96	38	0.333
Brood size	0.76	33	0.388	0.01	38	0.913

DISCUSSION

Males are usually the most conspicuous sex (Andersson 1994). This pattern has also been found in Great Tits (Slagsvold and Lifjeld 1985, Ferns and Hinsley 2008), and our results agree with previous ones.

Assortative mating has been found for several traits and organisms (Andersson 1994). This is predicted to occur when both sexes maintain sexually selected traits. Assortative mating can also result if elaborate traits function in both sexes as status signals, as males and females compete with same-sex rivals to gain access to the same resources (Murphy 2008). For Great Tits, several studies have shown assortative mating by colouration based on traits as the black crown (Hegyi et al. 2007), or the yellow breast (Ferns and Hinsley 2008), and even for the black stripe size (Quesada 2007, Quesada and Senar 2009). And yet for other traits, such as a yellow breast or breast stripe size, assortative mating has sometimes been found (Quesada 2007, Quesada and Senar 2009) and sometimes not (Hegyi et al. 2007, present study). Assortative mating was not detected for other traits tested here, specifically tarsus length and weight unlike found in other studies (Bortolotti and Iko 1992, Delestrade 2001).

Male plumage colouration may signal, among other traits, male genes, parental ability, or quality of the resources held (Alatalo et al. 1986a). In Great Tits, Quesada (2007) found a positive relationship between the yellow breast (chroma) of males and body condition, and this trait was a good indicator of the quality of the male. However, Hegyi et al. (2007) did not find relationships between the yellow breast and body mass or other components of the quality of the male. In our study, the yellow breast (brightness and chroma) was not related to the feeding effort of the males. An effect of male age may mask such relationships (Saetre et al. 1995), but no effects of male age were found. This lack of a relationship between male colouration and feeding effort has also been found in other species (e.g. Saetre et al. 1995, Smiseth et al. 2001). Nevertheless, we should recognize that it may be difficult to show a lack of relationship between plumage colour and feeding effort in one single year of study. On the other hand, male colouration did not signal benefits for female breeding success measured as nest productivity or as the probability of a nest to be predated. The absence of a relationship between brightness and nest predation in our population may be due to other traits (e.g. black band size, see Norris 1990b, Quesada and Senar 2007) are actually signalling nest male defense against predators. Although, Huhta et al. (2003b) found that plumage brightness of prey increased predation risk in 63 bird species, including Great Tits. The absence of a relationship between male colouration and traits important for female breeding success (e.g. parental care, predation) might be partly responsible for the lack of assortative mating in our population.

Other explanations for the absence of assortative mating, perhaps complementary to that above, is that females may pay more attention to habitat (e.g. predation risk, food availability, see Chapters

IV and VII) than to male characteristics (Alatalo et al. 1986a, Börjklund 1990). This happens when male traits are poorly related to female breeding success. A problem concerning territorial species is that male quality could be related to territory quality if better males hold better territories (Hill 1988, Norris 1990b, Ferns and Hinsley 2008). In this case, only experimental studies can solve which traits females are actually selecting (Alatalo et al. 1986a, Saetre et al. 1994). In cases where such relationship is lacking (male and habitat quality), females should show a clear trade-off between male and habitat features. In our study area, 67% of the total nest predation occurred when chicks were at the nest. In addition, predation on incubating females was also frequently observed. Based on the fact that predators identified in our study area, vision plays an important role in prey detection (Barbadillo et al. 1999), the choice of where to breed is clearly a vital one (Magnhagen 1991); even more so for bright individuals who are more conspicuous at the nest when feeding chicks (Huhta et al. 2003b, Post and Götmark 2006; see prey location for Gray Rat Snake *Elaphe obsoleta spiloide* in Mullin and Cooper 1998). Previous studies have suggested that nest predation could influence or drive female choice (Alatalo et al. 1986a, Björklund 1990), but empirical data were not presented. In our study area, nest predation was lower in territories with young vegetation (see also Chapter VII), probably because nest boxes were more concealed in these areas with higher vegetation density (Martin 1993). We suggest that bright, dominant females probably chose nest boxes placed in areas with dense vegetation because of their lower predation risk.

On the other hand, females may also pay attention to food available in the territory. Bright females, who occupied territories with more immature vegetation, provided more food per unit time to their chicks; although their feeding frequency was similar to that of dull females, they brought larger prey. Indeed, bright females had greater productivity in patches with young and dense vegetation. In contrast, the productivity of dull females was independent of vegetation age and stand density but lower than bright females. There are at least two possible reasons for why bright females provisioned larger prey: young and dense vegetation patches were richer and held, on average, larger prey, or bright females were better foragers. We have no data on food availability at the scale of territories, but the maturity of the vegetation patch was not related to the size of the prey brought by males, so there is no strong support for differential food availability. It seems, therefore, that bright females were better foragers. If this is the case then young vegetation patches were probably selected by bright females because of their safety against predation, therefore increasing nest success. Moreover, bright females seemed to be better at getting food, so their nest productivity was also higher.

Based on both all controversial results for the same species in mating choice showed above and our findings, it raises an interesting question of whether mate choice is mediated by several male traits (e.g. black crown, yellow breast and black stripe size) or is context-dependent (e.g. predation, Simcox et al. 2005). For instance, Hegyi et al. (2007) suggested that a system of multiple sexually selected traits with different information content may work in the Great Tit mate choice. Nevertheless, to answer such question, only experimental studies can solve it by controlling the effect of territory quality (Saetre et al. 1994).

Few studies to date have convincingly demonstrated that females actually preferred territory characteristics over male traits. It has been suggested (Alatalo et al. 1986a) that this might occur because of two main reasons: (1) when females do not take advantage of male traits to obtain direct benefits for their offspring; and (2) when territories consistently vary (nests surrounded by dense and young vegetation were less predated) in their effects on female reproductive success, and predation was focused on females and offspring. We have shown that both circumstances might be occurring in our studied population, and we suggest that these might contribute to explain the lack of assortative mating in this population. Knowledge of the determinants of female reproductive success is, therefore, crucial to understanding female mate choice (Björklund 1990). Finally, we are aware of the study period was just one year; therefore, the degree of generalization of our study is limited. Hence, long time series may reveal a more general pattern in the mating choice.

IX

NESTING HABITAT DESCRIPTION AND CHICK DIET IN MEDITERRANEAN CRESTED TITS

SUMMARY

Most bird species show specific habitat requirements for breeding and feeding. We studied here the pattern of habitat occupation, nestling diet and breeding performance of Crested Tits *Lophophanes cristatus* in a "typical" (coniferous) and an "atypical" (Holm Oak *Quercus ilex*) forest in eastern Spain during 2005-2007. We aimed to determine which microhabitat characteristics in the Holm Oak forest could account for the presence of Crested Tits, and checked whether the nestling diet in the Holm Oak forest resembled to that obtained in the pine forest. Vegetation maps were created using GIS from measures taken in the field (tree species, tree and shrub cover). Nestling diet was recorded through video surveillance. Crested Tits bred in low dense mature areas in the pine forest. Those breeding in the Holm Oak forest built their nests in areas including pine trees and avoided dense-forested areas. Birds breeding in the pine forest started laying by mid April, and

average clutch size was 5 eggs. In the Holm Oak forest, birds started laying by the end of April and average clutch size was also 5 eggs. Fledglings weighed around 12 g in both forests. Nestling diet, prey size and feeding frequency by the parents did not vary between forests. The main prey types consumed were Lepidoptera larvae and Diptera.

RESUM

Moltes espècies d'aus presenten requeriments específics per a la reproducció i alimentació. Al present capítol, nosaltres estudiàrem el patró d'ocupació de l'hàbitat, la dieta dels polls i l'èxit reproductor de la Mallerenga Emplomallada Lophophanes cristatus *en un bosc "típic" com és el de coníferes i en un bosc "atípic" per a l'espècie com és un Carrascar* Quercus ilex *a l'est d'Espanya entre 2005-2007. Els nostres objectius foren, determinar quines característiques del microhàbitat al bosc de Carrasca podrien permetre la presència de les Mallerengues Emplomallades, així com vore si la dieta dels polls nascuts al bosc de Carrasca es semblava a la registrada al bosc de pi. L'estudi es va dur a terme durant 2005-2007. Es van crear mapes de vegetació mitjançant SIG emprant les mesures preses al camp (espècie d'arbre, coberta arbòria i d'arbustos). La dieta dels polls fou registrada mitjançant la filmació. Les Mallerengues Emplomallades es reproduiren en zones madures i poc denses al bosc de pi. En canvi, aquells que es reproduiren al Carrascar construiren els seus nius en zones que presentaven pins, evitant zones denses en vegetació. Les aus al bosc de pi iniciaren la posta a meitat del mes d'Abril, i el tamany de posta promig fou de 5 ous. Al bosc de Carrasca, les aus*

començaren la posta a finals d'Abril, posant també uns 5 ous de mitja. Els polls eixiren del niu amb un pes promig de 12 g als dos boscos. La dieta dels polls, tamany de presa i la freqüència d'aprovisionament d'aliment pels pares no va variar entre boscos. El principal tipus de presa duta pels adults al niu foren larves de lepidòpters i dípters.

INTRODUCTION

Most bird species have specific habitat requirements for breeding (see Cody 1981, Holmes and Robinson 1981, Avery and Leslie 1990, Jones 2001, Mörtberg 2001). For instance, Crested Tits *Lophophanes cristatus* are adapted to coniferous forests (Cramp and Perrins 1993). In spite of this, Crested Tits also breed in other habitats, such as mixed (Perrins 1979, Díaz et al. 1998), Holm Oak *Quercus ilex* (Herrera 1978, Maícas and Fernández 2004) or even pure deciduous forests (Perrins 1979, Blondel 1985), though densities are generally low in these habitats (Díaz et al. 1998). Nevertheless, the conditions required for this species to occur in forest types other than coniferous ones remain unknown.

Tree species composition and vegetation structure may be important habitat traits for nest site selection (Avery and Leslie 1990, Denny and Summers 1996). Thus, a way to answer the above question might be studying the characteristics of the specific sites where birds are breeding within the uncommon habitat, and see whether those places resemble the characteristics of their preferred habitat. For instance, Pied Flycatchers *Ficedula hypoleuca*, a typical deciduous forest bird (Lundberg and Alatalo 1992, Martí and Del Moral 2003), has been found nesting in coniferous plantations, but only in patches including a few broadleaved trees (e.g. Avery and Leslie 1990). This type of studies gives the most useful information on tree-species preferences by birds, though they are relatively scarce (see Avery and Leslie 1990).

Floristic composition determines the dominant food type and food abundance for birds (Blondel et al. 1991, Lundberg and Alatalo 1992). Since the quality and quantity of food supply are crucial in determining breeding traits (see Martin 1987, Blondel et al. 1993), it is of interest to find out how bird species adapted to a specific habitat cope with the food resources available in different "atypical" habitats (e.g. Barba et al. 2004). Little is known on the nestling diet of Crested Tits, and most studies have been carried out in pine or spruce forests (Cramp and Perrins 1993, and references therein). Therefore, apart from how the birds consider the physical characteristics of the habitat for nesting in a non-coniferous habitat, it is of interest to know which prey types and sizes the adults bring to their nestlings in those "atypical" forests.

The original forests in the Mediterranean Basin were composed of different oak species, with Holm Oaks being the dominant evergreen tree species within altitudes ranging 500-1000 m (Blondel and Aronson 1999). However, Holm Oak forests have been largely replaced by pine plantations, which were virtually non-existent until a few decades ago in the south of the Iberian Peninsula (Maícas and Fernández 2004). Indeed, pine forests nowadays amount to 57% of the forests in the Community of Valencia, eastern Spain (Ara 2001). In the Mediterranean area, Crested Tits mainly occur in pine forests, though they have also been found in Holm Oak forests (see Tellería et al. 1999).

We studied Crested Tits in two forests in eastern Spain: a Holm Oak forest, which was an example of the ancient forests of the Mediterranean region, and a pine forest, an example of relatively new reforested areas, both placed at the same latitude. Our aim was to describe the nesting habitat, the nestling diet and the breeding performance of Crested Tits in a "typical" (coniferous) and an "atypical" (Holm Oak) forest. This will give insights into the microhabitat that Crested Tits use in these forests.

METHODS

The study was performed in two natural parks, Sierra Mariola (38º 44' N, 0º 33' W, 900 m a.s.l.) and Font Roja (38º 39' N, 0º 32' W, 1090 m a.s.l.) in eastern Spain. The distance between these areas was about 8 km. Sierra Mariola consists mostly of Aleppo Pine trees *Pinus halepensis*, and Font Roja of Holm Oaks. Despite that short distance, the vegetation composition and climate were different because of differences in altitude, orography and orientation. In both areas, human activity (e.g. silvicultural practices for preventing forest fires) has created a vegetation structure mainly characterized by regeneration of stands of even age.

During three breeding seasons (2005 to 2007), a total of 110-121 nest boxes in the pine forest and 118-140 in the Holm Oak forest were checked. All nest boxes were located using a geographic positioning system (GPS; Garmin 12). A detailed area description can be found in Chapter VII.

Breeding parameters and vegetation sampling procedure

Nest boxes were visited once a week, and active nests were visited with a pattern which allowed us to assess laying date (assuming that one egg was laid per day; 1 = 1 April), clutch size and hatching date. After hatching, nests were checked till fledging or failure, and the number of fledglings registered. Nestlings were weighed at day 14 (day of hatching = 0). Weight measurements of nestlings from the same nest were averaged to obtain a single value per nest (Eddison 2000), so the statistical unit was the brood. Only first clutches were used, and sample size varied according to the breeding trait analyzed due to nest losses along the nesting period.

Vegetation cover and species composition were quantified, and vegetation data processed according to described in Chapter VII. Three different buffers around each nest box (25, 50 and 75-m radius) were created, all within the normal foraging area for Crested Tits (Karlsson 1994). The shrub layer was included because Crested Tits were observed foraging on it (pers. obs.), and because shrubs may be considered as a secondary microhabitat for this species when food availability is scarce (Díaz et al. 1998).

We included in the sample all the nest boxes placed in the pine forest, but only 116 (83% of the maximum number present) in the Holm Oak forest; the remaining boxes were excluded for safety reasons, since the slope was too steep for vegetation sampling. All vegetation measurements were made by F. Atiénzar.

Principal component analyses (PCA) were carried out to reduce the number of habitat variables. Since we were interested in knowing the incidence of pine trees on nest placement in the Holm Oak forest, we used two measures of tree cover, one taking into account only the Aleppo Pine *Pinus halepensis* cover, and the second taking into account tree cover excluding pines. Based on broken stick analyses (Jackson 1993), PC1 and PC2 should be taken into account in further analyses for both study areas (see Table IX.1). Therefore, all the analyses were performed with PC1 and PC2, but none of the results including PC2 were significant and they are not presented here. Positive values for PC1 in the pine forest meant more mature territories, with low shrub cover and few young trees. On the other hand, as the value of PC1 in the Holm Oak forest decreased, the Aleppo Pine cover increased. We also repeated PCAs for the three buffers. Analyses were then performed with data of the three buffers, but results obtained for 50 m and 75 m were either not significant or redundant with those for 25 m, so they are not presented here.

Table IX.1. Summary of the two first components extracted from the principal component analyses for 25 m in both forests. Tree cover means the total amount of cover around the nest; Tree cover_b means the total amount of cover excluding Aleppo Pine cover. Significant correlations among the variables describing habitat structure and the factor are shown in bold.

Taula IX.1. *Resum dels dos primers factors extrets de l'anàlisi de components principals dins dels 25 m al voltant del niu als dos boscos. La coberta arbrària és la quantitat total de coberta al voltant del niu; la coberta arbrària_b és la quantitat total de coberta excloent la coberta de Pi Marítim. Els valors significatius per a cadascú dels dos primers components es mostren en negreta.*

	Pine forest		Holm Oak forest	
	PC1	PC2	PC1	PC2
Nº trunks 5-10 cm	**-0.50**	0.04	-0.13	0.13
Nº trunks > 30 cm	**0.88**	**0.17**	**0.91**	**0.27**
Mean diameter 5 thickest trees	**0.88**	**0.26**	**0.92**	0.14
Shrub cover (%)	**-0.61**	**0.53**	**0.22**	**0.66**
Aleppo Pine cover (%)			**-0.27**	**0.58**
Tree cover (%)	0.04	**-0.89**		
Tree cover_b (%)			**0.48**	**-0.72**
Eigenvalue	2.17	1.16	2.05	1.38
% variance accounted for	43.45	22.92	34.2	23.05

Diet sampling procedure

Diet was studied by videotaping (Currie et al. 1996) using digital video cameras (Sony DCR-DVD 203). They were recording during one hour per nest when nestlings were around 10 days-old (10.66 ± 0.17, range 10-13 days-old). Afterwards, DVDs were played and, for each visit, we recorded prey type and length. To identify prey types more easily, we placed wire cages (see Atiénzar et al. 2009) onto the front of the nest box before filming, so that birds entered the nest box slowly. Prey were assigned to several categories (see Table IX.2) by the same author (F. Atiénzar). Nestling diet was studied during the three years in the pine forest and only during the two first ones in the Holm Oak forest, since all nests failed in 2007.

Prey body length was estimated for all identified prey items, ignoring legs and other appendages. It was estimated by comparison with the bill length of the bird, both measured over the computer screen by placing graph paper. Actual mean bill length was measured on adult birds mist-netted in both forests when they were bringing food to their nestlings (mean bill length for the pine forest: 11.20 ± 0.20 mm, *n* = 18; for the Holm Oak forest: 10.85 ± 0.31 mm, *n* = 6, mean ± *SE*). To estimate prey length we used the appropriate mean bill length depending on the forest.

Samples collected in the pine forest belonged to 20 different nests (19 first and one second clutch) obtained between 14 April and 8 June. For the Holm Oak forest, data were obtained from 6 first clutches, 5 from nest boxes and one from a natural nest, between 12 May and 8 June.

Statistical analyses

To remove the possible non independence of data among years, when the same next box was chosen for breeding more than one year, only one data point was used for analyses concerning habitat characteristics. Thus, a total of 48 nests in which at least one Crested Tit egg was laid were used (pine forest = 35 nests, Holm Oak forest = 13 nests).

To analyze the likelihood of a nest box being occupied by Crested Tits we considered nest boxes occupied by this species (scored as 1) and those which remained empty (scored as 0). We excluded from this analysis nest boxes occupied by other putative competitors such as Great Tits *Parus major*, Coal Tits *Periparus ater*, Short-toed Treecreepers *Certhia brachydactyla* and House Wrens *Troglodytes troglodytes* (see Díaz et al. 1998), and therefore not available for Crested Tits. The best model was found using stepwise logistic regression. The effect of habitat type on breeding parameters (laying date, clutch size and the number of fledglings) and on prey sizes were analyzed using GLM (SPSS version 15.0, SPSS Inc., Chicago) showing the mean ± *SE* when needed. These nests in which no chicks fledged by predation were excluded from the analyses where the number of fledglings was involved. The effect size was calculated through the size of difference (*d*) between two variables (Nakagawa 2004). Only significant relationships and those variables included in the models will be discussed.

RESULTS

Habitat structure, nest box occupancy and breeding parameters

In their typical pine forest habitat, Crested Tits chose open mature areas including trees with a mean diameter higher than 30 cm immediately around the nest. Areas composed by young trees with a developed shrub layer were avoided (Fig. IX.1).

In the “untypical” Holm Oak forest habitat, the likelihood of a nest box to be occupied by Crested Tits increased with Aleppo Pine cover (Fig. IX.2). Mean pine cover around nest boxes where Crested Tits bred was 6.5 ± 1.8%. Instead, they avoided occupying nest boxes located in mature and dense areas and lacking pines.

Mean laying date of Crested Tits was 11 days earlier in the pine (16.43 ± 2.07) than in the Holm Oak forest (27.09 ± 2.71; $F_{1,51} = 6.15$, $d = 0.35$, $P = 0.016$). However, both mean clutch size (pine forest: 5.1

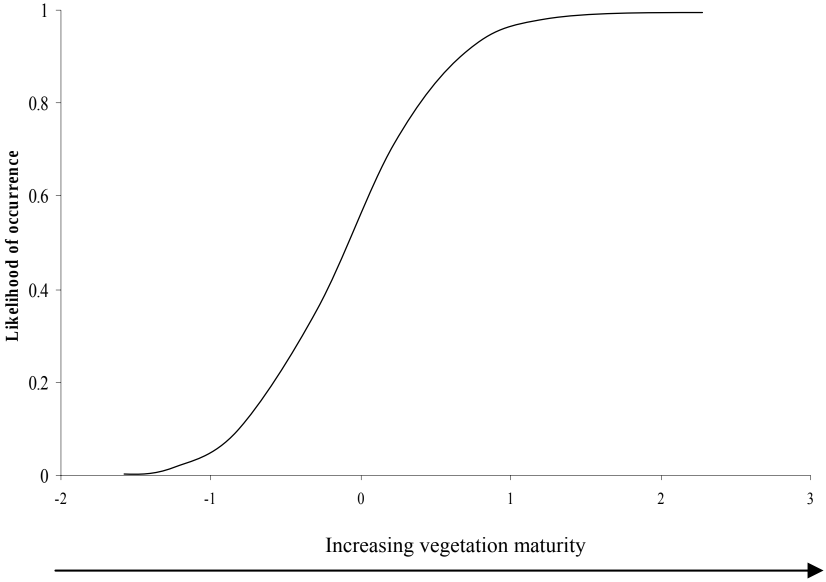


Figure IX.1. The probability of nest box occupancy by Crested Tits in the pine forest increased with the vegetation maturity of the territory within 25 m around the nest (Wald Statistic = 4.28, P = 0.039). It has been represented using $1/(1 + e^{(-(-0.30+ (3.36\cdot PC1\_25)))})$.

Figura IX.1. *La probabilitat de què una caixa niu fora ocupada per la Mallerenga Emplomallada al bosc de pins augmentà amb la maduresa de la vegetació del territori dins dels 25 m al voltant del niu (Wald Statistic = 4.28, P = 0.039). Per a la representació s’ha emprat la següent fòrmula* $1/(1 + e^{(-(-0.30+ (3.36\cdot PC1\_25)))})$.

± 0.2 eggs, *n* = 39; Holm Oak forest: 4.9 ± 0.4 eggs, *n* = 9; $F_{1,46}$ = 0.51, *d* = 0.37, *P* = 0.477) and the number of fledglings were similar between forests (pine: 4.4 ± 0.2, *n* = 24; Holm Oak: 3.5 ± 0.5, *n* = 4; $F_{1,26}$ = 2.38, *d* = 0.55, *P* = 0.135). Nestling weight did not differ significantly between forests (pine: 11.5 ± 0.2 g, *n* = 21; Holm Oak: 11.7 ± 0.3 g, *n* = 4; $F_{1,23}$ = 0.17, *d* = 0.57, *P* = 0.676).

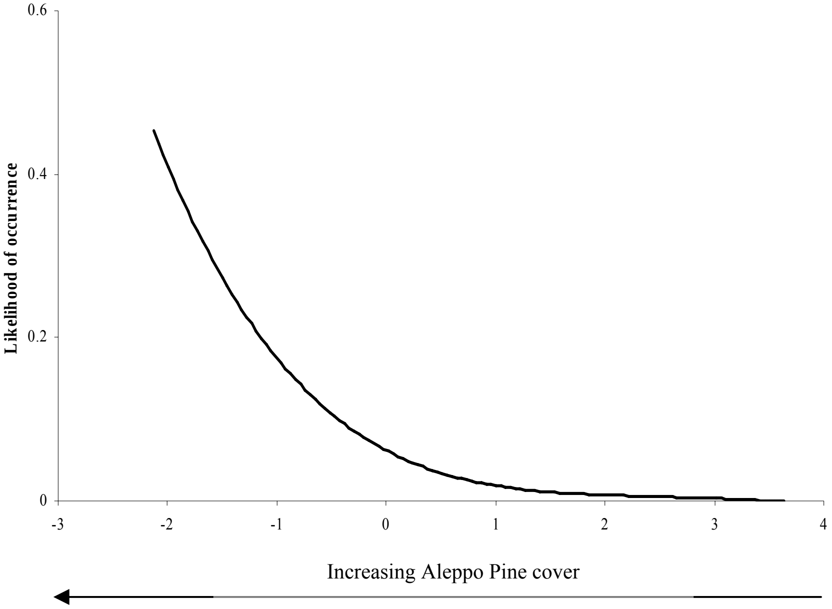


Figure IX.2. The probability of nest box occupancy by Crested Tits in the Holm Oak forest increased with the Aleppo Pine cover within 25 m around the nest (Wald Statistic = 7.80, P = 0.005). It has been represented using $1/(1+ e^{(-(-2.73 + (-1.18 \cdot PC1\_25)))})$.

Figura IX.2. *La probabilitat de què una caixa niu fora ocupada per la Mallerenga Emplomallada al bosc de Carrasca augmentà amb la coberta de Pi Marítim dins dels 25 m al voltant del niu (Wald Statistic = 7.80, P = 0.005). Per a la representació s'ha emprat la següent fòrmula* $1/(1+ e^{(-(-2.73 + (-1.18 \cdot PC1\_25)))})$.

Nestling diet, prey size and feeding frequency

A total of 362 prey was registered. We removed from this sample 68 flying ants recorded in one nest in one sampling session (in the pine forest), so sample size for further analyses was 294 prey items.

Considering the three main prey types (caterpillars, Diptera and spiders), diet composition of Crested Tit nestlings did not show differences between forests (χ^2_2= 1.63, P = 0.440). Thus, nestling diet was mainly composed by Lepidoptera larvae (64%) and Diptera (16%,

Table IX.2. Diet composition of Crested Tit nestlings in the Holm Oak forest (FR) and in the pine forest (SM), expressed as frequencies of appearance of the different food categories in the samples. Number of prey and nests are included for both sites.

Taula IX.2. *Composició de la dieta del polls de la Mallerenga Emplomallada al bosc de Carrasca (FR) i al bosc de pi (SM), expressat com les freqüències d'aparició de les diferents categories de presa a les mostres. S'inclouen el nombre de preses i nius per als dos boscos.*

	SM		FR	
	% prey	% nests	% prey	% nests
Lepidoptera adult	2.0	20.5	0.0	0.0
Lepidoptera larvae	60.1	95.0	68.3	100.0
Diptera	12.6	55.0	19.5	40.0
Spiders	5.9	55.0	2.4	20.0
Hymenoptera	3.2	25.0	0.0	0.0
Pupae	3.6	40.0	0.0	0.0
Homoptera	1.1	10.0	0.0	0.0
Coleoptera	0.8	10.0	0.0	0.0
Miriapoda	0.4	5.0	0.0	0.0
Odonata	0.4	5.0	0.0	0.0
Seeds	0.4	5.0	0.0	0.0
Not identified	9.5	50.0	9.8	60.0
Total number of prey/nests	253	20	41	6

mainly tipulids; see Table IX.2 for more details). Despite Crested Tits nestlings consumed 11 different prey types in the pine forest, though 9 of them accounted for less than 4% of the items. The percentage of unidentified prey was high in the Holm Oak, though excluding data from the natural nest, where prey identification was more difficult, it decreased to 9.8%, a similar level than in the pine forest.

Mean prey length did not vary significantly between study areas (pine: 1.89 ± 0.07 cm, *n* = 229; Holm Oak: 2.05 ± 0.16 cm, *n* =

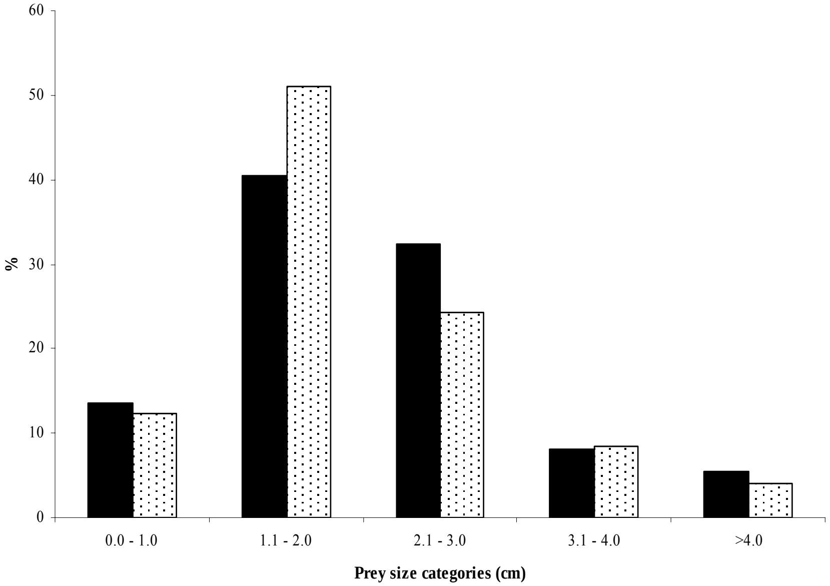


Figure IX.3. Range of prey sizes (cm) consumed by Crested Tit nestlings according to the percentage of occurrence for the Holm Oak (black bars) and for the pine forest (white-dotted bars).

Figura IX.3. *Rang de tamanys de presa (cm) consumits pels polls de Mallerenga Emplomallada en funció del percentatge d'aparició per al bosc de Carrasca (barres negres) i per al bosc de pi (barres a punts).*

37; $F_{1,264} = 0.76$, $P = 0.386$). The same result was obtained when only caterpillars were considered (pine: 2.13 ± 0.10, $n = 149$; Holm Oak: 2.06 ± 0.19 cm, $n = 28$; $F_{1,175} = 0.12$, $P = 0.735$). Prey length mostly ranged 1-2 cm in both areas. Prey above 3 cm were scarce (Fig. IX.3).

Finally, feeding frequency showed no differences between forests (pine: 11.99 ± 0.86 visits/h, $n = 18$ nests; Holm Oak: 12.29 ± 1.60 visits/h, $n = 4$ nests; $t_{20} = 0.153$, $d = 0.10$, $P = 0.880$). Each nestling received, on average, between 3 and 4 visits per hour (pine: 3.06 ± 0.26; Holm Oak: 3.85 ± 0.26 visits per hour per nestling).

DISCUSSION

Habitat requirements of Crested Tits in their typical habitat are poorly known. They excavate cavities on the trees to build their nests in dead and thick trees in open forests (Denny and Summers 1996, Mörtberg 2001). In cases where artificial nest boxes were used and this need is overcome, the species preferred areas which provided high vegetation cover created by thin trees (Summers et al. 1993). Our results showed that the probabilty of a nest box to be occupied by Crested Tits increased with the maturity of vegetation. It is difficult to explain the differences between our results and those presented by Summers et al. (1993) and Denny and Summers (1996), but differences in the overall forest structure, and in the methods to measure it, could have contributed. One plausible explanation would be the dominant Great Tits selected dense areas and thin trees (see Chapter VII) forcing

Crested Tits to occupy open areas composed by thick trees. However, the probability of nest occupancy by Great Tits was the same for those nest boxes located either in mature or in immature areas (unpubl. data; $P > 0.05$). This agreed with that found in the Chapter X, where nesting habitat characteristics were intermediate between immature and mature vegetation.

Crested Tits have their life-history mainly adapted to coniferous forests, but they also appear in other habitats, including those dominated by Holm Oaks (Herrera 1978, Maícas and Fernández 2004, present study). Some studies have reported that birds may use certain tree species within the forest (see Hartley 1953, Franzreb 1978, Holmes and Robinson 1981, Avery and Leslie 1990). For instance, Coal Tits *Periparus ater* preferred mostly coniferous trees for feeding in mixed forests (Hartley 1953). Similarly, Wood Warblers *Phylloscopus sibilatrix* occur mainly in deciduous forests, and they select patches of deciduous trees when they are breeding in coniferous forests (Avery and Leslie 1990). In the present study, we have shown that Crested Tits preferred breeding in territories including pines within the Holm Oak forest. Birds may select trees because they provide different nesting opportunities, but since we used nest boxes, this explanation could be left out. On the other hand, choosing certain tree species may be an useful strategy to further segregate the habitat among other competitors (Balda 1969). However, only 45% of the nest boxes placed in the Holm Oak forest was used for nesting by putative competitors, so competition for nesting sites should be low. Finally, differences in food availability (Díaz et al. 1998, Tremblay et al. 2003) and type (Blondel et al. 1991) that trees may contain may justify our results. It probably was not an issue of food quantity, since Holm Oaks hold more food than pines (Tremblay et al. 2003). A most suitable explanation is that Crested Tits searched for pine trees because birds might find in pines some prey types and prey species not present in Holm Oak trees. Actually, we did not find any difference in the nestling diet between nests in pine and Holm Oak forests, though we are aware that we did not identify the prey to species level and differences might arise at this level. Finally, we can not reject the idea that birds just chose for nesting microhabitats more familiar to them, selecting then those nest boxes with some pines around. In any case, it is clear from our results that Crested Tit distribution within the Holm Oak forest was affected by pine tree distribution.

Crested Tits started to breed around 10 days later in the Holm Oak forest. A similar difference was found by Maícas and Fernández (2004) when comparing two Crested Tit populations occupying similar habitats. Several factors may be behind these differences. First, there is a general pattern of delaying the starting of reproduction as altitude increases, mainly due to delays in vegetation phenology associated to a decrease in temperatures (Sanz 1998). Indeed, the peak of caterpillar abundance was later in the Holm Oak forest (see Chapter IV). Hence, this might contribute to the observed difference in our study. Second, competition with other tit species for nest boxes, along with low food availability in coniferous forests (Tremblay et al. 2003) could force

Crested Tits to breed earlier (Maícas and Fernández 2004). Indeed, 75% of the nest boxes were occupied in the pine forest, compared with the 45% in the Holm Oak forest.

Food availability depends on the floristic composition of the habitat (Díaz et al. 1998, see also Chapter IV). Considering the positive relationship between food availability and clutch size (Klomp 1970), differences reported by Tremblay et al. (2003) in food availability among forests should result in larger clutches in the Holm Oak forest. However, no differences in clutch size between forests were detected. Also, nestling diet composition, prey size, and feeding frequency did not differ between forests, suggesting that Crested Tits experienced similar food conditions in both areas. Indeed, no differences in fledgling weight were detected. Thus, our results suggest that Crested Tits breeding within the Holm Oak forest managed relatively well, though we are aware that sample sizes for the Holm Oak forests were low, and more data should be collected to be conclusive. Breeding traits observed in the pine forest agreed with those previously obtained in this habitat type (Denny and Summers 1996, Maícas and Fernández 2004). To the best of our knowledge, no previous breeding data from Holm Oak forests are available.

Not surprisingly, the few available studies on Crested Tit nestling diet have been mostly performed in coniferous forests. In these habitats, spiders and caterpillars were reported to be the main prey types consumed, although pine seeds were also found in significant quantities (Cramp and Perrins 1993 and references therein). In our study areas, Crested Tit nestlings were fed mainly with insects, and occasionally with vegetal matter. Caterpillars and Diptera amounted to 72% of total animal prey types. Contrasting with most previous studies, spiders were not the main prey type consumed. On the other hand, based on the effect of tree species over food types present (Blondel et al. 1991), one would expect to find differences in chick diet among types of forests. However, adult Crested Tits fed their chicks with similar main prey types and prey sizes in Holm Oak and pine forests. To this result might have contributed that Crested Tits in the Holm Oak forests selected mainly nearby pines to find food, and that our level of precision in the determination of prey was too rough.

Summing up, the present study has showed that those Crested Tits inhabiting in a Holm Oak forest bred surprisingly well despite being an unusual breeding habitat for the species. Clutch size, number of fledglings, nestling diet (prey type and size) and feeding frequency did not differ from those observed in a pine forest. We found that, within the Holm Oak forest, Crested Tits selected patches including pine trees for placing the nest, so the presence of pine trees around the nests might have favoured the similarity of the breeding traits between the two populations. We are certainly aware that sample sizes are low for some parameters, and further studies on these Mediterranean habitats would be desirable.

X

MECHANISMS OF COEXISTENCE OF TITS BREEDING IN A MEDITERRANEAN PINE FOREST

SUMMARY

In the nature, a matrix of organisms of many species interacting among them, lives together in the same area. Hence, some mechanisms should have evolved to allow the coexistence of close species (putative competitors). Such mechanisms have been well studied in small passerines (e.g. *Paridae*) through experiments carried out mainly during the winter. But, during the breeding season, mechanisms of coexistence are poorly known. In the present study, we looked for the mechanisms explaining the coexistence among Great *Parus major*, Crested *Lophophanes cristatus* and Coal Tits *Periparus ater* breeding in a Mediterranean pine forest. Among potential mechanisms, we explored (1) differences in the nestling diet, through the analysis of nestling diet and prey size diversity and overlap; (2) differences in nesting habitat characteristics, by using GIS techniques; and (3) differences in timing, by looking at temporal overlaps in their breeding cycles. Great Tit nestling diet was as diverse as that of Crested Tit, both preying mostly on caterpillars of similar sizes. Instead, prey diversity was lower for Coal Tits, who also fed on shorter caterpillars. Coal Tits built their nests preferently in nest boxes surrounded by mature vegetation, while Great Tits preferred those surrounded by immature vegetation; Crested Tits selected intermediate vegetation territories, not differing significantly from those of the other two species. Finally, both Great and Coal Tits overlapped to a great extent their respective breeding cycles. Instead, Crested Tits bred earlier, reducing the overlap with their congeners. Summarizing, we found differences in the three niche dimensions explored which might contribute to the coexistence of the three tit species. Crested Tits differed from Great and Coal Tits in the period of maximum food demand, and from Coal Tits also in prey size, while Great and Coal Tits differed in prey size and nest site selection, greatly overlapping their periods of maximum food demand.

RESUM

A la natura, una matriu d'organismes de vàries espècies interactuant entre ells, viuen junts al mateix hàbitat. Per tant, alguns mecanismes deuen haver-se desenvolupat per poder permetre la coexistència d'espècies pròximes (competidors).

Aquests mecanismes han sigut ben estudiats en petits paseriformes (p.e. Paridae*) mitjançant experiments duts a terme principalment durant l'hivern. Malgrat això, durant el període reproductor, els mecanismes de coexistència són poc coneguts. Al present estudi, nosaltres ens vam interessar pels mecanismes de coexistència entre la Mallerenga Carbonera* Parus major*, la Mallerenga Emplomallada* Lophophanes cristatus *i la Mallerenga Petita* Periparus ater *reproduïnt-se a un bosc Mediterrani de pi. Entre els mecanismes possibles, vàrem explorar (1) diferències en la dieta dels polls mitjançant l'anàlisi de la diversitat i solapament de la dieta dels polls i dels tamanys de presa; (2) diferències en les característiques de la vegetació del lloc de reproducció, emprant tècniques SIG; i (3) diferències en el moment d'inici de la reproducció, analitzant el solapament temporal dels cicles reproductors. La dieta dels polls de la Mallerenga Carbonera fou tan diversa com l'obtesa en polls de Mallerenga Emplomallada, tot dos alimentant-se d'orugues de tamany similar. En canvi, la diversitat de la dieta en polls de Mallerenga Petita fou menor, composta per orugues més menudes. Dita espècie va niuar a caixes nius envoltades per vegetació madura, mentre que les Mallerengues Carboneres ho feren als llocs on predominava la vegetación inmadura; les Mallerengues Emplomallades seleccionaren un tipus de vegetació intermèdia, no sent diferent en comparació a les altres dos espècies. Finalment, ambdúes espècies, la Mallerenga Carbonera i la Mallerenga Petita solaparen en gran mesura els seus cicles reproductors. Per altra banda, les Mallerengues Emplomallades es reproduiren abans, reduint el solapament amb les altres espècies. En resum, vàrem trobar diferències en les tres dimensions de níntxol explorades que podrien permetre la coexistència de les tres espècies d'aus. Les Mallerengues Emplomallades es diferenciaren de les altres dos en el moment en què els polls mostraven màxima demanda d'aliment, i a més, amb* *la Mallerenga Petita en relació al tamany de presa. Mentre, la Mallerenga Carbonera i la Petita es diferenciaren en el tamany de presa i lloc per a la reproducció, no així amb els seus respectius cicles reproductors que es solaparen en gran mesura.*

INTRODUCTION

A central issue of community ecology is searching for mechanisms allowing the coexistence of similar species whose distributions overlap geographically and that share some resources present in the environment (Begon et al. 2006). Such species with similar requirements (e.g. prey sizes) may coexist in the same habitat if one of the two coexisting species "displaces" the other in one or more morphological, ecological or physiological characters (Brown and Wilson 1956, Martin and Thibault 1996). For instance, in birds, having beaks of different sizes allows preying on different prey sizes, therefore reducing competition (Török 1987, Matthysen et al. 1991, Grant and Grant 2006). Additionally, putative competitors may coexist by selecting different vegetation types/characteristics for breeding (Fasola and Alieri 1992, Dellinger et al. 2007). For example, Fasola and Canova (1992) suggested that interspecific differences in habitat preferences for breeding permitted the coexistence of different seabird species by decreasing territorial aggression. On the other hand, species could also coexist by displacing their periods of maximum food demand, i.e. not overlapping the breeding cycle. For instance, both Balearic *Procellaria puffinus mauretanicus* and Cory's Shearwaters *Calonectris diomedea* take similar food and breed at the same area, but the first species displaced its breeding cycle earlier than usual, thus reducing competition (Brown and Wilson 1956).

Most of studies on small passerines analyzing the mechanisms of coexistence of putative competitors have been carried out during winter (Hogstad 1978, Alatalo 1982, Fraticelli and Guerrieri 1988, Dhondt 1989, Sorensen 1997, Park et al. 2005). The general trend is a greater segregation in foraging sites among coexisting species (Alatalo 1982, Alatalo et al. 1986b, Dhondt 1989). Instead, studies on competition during the breeding season in natural conditions are scarce (Minot 1981, Török 1987, Dellinger et al. 2007), though competition also occurs during this season (Dhondt 1977, 1989, Minot 1981, Török and Tóth 1999). Here, differences in prey size, nesting habitat characteristics, or breeding time acquired more relevance in the competition process (Brown and Wilson 1956, Török and Tóth 1999).

European tits *Parus* spp. is one of the best studied groups of birds in terms of mechanisms of coexistence (Alatalo 1982 for a review), because their activity is relatively easy to observe in the field and because several tit species usually coexist in the same habitat (Perrins 1979, Cramp and Perrins 1993). The mechanisms of coexistence between Great *Parus major* and Blue Tits *Cyanistes caeruleus* are well known. As an example, Blue Tits depleted the food supply sufficiently to affect negatively Great Tit breeding success (Minot 1981). Both species could coexist because Blue Tits are better exploiting smaller caterpillars, the most abundant caterpillar sizes. Hence, fewer caterpillars get larger sizes to be consumed by Great Tits (Török 1987).

Great Tits are often sharing the same habitat with other tit species such as Crested *Lophophanes cristatus*, and Coal Tits *Periparus ater* (Cramp and Perrins 1993) showing high overlap in the space used for feeding (Obeso 1987, see also Hartley 1987). Apart from it, little more is known over the mechanisms of coexistence during the breeding season (Park et al. 2005), when the amount of food can be limited even during the peak of food abundance (e.g. evergreen forests, Tremblay et al. 2003, see also Chapter IV). Furthermore, to the best of our knowledge, no studies are available on other mechanisms of coexistence as differences on either timing of breeding or nest site selection.

Given a stable tit community coexisting in sympatry in a pine forest, we focused on how its constituent species have come to share the same habitat, by looking for some mechanisms of coexistence: prey diversity and size in the nestling diet, nesting habitat characteristics, and degree of overlap in the period of maximum food needs.

METHODS

The study was carried out in a natural park, Sierra Mariola, 38º 44' N, 0º 33' W, 900 m a.s.l.) in eastern Spain. For further information, see Chapters II and VII.

Breeding phenology

Data on breeding traits were gathered during 2005-2007. A total of 121 nest boxes were visited once a week. Active nests were visited with a pattern which allowed us to assess important breeding traits for the present study such as laying date (assuming that one egg was laid per day; 1 = 1 April) and hatching date. This last parameter was useful to assess the overlap in the period of maximum food needs, i.e. hatching date + 10 days (Barba et al. 2009). Differences in mean laying date among species were conducted with linear mixed models (LMM). We included year and species as fixed factors; female identity as a random effect; and laying date as dependent variable.

To calculate the overlap in the breeding cycle among species, we used the index $C_{\hat{o}} = 1\text{-}0.5 \cdot (\Sigma \left| p_{xi} - p_{yi} \right|)$. For it, we created periods of 5 days long. For each period and for each species, we assessed the proportion of nests containing chicks 10 days-old. Therefore, p_{xi} is the proportion of nests for the species x during the period i (Schoener 1970). Values of niche overlap range from 0 (lack of overlap) to 1 (complete overlap).

Nestling diet

Food consumed by the nestlings was recorded by filming a total of 129 first clutches (86 Great, 20 Crested and 23 Coal Tits) containing chicks 8-12 days-old. Animal prey were identified to the level of order when possible. Filming was done during three years, 2005-2007.

Prey body length was estimated for all identified prey items, ignoring legs and other appendages. It was estimated by comparison with the beak length of the bird, both measured over the computer screen by placing graph paper (Atiénzar et al. 2009). Actual mean beak length was measured on adult birds mist-netted in the study area. Only measures of caterpillars, the main prey consumed by tits (Perrins 1979), will be used for further analyses. To look for the most consumed caterpillar sizes as well as to estimate prey size diversity, caterpillar sizes were assigned to six categories (< 10 mm, 10-14, 15-19, 20-24, 25-29, > 29 mm, Gibb and Betts 1963). Data were analyzed by using GLM, showing the mean ± *SE* when needed.

We estimated the Shannon-Weaver diversity index ($H' = \Sigma$ $p_i \cdot \ln p_i$) in which p_i is the proportion of the *i*th prey (or size) category created (e.g. Herrera 1976, Magurran 1988). For the niche overlap we used the same formula used above for the overlap in breeding cycles. Here, p_{xi} is the frequency of food group i (prey type or size class) in the diet for the species x. t-tests were used to assess for differences in prey diversity (e.g. Magurran 1988).

Nesting habitat characteristics

Vegetation cover and species composition were quantified, and vegetation data processed according to described in Chapter VII. Because of a proper scale in studies of habitat segregation by congeners is primordial (Haila and Hanski 1987, Martin and Thibault

1996), we estimated different environmental variables for three different buffers around each nest box (25, 50 and 75-m radius). Vegetation maps were created for a total of 247 first clutches (94 great, 31 crested and 43 coal tits) in which at least one egg was laid. When a certain nest box was occupied for the same species for more than one year, only one data point was used for the analyses.

A principal component analysis (PCA) was carried out to obtain a small set of factors that summarized vegetation structure (Table X.1). Two factors were extracted from the analyses. For the analyses we chose the PC1, which summarized the degree of maturity of the vegetation in the area considered: positive values of PC1 meant

Table X.1. Correlations among the variables describing habitat characteristics and the two first principal components for the three buffers performed. The percentage of variance explained for both components and for each buffer is also presented. Significant correlations among the variables describing habitat structure and the factor are shown in bold.

Taula X.1. *Correl.lacions entre les variables que descriuen les característiques de l'hàbitat i els dos primers components principals per als tres radis creats. Es mostra el percentatge de la variança per als dos components principals i per a cadascú dels radis. Els valors significatius per a cadascú dels dos primers components es mostren en negreta.*

	25 m		50 m		75 m	
	PC1	PC2	PC1	PC2	PC1	PC2
Nº trunks 5-10 cm	**-0.73**	**0.12**	**-0.72**	0.09	**-0.71**	-0.07
Nº trunks > 30 cm	**0.83**	**0.21**	**0.83**	**0.12**	**0.83**	-0.07
Mean diameter 5 thickest trees	**0.88**	**0.23**	**0.88**	**0.19**	**0.88**	-0.12
Shrub cover (%)	**-0.54**	**0.64**	**-0.55**	**0.57**	**-0.58**	**-0.50**
Tree cover (%)	-0.06	**-0.85**	**-0.13**	**-0.86**	**-0.20**	**0.89**
Eigenvalue	2.27	1.24	2.30	1.13	2.35	1.06
% variance accounted for	45.43	24.77	46.01	22.62	46.92	21.25

areas where the vegetation was more mature. PC1 was used in GLM analyses to assess for the mean nesting habitat characteristics around the nests. All analyses were carried out using SPSS (version 15.0, SPSS Inc., Chicago).

Table X.2. Nestling diet composition in Great (Pm), Crested (Lc) and Coal Tits (Pa) in the pine forest expressed as frequencies of appearance of the different food categories in the samples.

Taula X.2. *Composició de la dieta en polls de Mallerenga Carbonera (Pm), Mallerenga Emplomallada (Lc) i Mallerenga Petita (Pa) al bosc de pi, expressat com la freqüència d'aparició de les diferents categories d'aliment a les mostres.*

Prey types	Pm	Lc	Pa
Lepidoptera larvae	55.7	60.1	61.6
Not identified	11.2	9.5	15.2
Pupae	8.1	3.6	1.7
Spiders	6.3	5.9	12.7
Orthoptera	4.9	0.0	3.0
Diptera	3.8	12.6	3.4
Seeds	4.4	0.4	0.0
Insect eggs	2.6	0.0	0.0
Himenoptera	1.4	3.2	0.8
Coleoptera	0.7	0.8	0.8
Lepidoptera adult	0.4	2.0	0.0
Odonata	0.2	0.4	0.4
Blattaria	0.1	0.0	0.0
Hemiptera	0.0	0.0	0.4
Miriapoda	0.0	0.4	0.0
Homoptera	0.0	1.2	0.0
Total samples	**837**	**253**	**237**

RESULTS

Prey type and size: prey diversity and niche overlap

A total of 19 prey types were distinguished in the diet of the nestlings of the three studied tit species. Caterpillars were the main prey type brought in all species, amounting to more than 55% (Table X.2). Pupae, Diptera and spiders were the second prey type most consumed by Great, Crested and Coal Tits respectively. Spiders were consumed by all species with percentages of occurrence higher than 5%.

Dietary diversity was similar for Great and Crested Tits, while that for Coal Tits was lower (Table X.3). Dietary overlap for all possible combinations of the three species was relatively high ($C_{\hat{o}} \approx 0.83$).

Prey size diversity was similar for all three species. The overlap was higher between Crested and Great Tits ($C_{\hat{o}} = 0.93$) indicating almost complete overlap, being $C_{\hat{o}}$ around 0.78 for the remaining combinations. On the other hand, differences in beak lengths appeared among all three species ($F_{2,154} = 33.23$, $P < 0.001$; Tukey *post hoc* tests, $P < 0.05$ in all cases). Great Tits had the largest beak (11.68 ± 0.08 mm, $n = 78$), Crested Tits intermediate beak sizes (11.20 ± 0.21 mm, $n = 18$) and, Coal Tits the shortest beak (10.75 ± 0.07 mm, $n = 61$). Mean caterpillar size consumed differed also among species ($F_{2,725} = 14.05$, $P < 0.001$), Coal Tits consuming shorter caterpillars than Great and Crested Tits (see Table X.3; Fig. X.1).

Table X.3. Indexes of prey type and size diversity in Great (Pm), Crested (Lc) and Coal Tits (Pa) as well as caterpillar size (mean ± *SE*, cm). Differences in such indices were assessed using t-tests. ANOVAs were used for differences in caterpillar sizes. Tukey *post hoc* tests were used to assess different statistically groups. Sample sizes in brackets.

Taula X.3. *Índexs de la diversitat del tipus d'aliment i de tamany de presa així com el tamany d'oruga (mitja ± ES, cm) en la Mallerenga Carbonera (Pm), Mallerenga Emplomallada (Lc) i Mallerenga Petita (Pa). Per evaluar les diferències en dits índexs, es van emprar el test de la t. En canvi, anàlisis de la variança s'empraren per evaluar les diferències en tamanys d'oruga. Tests a posteriori s'empraren per veure grups que diferien estadísticament. Els tamanys mostrals apareixen entre parèntesi.*

	Pm	Lc	Pa	Pm-Lc	Pm-Pa	Lc-Pa
Prey type diversity index (H')	1.35	1.20	0.97	$t_{362} = 1.63$, $P > 0.05$	$t_{348} = 9.73$, $P < 0.05$	$t_{416} = 2.00$, $P < 0.05$
Prey size diversity index (H')	1.71	1.66	1.64	$t_{192} = 1.34$, $P > 0.05$	$t_{184} = 1.46$, $P > 0.05$	$t_{268} = 0.60$, $P > 0.05$
Caterpillar size	2.21 ± 0.47 (454)	2.27 ± 0.92 (133)	1.74 ± 0.63 (141)	$P = 0.790$	$P < 0.001$	$P < 0.001$

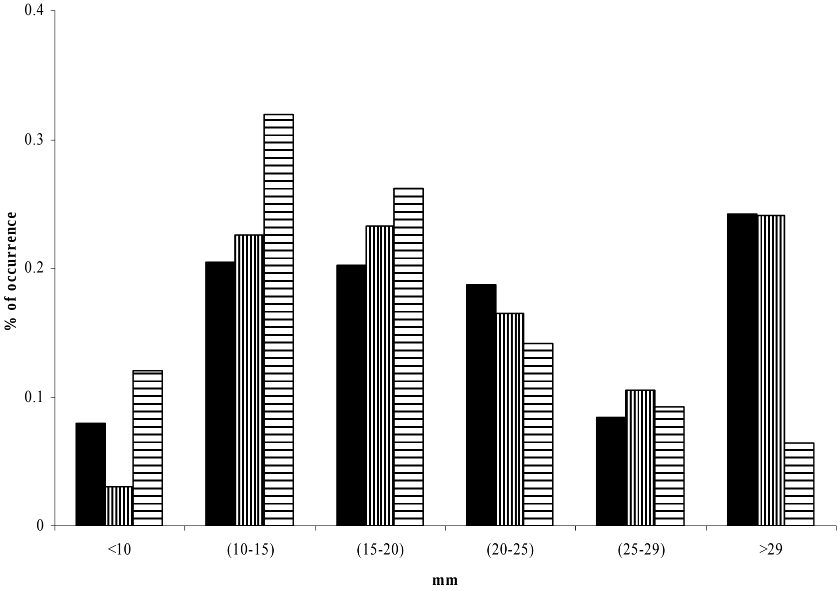


Figure X.1. Percentage of caterpillar prey size occurrence in the diet of Great Tit (black columns), Crested Tit (vertical lines) and Coal Tit nestlings (horizontal lines) in the pine forest.

Figura X.1. *Percentatge d'aparició de tamanys d'oruga a la dieta dels polls de la Mallerenga Carbonera (barres negres), Mallerenga Emplomallada (línies verticals) i Mallerenga Petita (línies horitzontals) al bosc de pi.*

Nesting habitat characteristics

The maturity of vegetation around the nest differed among the three tit species ($F_{2,165} = 4.45$, $P = 0.010$). Coal Tits bred in areas where the vegetation was more mature, whilst Great Tits did it preferently in immature areas when considering 50-m radii (Fig. X.2; Tukey *post hoc* tests, $P < 0.05$). The maturity of the vegetation patch surrounding Crested Tit nests was between those of Great and Coal Tits (Fig. X.2), not differing significantly from none of them (Tukey *post hoc* tests, $P > 0.1$ in both cases). Similar findings were obtained for 25 m and 75 m (all $P < 0.05$). Finally, there were no differences among years in the mean nesting habitat characteristics ($P > 0.1$).

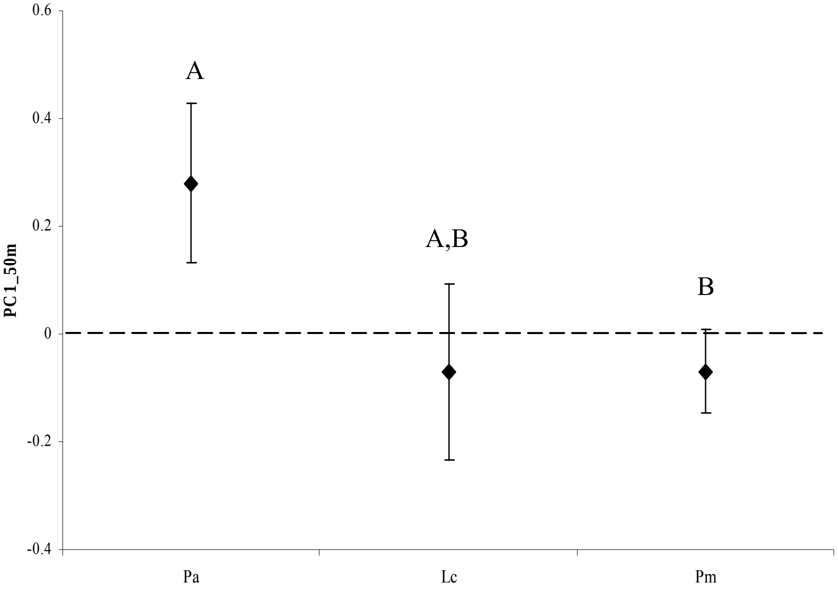


Figure X.2. Mean nesting habitat requirements for Coal Tits (Pa), Crested Tits (Lc) and Great Tits (Pm) in the pine forest 50 m around nest boxes. Letters above the standard error meant different statistically groups. Mean ± *SE* are also showed.

Figura X.2. *Promig dels requeriments d'hàbitat per niuar en les Mallerengues Petites (Pa), Mallerengues Emplomallades (Lc) i Mallerengues Carboneres (Pm) als 50 m al voltant del niu al bosc de pi. Les lletres assenyalen els grups estadisticament diferents. Es mostren les mitges ± ES.*

Timing of breeding

Crested Tits started breeding earlier (16.43 ± 2.07, $n = 42$ nests) than both Great (29.34 ± 0.77, $n = 164$) and Coal Tits (33.58 ± 1.32, $n = 45$; $F_{2,247} = 33.70$, $P < 0.001$; Tukey *post hoc* tests). As a consequence, there were differences among species in the time when chicks were 10 days-old: Crested Tit nestlings reached 10 days, 15 days earlier (43.91 ± 2.14, $n = 33$) than Great Tits (58.11 ± 0.76, $n = 137$), and those of Coal Tits even one week later (64.82 ± 1.73, $n = 33$; $F_{2,200} = 41.63$, $P < 0.001$, Tukey *post hoc* tests, all pairwise comparisons with $P < 0.05$). Thus, the overlap in the dates of maximum food demand was relatively low: 0.31 between Great and Crested Tits, and 0.13 between Crested and Coal Tits, being higher (0.50) between Great and Coal Tits.

DISCUSSION

The diet of Great Tit nestlings is well known in many environments (Cramp and Perrins 1993). The amount of caterpillars found here was in accordance with that found in other studies carried out in pine forests (49-60%, Cramp and Perrins 1993).

Nestling diet of Coal Tits is also known, with a variety of results with either spiders or aphids as the main prey (see Cramp and Perrins 1993; Monrós et al. 1997). In coniferous forests, caterpillars have been reported to amount between 0.70% and 23%, being the main prey type in nestling diet very seldom (Cramp and Perrins 1993). In this context, it is noticeable the high contribution of caterpillars to the nestling diet found in the present study, being of the same magnitude as for the other two tit species studied. Our results resembled to those found in deciduous forests, where caterpillars amounted to 51% of the total prey items (Cramp and Perrins 1993). Spiders seem to have great relevance on Coal Tit nestling diet because they are always among the two main prey types consumed (Cramp and Perrins 1993, Monrós et al. 1997, present study).

Finally, few studies on the Crested Tit nestling diet performed in coniferous forests are available. Spiders and caterpillars were reported to be the main prey types consumed, although pine seeds were also found in significant quantities (Cramp and Perrins 1993, and references therein). In the present study, caterpillars and Diptera amounted to 72% of total prey (see Chapter IX). Contrasting with most previous studies, spiders were not the main prey type consumed.

In our study area, nestling diet was similar for Crested and Great Tits. In fact, dietary diversity did not differ much, with values of diet overlap close to 0.90. Though Coal Tits preyed on less prey diversity, they also showed high diet overlap with their congeners. Hence, our results would indicate that all three tit species had similar nestling diet. We are aware that our level of prey identification was too rough, and that identifying caterpillars to the level of species might have produced more differences. For instance, Török (1985) showed that Great and Blue Tits fed on similar prey types, but both species were segregated through prey species consumed.

Prey size is an important element to take into account to understand the mechanisms of coexistence (e.g. Guitián 1985, Török 1985, 1986, Török and Tóth 1999, García and Arroyo 2005). In tits, most studies considering prey size to study coexistence of putative competitors have been done with Great and Blue Tits, generally concluding that Blue Tits consumed smaller prey and this facilitates their coexistence (Török and Tóth 1999). Following the reasoning that species with shorter beak should prey upon smaller prey (Betts 1955, Guitián 1985), and considering that the Coal Tit is a subordinate species in the competition process (Suhonen et al. 1994, Fyhn and Sorensen 1997), we would expect that Great Tits would prey upon larger caterpillars than Coal Tits, even when feeding on the same prey species on the same dates and in the same habitat (see also Gibb and Betts 1963, Monrós et al. 1997, Park et al. 2005). Our results agreed with expectations, Coal Tits taking significantly shorter prey than Great Tits. Moreover, prey sizes for both species were within normal values obtained in other studies (Török 1985, Gibb and Betts 1963, Monrós et al. 1997, Török and Tóth 1999). Such expectations were also accomplished for the Crested-Coal Tit comparison: Crested Tits, with longer beaks, preyed on longer caterpillars than Coal Tits. Finally, we would also expect that Crested Tits preyed upon shorter prey than Great Tits, but differences in beak lengths between these species were not translated into different prey sizes. We are not aware of information over prey sizes consumed by Crested Tits in other places, so could not tell whether prey sizes consumed here are within the normal range for the species. In any case, prey size would not be an important factor of food segregation between Great and Crested Tits, but it seems to be suitable to explain the coexistence of Coal Tits with their congeners.

Sometimes, subtle differences in nesting habitat characteristics make possible the coexistence of putative competitors (Fasola and Canova 1992). Here, Great and Coal tits bred clearly in different areas, the former did it in territories with immature vegetation whilst the latter did it in mature ones. We are not aware of information over other studies analyzing the vegetation characteristics around nests for those species. On the other hand, Crested Tits did not differ in mean nesting characteristics from their congeners. We may conclude that nesting habitat characteristics could act as mechanism of coexistence between Great and Coal Tits, but not so for Crested Tits.

A third niche dimension considered in this study was the timing of breeding. Breeding at different times would avoid the coincidence of the periods of maximum food demand among species with similar needs. Indeed, we found that the difference among such periods between Crested and Great Tits was 15 days, showing, therefore, low overlap. Breeding too early might cause problems if the period of maximum food demand occurs when food availability is not at its peak (Naef-Daenzer and Keller 1999, see also Chapter IV).

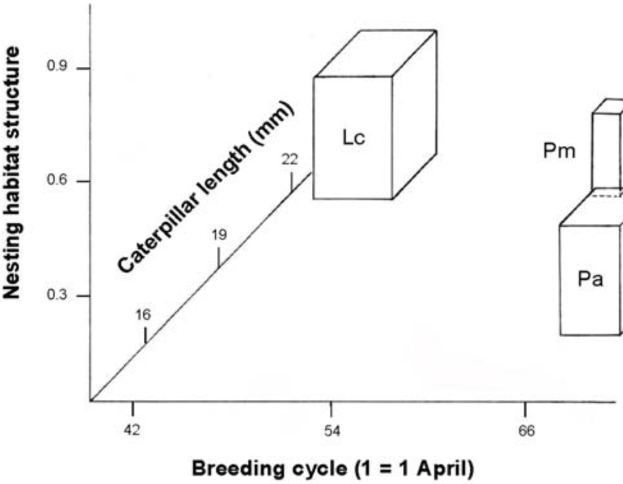


Figure X.3. Overview of the ecological niche with three dimensions, breeding cycle, caterpillar length and nesting habitat structure of Great (Pm), Crested (Lc) and Coal Tits (Pa).

Figura X.3. *Visió general del níntxol ecològic amb les tres dimensions considerades, cicle reproductor, llargària de les orugues i l'estructura de l'hàbitat al lloc de reproducció de la Mallerenga Carbonera (Pm), Mallerenga Emplomallada (Lc) i Mallerenga Petita (Pa).*

However, when Crested Tit chicks were 10 days-old, caterpillar biomass in the environment (18.11 mg/day $\cdot$m^2) was within the mean range during the peak of caterpillar abundance (17.87-20.53 mg/day $\cdot$m^2, Chapter IV) and, in fact, the mean length of caterpillars brought to their chicks was similar to those of Great Tits. On the other hand, Coal Tits bred not much later than Great Tits causing a relatively high overlap in their breeding cycles. Differences in the timing of the breeding season might also be due to differences in life-history strategies. Laying earlier for example may allow the crested tits to lay second clutches (e.g. Cramp and Perrins 1993).

Without doubt, well-done experiments provide the most convincing tests to assess the existence of competition. The role of nonexperimental results is much less clear, since it is difficult to identify all the possible alternative environmental causes on niche variation (Alatalo 1982, Alatalo et al. 1986b). However, the patterns found in nature are crucial for the formulation and evaluation of hypothesis that provides possible causal explanations of natural phenomena (see Beaver and Baldwin 1975). Therefore, it is not legitimate to omit nonexperimental evidences if reasonable alternative explanations cannot be pointed out (Alatalo et al. 1986b). Our results highlight that not only one niche dimension can be important in explaining the mechanisms of coexistence among similar species, but some sort of complex combination of prey type, prey size, microhabitat characteristics, and the timing of breeding could contribute to the coexistence (Fig. X.3., see also Beaver and Baldwin 1975, Herrera 1981).

XI

MAIN RESULTS AND GENERAL DISCUSSION

In the present thesis, several life-history traits have been treated from different points of view. As a whole, it has been showed how birds breeding in Mediterranean evergreen habitats have coped with several environmental constraints and trade-offs. Here, I will highlight and discuss the main results obtained.

The Mediterranean region is characterized by strong seasonality (Blondel and Aronson 1999); hence there is only a limited period each year in which conditions for growth and reproduction are optimal. Therefore, a relevant question to ask is how organisms can time their reproduction to the right time of their prey cycle. Great Tits *Parus major* living in temperate forests use temperature as a cue to time their breeding activities (Visser and Both 2005). Thus, birds start laying earlier in warm springs because trees start leafing earlier, and insects emerge earlier (van Asch 2007). In such forests, a right timing of bird reproduction to prey cycle has positive effects on fitness (Perrins 1991). However, how Great Tits time their reproduction, and the fitness consequences of it are poorly known in evergreen forests in the Mediterranean region (Belda 1996, Iglesias 1996).

We addressed these questions by studying two Mediterranean Great Tit populations breeding in Mediterranean evergreen forests, a Holm Oak *Quercus ilex* and a pine forest. By using frass-collectors under the canopy, we could monitor food availability and food phenology (see more in Chapter IV). The window when food was more abundant ranged between one (Holm Oak forest) and two weeks (pine forest), which is relatively short compared with the three weeks found in deciduous forests (Visser et al. 2006). Thus, this was an important reproductive constraint in those evergreen habitats. Indeed, we found that fledglings produced by birds which mistimed reproduction (i.e. those for which the peak of food demand by the nestlings were outside the window of maximum prey availability) were lighter than those produced by birds which timed correctly. Based on the fact that nestling weight is translated to survival prospects (Greño et al. 2008), and thus on recruiment rate, there should be a strong pressure to time reproduction to a small time window.

As found in previous studies, Great Tits of our two studied populations in forest habitats used ambient temperature as cue to start breeding, delaying reproduction in colder springs. However, only for birds breeding in the pine forest this cue was really effective, and this population correctly timed reproduction to food phenology (see Chapter IV). On the other hand, birds breeding in the Holm Oak forest, though also responded to the same environmental cue, failed to time properly the peak of food needs with that of food availability – i.e. they were maladapted to local feeding conditions. We suggest that this was probably caused by asymmetrical dispersal from the surrounding and most common habitat (pine forest) where Great Tits did match food phenology.

Nestlings of nidicolous birds depend completely on adults to get the necessary nutrients for their development. Therefore, adult care through feeding trips is required to satisfy the food demands of the rapidly developing young (Chapter V). The record of feeding behaviour allows having a better identification of the factors which might affect parental care, and how adults respond to them. By using mechanical counters in a large number of Great Tit nests, we found that feeding rates (1) increased with nestling age up to the 10-12 d of life, keeping constant afterwards; (2) increased linearly with brood size; (3) declined along the season; and (4) did not vary with time of day (Chapter V). The general patterns found here agreed with those previously found in this and other species, though this is the first study with such a large number of samples (more than 200 nests) and with a proper statistical treatment.

This study also clarified the cause of some patterns. For instance, the lack of increment of feeding rates towards the end of the nestling phase was mostly a consequence of brood reduction, and not to fatigue of adults as it was claimed in previous studies. Also, the increase of per nest feeding rates with brood size was accompanied by a decrease in per-nestling effort. This agreed with the Trade-off Hypothesis (see more in Chapter V), i.e. parents might be optimizing costs and benefits of feeding nestlings in the long term (Nur 1984a). Since brood size experiments are required to demonstrate this, we tackled this question in Chapter VI.

One of the central questions in parental investment is whether the number of offspring raised is adjusted to parental capacity, i.e. the fitness consequences of clutch size variation (see for a review Both 1998, Pettifor et al. 2001). To solve such question, brood size experiments, where the fitness of enlarged and reduced broods could be compared with that of original brood sizes, are required (Both 1998). Some studies have shown that the chosen (original) clutch size maximized fitness, while others showed that birds were able to raise clutch sizes larger than the original one (see also Chapter VI). We designed an experiment where three experimental groups, with similar hatching dates and clutch sizes, were created by exchanging newly born nestlings: enlarged, control and reduced broods. We analyzed the effects of brood manipulations over some factors, as adult feeding behaviour, adult and nestling weight and condition, number of fledglings, fledging success, and the estimated number of recruits. What we obtained was that birds did not increase their effort with brood size, so each nestling received fewer visits than those from control broods. Adult weight and fledging success were not affected by brood manipulations. Enlarged broods raised more but lighter fledglings, but they showed lower post-fledging survival probabilities. As a consequence, fewer fledglings were expected to be recruited in the following season. On the other hand, birds rearing reduced broods decreased their effort proportionally. As a consequence, each nestling received similar amount of visits than those from control broods. There were no differences in post-fledging survival probabilities between control and reduced broods, although the estimated number of chicks to be recruited in the following season was lower in reduced ones (see Chapter VI). Our results were in accordance with the life-history for our studied tit population – a higher inter-annual adult survival probability selected for individuals who limit current reproductive investment (Belda and Orell 2003). These results support the Individual Optimization Hypothesis (see Chapter VI), i.e. Great Tits were raising a brood size that maximizes their individual fitness. Therefore, what the descriptive study suggested (see above, also Chapter V) was refuted later experimentally.

The environment or habitat surrounding nests of forest songbirds has been found to influence reproductive success. Several studies have analyzed different habitat features (e.g. habitat fragmentation, Olson and Grubb 2007). In Great Tits, landscape studies have been carried out across their distribution range (see more in Chapter VII). Those studying the effect of forest type found that birds breeding in deciduous forests showed higher breeding success than those breeding in evergreen forests. The underlying factor explaining these results was the greater food abundance present in deciduous forests (Tremblay et al. 2003, see more in Chapter IV). However, various factors affecting individuals may act at different spatial scales. For example, Huhta et al. (1998) found that, whilst nest site selection in Pied Flycatchers *Ficedula hypoleuca* occurred at two levels of scale, differences in reproductive success existed only at the microhabitat scale.

Nowadays, there is not a solid understanding of the processes underlying patch use in breeding Great Tits. In the present study, we analyzed the effects of habitat features over breeding traits in two Great Tit populations by using a multilevel approach, macrohabitat and microhabitat. For the macrohabitat level, we found that birds breeding in the Holm Oak forest started laying one week later, laid more eggs per clutch, produced more hatchlings and fledglings, and their chicks fledged in better condition, than those of the pine forest. Such results agreed with the fact that Holm Oak forests held more food than pine forests (Chapter IV). On the other hand, for the microhabitat level, we measured some variables related to vegetation structure around each nest box (Chapter VII). Breeding success was higher in those nests located in immature territories, characterized by dense vegetation, since nest predation was lower there (Chapters VII and VIII). This agreed with the total-foliage hypothesis that predicts a decrease in predation risk as the total vegetation increases around the nest. The mechanism proposed is that greater foliage density inhibits, among others, transmission of visual cues by prey (Martin 1993). Therefore, different factors seemed to be operating at different levels:

food availability at the macrohabitat level and nest predation at the microhabitat level. These constraints contribute to explain differences in breeding success of the Great Tit populations studied across and within-forests.

Using different spatial scales allows also knowing why some untypical species could occur in certain habitats (see more in Chapter IX). Hence, we also used two levels of analysis to answer why Crested Tits *Lophophanes cristatus*, a coniferous bird species, were breeding in an untypical forest (Holm Oak forest, see Chapter IX). Moreover, we were interested in knowing how differences in the dominant type of vegetation might influence some breeding traits and feeding ecology (nestling diet, prey size and feeding frequency) of this species. We found that Crested Tits bred in those areas within the Holm Oak forest containing at least 5% of pine tree cover. On the other hand, nestling diet was similar between populations breeding in Holm Oak and pine forests, and was mainly composed by caterpillars. Moreover, both prey size, ranging from 1 to 2 cm length, and breeding success (clutch size, number of fledglings, fledgling weight) were similar between forests. Finally, adults visited nest boxes at a similar rate in both forests. Therefore, we have showed that those Crested Tits inhabiting a Holm Oak forest bred surprisingly well despite being an unusual breeding habitat for the species, as long as there were some pines around the nest box. This study was the first describing the nestling diet of this species in a Holm Oak forest, and gives more information about nestling diet in coniferous forests (Cramp and

Perrins 1993). Additionally, this thesis also highlights the importance of multilevel approaches in habitat-species relationships, showing the importance of pine trees for the presence of Crested Tits in a non coniferous forest.

Birds are the best studied group in terms of sexual selection by means of conspicuous colours and other visual signals (Andersson 1994). One of the most striking questions in studies of sexual selection is why individuals mate assortatively. Such type of mating occurs when male colouration signals some benefit for female breeding success (see Chapter VIII). To the best of our knowledge, most of studies which have searched for assortative mating by plumage colouration in Great Tits and other species have found it (Andersson 1994; see Hegyi et al. 2007 for an exception). However, few studies have introduced habitat quality as a potentially relevant variable in the analyses. For example, Alatalo et al. (1986a) showed that Pied Flycatchers did not mate assortatively. In this population, male colouration did not signal benefits for female breeding success, and females paid more attention to habitat features than to male colouration.

Here, we were interested in knowing whether two Mediterranean Great Tit populations mate assortatively under the constriction of high predation level using plumage colouration, tarsus length and body weight. Males were more colourful than females. However, there was not assortative mating by any trait analyzed (see Chapter VIII). Male colouration was related neither to nest productivity nor to feeding rates. Hence, these male characteristics were not related to female breeding success. On the other hand, female colouration was related to nest productivity through vegetation characteristics: bright females showed high nest productivity in immature vegetation patches. Nest productivity for dull females was not affected by the vegetation features. Nest predation was lower in immature vegetation patches (Chapters VII and VIII). Therefore, it seemed that in environments where nest predation is high, colourful females paid more attention to habitat features than to male characteristics. Few studies to date have convincingly demonstrated that females actually preferred territory characteristics rather than male ones (see Chapter VIII). We have shown that nest predation is a constraint affecting not only breeding success, but also female mate choice.

Some mechanisms have evolved to allow the coexistence among putative competitors living in the same area. In small passerines, these mechanisms in small passerines have been analyzed during the winter, when food is supposed to be in short supply (Alatalo 1982 for a review). Few studies have addressed it during the breeding period (see Chapter X). Here, we aimed to analyze some mechanisms potentially allowing the coexistence of three tit species, Great, Crested and Coal Tits *Periparus ater* inhabiting a Mediterranean pine forest. We showed that Coal Tits differed in prey type, prey size and nesting vegetation characteristics from Great Tits (the best competitor). Thus, Coal Tits preyed on shorter caterpillars and nested in mature vegetation patches, while Great Tits did it in immature vegetation patches preying on larger prey. Therefore, niche overlap between these two species was low. There was a relatively high temporal overlap in the breeding cycles of these two species. On the other hand, Crested Tits fed on similar prey types and sizes that Great Tits, and both species mostly nested in immature vegetation patches. However, Crested Tits bred earlier than Great Tits, thus avoiding overlap in the periods of maximum food demand by their nestlings. With the present study we have stressed the importance of some sort of complex combination of niche dimensions in explaining the coexistence of putative competitors.

The general objective of the present thesis was studying how organisms cope simultaneously with numerous aspects of their environments (food phenology, physical environment, predation, intra and interspecific competition…), and how they trade-off conflicting demands. We have shown that birds used environmental temperature to cope with variation in food phenology, or they used vegetation characteristics to reduce predator detection. Birds also coped with some environmental and intrinsic factors when feeding chicks, by decreasing or increasing their effort. We have also showed how birds traded-off conflicting demands, for instance, between bird colouration and nest predation. Colourful females avoided nest predation by choosing concealed places. Additionally, we have shown how Crested Tits breeding in an untypical forest coped with the new environmental conditions by looking for nest boxes surrounded by pine trees. Finally, the three tit species used here coped with the problem of sharing the same habitat by differing in prey size, nesting habitat characteristics or breeding time.

Finally, it is important to highlight that data were gathered by using nest boxes. Hence, some results may be not relevant in cases of studying birds in natural holes due to differences in, for instance, predation pressure. Moreover, pressures may be also different depending on whether the bird breeds in a nest box or in a natural hole.

SÍNTESI DE LA TESI EN VALENCIÀ

Un dels reptes més excitants de l'ecologia moderna és intentar entendre la correspondència i les adaptacions entre les diferents etapes del cicle vital dels organismes i el medi (p.ex. Southwood 1977). Els organismes estan adaptats al seu medi per tal de sobreviure i reproduir-se de manera exitosa (p.ex. Darwin 1859). Molts d'ells s'han d'enfrontar simultàniament amb diversos aspectes del seu medi (fenologia de l'aliment, medi físic, predació, competència intra i interespecífica…), i per tant, a moltes situacions de trade-off entre demandes conflictives (p.ex. Pianka 1974). La predació és, per exemple, una constricció important durant la reproducció. En el cas de les aus, als llocs on hi ha un elevat risc de predació, tindre colors pàlids/críptics reduix el risc de ser predat, però també reduix les oportunitats d'emparellar-se (p.ex. Lyon and Montgomerie 1985, Magnhagen 1991). Per tant, es requerix un adequat coneixement de dites constriccions per a un millor enteniment de cóm els animals estan adaptats al seu medi i cóm les espècies han arribat a coexistir. Aquest coneixement adquirix gran importància en ambients estacionals i escassos en aliment (p.ex. boscos perennifolis al Mediterrani, Blondel and Aronson 1999), on la fluctuació i manca de recursos estan considerats com uns dels factors més importants que influixen sobre l'èxit reproductor actual i venider (p.ex. Martin 1987, Barba et al. 1994, Rytkönen and Krams 2003). A més, la predictibilitat de les situacions externes que pot *limitar la reproducció adquirix un paper rellevant en ambients estacionals. Açò està relacionat amb el grau amb el que els recursos o condicions ambientals poden ser emprats per un organisme en tal de maximitzar el nombre de polls produïts per a la següent generació (Kuitunen 1989).*

Els ambients estacionals mostren un període limitat durant l'any quan les condicions són suficientment favorables per a reproduir-se o crèixer, i on les plantes i animals exhibixen patrons estacionals a les seues activitats. Si la reproducció o el creixement ocurrix fora del període quan les condicions són favorables, sovint hi ha conseqüències negatives sobre l'èxit reproductor (veure revisió en Visser and Both 2005). A més, si la fenologia d'una espècie canvia a una taxa diferent a la que ho fa l'espècie/organisme que forma part de les seues condicions ecològiques (preses, hoste, etc.), això durà a un desajustament de les seues activitats estacionals (Visser et al. 2006). A les aus, la reproducció suposa un elevat cost energètic. Per tant, ajustar la reproducció amb la fenologia de la presa és realment important (Martin 1987). Per exemple, a la Daurada Grossa Pluvialis apricaria*, l'èxit reproductor depén de la sincronia de l'eclosió dels seus polls amb el període quan els tipúlids adults, la seua presa principal, són més abundants. Això suposa una clara presió sobre l'ajustament de la reproducció (més exemples de pardals en, Visser and Both 2005). Per tant, les aus han d'emprar senyals que els permitisca ajustar la seua reproducció a la fenologia de l'aliment (p.ex. temperatura ambiental, Visser and Both 2005). Malgrat això, moviments dispersius asimètrics entre hàbitats podria previndre que les poblacions s'adaptaren en ambients heterogenis. Els moviments dispersius són direccionals, des de l'hàbitat més comú fins al menys comú causant una maladaptació aparent a les condicions locals. Per tant, s'esperaria que les aus que viuen en dits ambients, mostraren un desajustament entre la reproducció i la* *fenologia de l'aliment (p.ex. Dias and Blondel 1996a). Per altra banda, moltes espècies d'insectes herbívors sols poden desenvolupar-se sobre material vegetal jove. Per a estes espècies, la fenologia del creixement de les fulles o dels brots pot ser emprat com a criteri per als canvis fenològics del seu desenvolupament larvari. Un clar exemple d'açò occurrix en la interacció entre una espècie de larva de lepidòpter* Operophtera brumata *i els roures. Els ous d'esta espècie que eclosionen abans o després de l'aparició dels brots veuen reduït el seu fitness (van Asch 2007). Hi ha també exemples procedents del medi aquàtic: el següent bivalvo intermareal* Macoma balthica*, està sota la selecció de la variació temporal del seu recurs alimentici, el fitoplàncton (per a una revisió més extensa, Visser and Both 2005).*

Els individus probablement estan emprant senyals ambientals per tal d'ajustar la seua inversió reproductiva, i maximitzar així el seu fitness. Malgrat això, dins d'una mateixa població, alguns individus invertixen més que altres. Tenint en compte que individus que invertixen més (p.ex. a les aus, posar les femelles més ous) tendixen a ser més exitoses que aquells que invertixen menys (Nur 1984a), per què eixes diferències en inversió dins la mateixa població? En paseriformes menuts, dos hipòtesi principals han sigut proposades per tal d'aclarir la qüestió abans esmentada: la Hipòtesi del Trade-Off o del Compromís (HTO) i la Hipòtesi d'Optimització Individual (HOI). La HTO postula que posar més ous té un cost reproductiu (p.ex. una disminució en la fecunditat futura) i beneficis (p.ex. més polls són reclutats a la següent estació reproductora, Werf 1992, Pettifor et al. 2001). Per tant, els individus estarien posant un nombre d'ous de tal mode que els beneficis foren majors que els costos a llarg termini. Els costos deguts a la reproducció han sigut examinats en una gran varietat d'espècies animals i vegetals, emprant mètodes observacionals i experimentals (per a una revisió, veure Harper *and White 1974, Zera and Harshman 2001, Obeso 2002). Per altra banda, la HOI postula que els individus estarien posant un nombre d'ous que es correspondria amb el màxim nombre de polls que ells podrien alimentar de manera satisfactòria. Per tant, posar més o menys ous no seria avantatjós. L'argument és que hi ha restriccions energètiques i de temps actuant sobre els pares, així que ells no poden invertir més de lo que ho fan. Alguns estudis han recolzat la HTO (Nur 1984a, Both 1998, veure més referències al Capítol VI). En canvi, la HOI ha sigut menys recolzada a dia d'avui (Both 1998, Pettifor et al. 2001, veure també Lindén 1990). Donat que les estratègies d'inversió podrien dependre dels costos i beneficis experimentats per les aus, caldria esperar-ne que les poblacions que visquen sota diferents restriccions ambientals mostraren diferents estratègies d'inversió. Per tant, per comprendre la plasticitat de l'estratègia d'una espècie durant el seu cicle vital, dites hipòtesi deurien de ser testades en tots aquells ambients possibles on l'espècie és capaç de reproduir-se satisfactòriament.*

El comportament animal pot ser estudiat des de diferents angles, intentant respondre cóm s'ha produït un determinat comportament, i per quins mecanismes (Tinbergen 1963). El comportament d'alimentació dels animals és un dels principals temes de l'ecologia comportamental, i els animals a sovint poden respondre de molt diverses formes a la situació en la que ells mateixos es troben. Algunes restriccions afecten a dit comportament (p.ex. la duració del dia, Kuitunen 1989), traslladant-se això a l'èxit reproductor. A les aus nidícoles, on la descendència és dependent dels dos membres de la parella, l'èxit reproductiu pot estar limitat per la taxa a la que l'aliment es dut al niu, així com per la qualitat i quantitat d'aliment dut.

Diferents tipus d'animals vivint junts al mateix lloc poden interactuar i competir potencialment pels recursos limitants com són l'aliment, espai, etc. (Krebs 2001). Dita competència és major en espècies germanes vivint en simpatria i fent ús de recursos semblants (Pianka 1974). Hi ha dos modes diferents de competència entre els animals: explotació i interferència. El primer té lloc quan un nombre d'organismes (de la mateixa o de diferent espècie) utilitzen recursos en comú que són escasos en abundància (p.ex. els lleons i els guepards competixen per les gacel.les a les planícies africanes). El segon té lloc directament entre els individus via l'agressió, quan s'interferix en l'aliment, supervivència, o en la reproducció d'altres organismes, o directament prevenint l'establiment físic a una part de l'hàbitat inclusive si el recurs no és escàs (Krebs 2001). Per exemple, la Perdiu d'Escòcia Lagopus lagopus scoticus *defén les àrees riques de les brugueres com a territoris d'alimentació i reproducció, mentre que les aus excloses han d'explotar ambients més pobres on les probabilitats de supervivència són baixes (Krebs and Davies 1993). La competència és, per tant, considerada com una limitació reproductiva degut a les conseqüències negatives relacionades amb el fitness del pitjor competidor (Török 1987). La qüestió que uno es planteja és, cóm els organismes que viuen junts al mateix hàbitat han evolucionat dins del context de la competència. L'ús diferencial de l'aliment i/o de l'hàbitat podria permetre la coexistència de competidors al mateix ambient. Per exemple, dos espècies d'aus semblants podrien coexistir al mateix bosc mitjançant l'especialització en el tipus de presa (o tamany), o en el lloc o en la forma d'alimentar-se (Pianka 1974). Per tant, per a una millor comprensió de la coexistència animal, és interessant tindre un coneixement adequat de les restriccions que podrien afectar-la.*

La disponibilitat d'aliment i la predació són dos constriccions reproductives importants (veure més abaix) relacionades amb l'hàbitat en el que una espècie viu (Sargent and Gebler 1980, Dobkin 1985, Kuitunen 1989, Stokes and Dee Boersma 1998). Malgrat això, les relacions hàbitat-espècie sovint són complexes i dependents de l'escala considerada (p.ex. selecció d'hàbitat, WallisDeVries et al. 1999, Quevedo et al. 2006). L'hàbitat podria definir-se a varies escales espacials, des de l'escala geogràfica o macrohàbitat fins a una escala local o microhàbitat. L'escala de macrohàbitat per a les aus és examinada principalment a nivell de paissatge (Otter et al. 2007). Això comprén algunes característiques que podrien afectar a l'èxit reproductor com el tamany/àrea i aïllament del terreny, tipus d'usos del terreny dins del paissatge, i inclusive el tipus de vegetació predominant (p.ex. caducifoli vs. perennifoli). En canvi, l'escala de microhàbitat comprén la complexitat estructural de les característiques dels voltants del niu (p.ex. densitat d'arbres). Dites característiques podrien afectar l'èxit reproductiu. Per exemple, el fet de què la vegetació siga densa influix en l'habitat i visibilitat dels predadors per trobar nius, augmentant l'èxit reproductor (Martin 1993, Tarvin and Garvin 2002). Per tant, l'anàlisi a diferents escales és important per entendre els processos subjacents de cóm les aus responen en un paissatge estructurat, especialment quan el tipus de vegetació no és homogeni, així com per a entendre les constriccions que afecten a la reproducció.

En molts sistemes animals, la predació és una de les majors forces selectives en la selecció d'hàbitat i coloració animal degut als seus efectes sobre l'èxit reproductor (Magnhagen 1991, Martin 1993, Godin and McDonough 2003). A les aus, la selecció natural deu afavorir les aus que elegixen llocs per reproduir-se amb baixa incidència de predació de nius, o organismes amb coloracions críptiques *per evadir als predadors (p.ex. Götmark 1997). Per exemple, les aus que es reproduixen als llocs de vegetació densa i altament heterogènia, manifesten una baixa taxa de predació (Martin 1993). En alguns peixos (p.ex. els Guppies de Trinitat* Poecilia reticulata*), els mascles es fan menys colorits quan el risc de predació és elevat. Basat en la selecció sexual, dits mascles mostrarien menys probabilitats d'emparellar-se (Magnhagen 1991). Malgrat això, tindre una coloració vistosa suposa tindre també beneficis reproductius mitjançant l'augment de la competència mascle-mascle o ser elegit per la femella (Andersson 1994, Hill and McGraw 2006a). La coloració dels mascles assenyala algunes característiques d'ells mateixos, com pot ser una elevada contribució en el procés d'alimentació dels polls (Senar et al. 2002). Per tant, la selecció sexual deu afavorir el desenvolupament i manteniment dels colors vistosos que faciliten les oportunitats d'emparellament (Andersson 1994). És a dir, la predació és, mitjançant la coloració, una altra constricció reproductiva que s'ha de tindre en compte en estudis d'ecologia reproductiva.*

Les mallerengues (Família Paridae) com espècies model

Les espècies de la família Paridae *es troben entre les espècies d'aus canores més conegudes (p.ex. Perrins 1979, Cramp and Perrins 1993). Des de 1997 fins ara, més de 1200 estudis s'han publicat directa o indirectament involucrant a la Mallerenga Carbonera* Parus major *(ISI Web of Knowledge) cubrint diverses branques d'investigació des dels gens fins a la selecció d'hàbitat. Per tant, per què vàrem plantejar fer una tesi sobre espècies de mallerenga quan ja hi ha gran quantitat d'informació disponible? Malgrat la gent ha estat parlant sobre pardals* *des de fa prou temps, des de què existixen records històrics, realment encara no entenem les estratègies dels cicles vitals de les aus sota gran part de les condicions ecològiques. Per exemple, les estratègies reproductores així com les característiques de les històries de vida de les Mallerengues Carboneres han sigut ben estudiades al centre i nord d'Europa (Perrins 1979, Gosler 1993), però han sigut molt poc estudiades al sud del seu rang de distribució (Cramp and Perrins 1993). De fet, és important estudiar les característiques individuals i poblacionals i les adaptacions de l'espècie al llarg de la seua distibució en tots aquells ambients possibles de ser ocupats per l'espècie (Zink 1989). Açò adquirix relevància si tenim en compte que les relacions trobades a nivell o escala local podrien no ser les mateixes quan es té en compte tota la seua àrea de distribució. Per exemple, Belda and Orell (2003) trobaren que la supervivència dels adults de Mallerenga Carbonera fou relativament major a l'àrea Mediterrània, i aquest fet podria fàcilment afectar altres trets del cicle vital.*

Uns dels trets característics de la família de les mallerengues és el seu hàbit reproductor. Totes les espècies construixen els seus nius en forats, a sovint emprant forats en arbres vells o arbres mig caiguts, malgrat que les Mallerengues Emplomallades i Capnegres Poecile montana*, normalment excaven els seus propis forats en arbres prodits (Perrins 1979, Denny and Summers 1996). La majoria de les espècies de mallerenga accepten ràpidament nius artificials, vulgarment coneguts com caixes niu, per reproduir-se. A més, l'ús de les caixes niu facilita la seua revisió així com la presa de mesures als polls. A més, aquestes espècies d'aus ens permitix dur a terme experiments al camp no sols perquè utilitzen les caixes niu sinó perquè són aus fàcils de capturar i marcar. Les mallerengues estan ampliament distribuïdes, reproduint-se en diferents hàbitats des* *de jardins fins a boscos (Cramp and Perrins 1993). Per tant, aquestes experimenten condicions ambientals diferents (aliment, clima, tipus de vegetació, predació…), que les fa ideals per a estudis comparatius a una escala geogràfica gran (p.ex. Visser et al. 2003, van den Steen et al. 2009).*

Perfil de la tesi

L'objetiu general perseguit a la present tesi fou assolir una millor comprensió de cóm les aus estan adaptades al seu ambient. En particular, examinar l'existència i les conseqüències de la limitació d'aliment en ambients perennifolis Mediterranis, mitjançant un adequat coneixement de les limitacions o constriccions que afecten el comportament tròfic i l'èxit reproductor. Amb això, es pot interpretar més correctament gran part dels aspectes relacionats amb la vida d'un individu.

Emprant les mallerengues pertanyents a tres poblacions de l'est d'Espanya reproduint-se en caixes niu com a espècies model, els objetius específics perseguits a la present tesi són els següents:

Capítol III. *Desenvolupament d'un aparell o estructura metàl.lica per facilitar la filmació del comportament tròfic dels adults des de l'exterior de la caixa niu. Açò fou necessari per assolir alguns dels objetius proposats en altres capítols.*

Capítol IV. *Cercar les senyals ambientals encarregades d'iniciar la reproducció a les Mallerengues Carboneres* Parus major*, i cóm les aus les utilitzen per a ajustar la reproducció a la fenologia de l'aliment: conseqüències sobre l'èxit reproductor degut a la manca d'ajust.*

Capítol V. *Descriure els patrons de comportament tròfic o d'aprovisionament d'aliment i les seues conseqüències sobre els adults i polls.*

Capítol VI. *Testar, mitjançant experiments de manipulació del tamany de pollada, si les aus estan optimitzant el tamany de posta.*

Capítol VII. *Investigar cóm el tipus de bosc i l'estructura de la vegetació afectava l'èxit reproductor: una aproximació multi-nivell.*

Capítol VIII. *Analitzar l'elecció de parella a les Mallerengues Carboneres baix l'escenari d'un elevat nivell de predació de nius: el paper de la qualitat de l'hàbitat en la decisió d'elecció de la parella per la femella.*

Capítol IX. *Descriure les característiques de l'hàbitat al voltant dels nius de les Mallerengues Emplomallades* Lophophanes cristatus *en boscos atípics i típics per a l'espècie, tractant de conèixer cóm dita espècie ha adaptat el seu cicle reproductor a les noves condicions ambientals, i cóm això podria afectar alguns paràmetres de la seua història vital i la dieta dels polls.*

Capítol X. *Analitzar alguns dels mecanismes de coexistència entre forts competidors, Mallerenga Carbonera, Emplomallada i Menuda* Periparus ater*: tamany de l'aliment, requeriments d'habitat per a l'ubicació dels nius i l'inici de la reproducció.*

A la present tesi, diversos trets o variables del cicle vital han sigut analitzats des de diferents punts de vista. En general, s'ha demostrat com les aus que s'han reproduit en ambients perennifolis al Mediterrani han solventat les diverses constriccions *ambientals i compromissos. Ací vull destacar i discutir els principals resultats obtinguts.*

La regió Mediterrània es caracteritza per la forta estacionalitat (Blondel and Aronson 1999); per tant, cada any hi ha sols un període limitat durant el qual les condicions per al creixement i reproducció són òptimes. Arrel d'això, una pregunta important a resoldre és, com els organismes poden ajustar la seua reproducció al moment just del cicle vital de la seua presa. Les Mallerengues Carboneres Parus major *que viuen als boscos templats utilitzen la temperatura com a senyal per ajustar les seues activitats reproductives (Visser and Both 2005). És a dir, les aus comencen a posar-ne ous més prompte en primaveres càlides perquè els arbres brollen més prompte, i els insectes emergixen abans (van Asch 2007). En aquestos boscos, un ajust correcte de la reproducció de les aus amb el cicle vital de la presa té efectes positius sobre el fitness (Perrins 1991). Malgrat això, poc es conegut sobre com les Mallerengues Carboneres ajusten la seua reproducció, i les conseqüències d'això sobre el fitness en boscos perennifolis a la regió Mediterrània (Belda 1996, Iglesias 1996).*

Vam abordar dites qüestions estudiant dos poblacions de Mallerenga Carbonera reproduint-se en boscos perennifolis al Mediterrani, un Carrascar Quercus ilex *i un pinar. Mitjançant l'ús d'embuts disposats baix de les copes dels arbres vam fer el seguiment de la disponibilitat i fenologia de l'aliment (veure més al Capítol IV). La finestra temporal durant la qual l'aliment era abundant comprenia entre una (Carrascar) i dos setmanes (pinar), això és relativament poc si ho comparem amb les tres setmanes que comprén als boscos caducifolis (Visser et al. 2006). Per tant, el curt temps durant el qual hi ha prou aliment al medi és una* *restricció als boscos perennifolis. De fet vam trobar que els polls criats per individus que no ajustaren la reproducció (és a dir, aquells individus als quals el pic de màxima demanda d'aliment per part dels polls estava fora del moment de màxima disponibilitat d'aliment al medi), pesaren menys que aquells criats per individus que sí que ajustaren. Per tant, deu d'haver una forta pressió per a ajustar la reproducció a dit curt període d'abundància d'aliment.*

D'acord amb el que s'ha trobat en estudis previs, les nostres poblacions estudiades de Mallerenga Carbonera als boscos perennifolis empraren la temperatura ambiental com a senyal per a iniciar la reproducció, retardant-la a les primaveres més fresques. Malgrat això, sols els individus que es van reproduir al bosc de pi empraren de manera satisfactòria dita senyal, i per tant aquesta població ajustà la reproducció a la fenologia de l'aliment (veure Capítol IV). En canvi, les aus que es van reproduir al Carrascar, malgrat van respondre de igual forma a la senyal ambiental, fracassaren ajustant correctament el punt de màxima demanda d'aliment amb el pic de màxima abundància d'aliment – és a dir, els individus d'aquesta població estaven maladaptats a les condicions tròfiques locals. Aquestos resultats sugerixen que la falta d'ajustament podria ser degut a una dispersió asimètrica d'individus procedents de l'hàbitat del voltant, que al mateix temps és el més comú (pinar) on les Mallerengues Carboneres sí que estaven adaptades.

Els polls d'aus nidícoles depenen completament dels adults per obtindre els nutrients necessaris per al seu desenvolupament. Per tant, es requerix la cura parental mitjançant les anades i vingudes al niu per satisfer les demandes d'aliment durant el ràpid procés de desenvolupament dels polls (Capítol V). L'enregistrament del comportament tròfic permitix una millor identificació dels factors que podrien *afectar a la cura parental, així com conèixer com els adults responen a aquestos factors. Mitjançant l'ús de contadors mecànics posats a una gran quantitat de nius de Mallerenga Carbonera, vàrem trobar que el nombre de visites (1) augmentà amb l'edat dels polls fins els d'10-12 dies d'edat, mantenint-se constant posteriorment; (2) augmentaren linialment amb el tamany de pollada; (3) varen disminuir al llarg de l'estació; i (4) no variaren amb el moment del dia (Capítol V). Els patrons generals trobats al present estudi coincidiren amb aquells trobats a les mallerengues i altres espècies, malgrat aquest estudi és el primer que empra una gran quantitat de nius (més de 200) i amb un tractament estadístic més oportú a les dades.*

El present estudi també aclarix la causa d'alguns patrons. Per exemple, la manca de creixement en l'esforç parental cap a la fi del període d'estància dels polls al niu fou degut majoritàriament a una reducció del tamany de pollada, i no al cansament dels adults com estudis previs sugerien. A més, l'increment de la taxa de visites per niu es va traduir en una disminució del nombre de visites que cada poll va rebre. Aquest fet suportava la Hipòtesi del Trade-Off (veure més al Capítol V), és a dir, els pares podrien estar optimitzant els costos i els beneficis a llarg termini durant el procés d'alimentació dels polls (Nur 1984a). Donat que es requerix de la manipulació del tamany de posta per demonstrar això, abordàrem dita qüestió al Capítol VI.

Una de les qüestions centrals en la inversió parental és si el nombre de descendents obtinguts s'ajusta a la capacitat parental, és a dir, les conseqüències sobre el fitness a conseqüència de la variació en el tamany de posta (per a una revisió, veure Both 1998, Pettifor et al. 2001). Per a resoldre dita qüestió, es *requerix com s'ha dit dalt, d'experiments de manipulació del tamany de posta on el fitness de postes augmentades i reduïdes es puga comparar amb el de postes originals (Both 1998). Alguns estudis han demostrat que el tamany de posta elegit (original) maximitzava el fitness, mentre que altres mostraren que les aus eres capaços de dur endavant tamanys de posta majors que els originals (veure també el Capítol VI). Nosaltres vàrem dissenyar un experiment on els tres grups experimentals (postes augmentades, control i reduïdes) foren creats intercanviant polls recent nascuts procedents de nius amb dates d'eclosió i tamanys de posta semblants. Analitzàrem els efectes de la manipulació del tamany de posta sobre alguns factors com el comportament tròfic dels adults, pes i condició dels polls i dels adults, nombre de volantons, èxit de vol, i el nombre estimat de polls reclutats a la població. El que vam obtindre fou que les aus no augmentaren el seu esforç amb el tamany de posta, per tant cada poll va rebre menys visites que aquells procedents de postes control. Tant el pes dels adults com el dels polls i l'èxit de vol no van variar en funció del tractament o tipus de manipulació. Les postes augmentades obtingueren més polls, però també mostraren una menor probabilitat de supervivència a l'eixir del niu. Això dugué a què menys polls foren reclutats a la següent estació reproductora. Per altra banda, les aus de postes reduïdes van disminuir proporcionalment el seu esforç o taxa de visites al niu. El resultat fou que, cada poll va rebre una quantitat de visites semblants a aquells de postes control. No hi hagué diferències en les probabilitats de supervivència dels polls al abandonar el niu entre aquests dos tractaments, malgrat que el nombre estimat de polls reclutats fou menor a les reduïdes (veure Capítol VI). Els nostres resultats estigueren d'acord amb la història vital per a la nostra població de mallerenga – una major probabilitat de supervivència adulta interannual seleccionada pels* *individus que limitaven l'actual inversió reproductiva. Aquests resultats recolzen la Hipòtesi d'Optimització Individual (veure Capítol VI), és a dir, les Mallerengues Carboneres estaven duent endavant tamanys de posta que maximitzaven el seu fitness individual. Per tant, allò que l'estudi descriptiu va sugerir (veure dalt, també el Capítol V) fou rebutjat més tard experimentalment.*

S'ha trobat que l'ambient o l'hàbitat al voltant dels nius en aus forestals influix l'èxit reproductiu. Diversos estudis han analitzat diferents característiques de l'hàbitat (p.ex. fragmentació de l'hàbitat, Olson and Grubb 2007). A les Mallerengues Carboneres, estudis relacionats amb el paissatge s'han fet al llarg i ample de la seua distribució (veure més al Capítol VII). Aquells estudis que analitzaven l'efecte del tipus de bosc, trobaren que les aus que es reproduïen als boscos caducifolis tingueren un major éxit reproductiu que aquells que ho feren als perennifolis. El factor subjacent que explicava aquests resultats fou una major abundància d'aliment als boscos caducifolis (Tremblay et al. 2003, veure més al Capítol IV). A pesar d'això, diversos factors que afecten als individus podrien estar actuant a diferents escales espacials. Per exemple, Huhta et al. (1998) va trobar que, mentre la selecció d'hàbitat per a la ubicació dels nius als Mastegatatxes Ficedula hypoleuca *es donava a dos nivells d'escala, diferències en l'èxit reproductio existia sols a nivell de microhàbitat.*

Actualment no hi ha una comprensió sòlida dels processos subjacents a l'ús de l'hàbitat a les Mallerengues Carboneres reproductores. Al present estudi vàrem analitzar els efectes de les característiques de l'hàbitat sobre alguns trets reproductors a dos poblacions de Mallerenga Carbonera mitjançant una aproximació multinivell, macrohábitat i microhàbitat. Per al primer nivell, *nosaltres vàrem trobar que les aus que es reproduïen al Carrascar començaren la posta una setmana més tard, posaren més ous, eclosionant-ne més i així, més volantons s'obtingueren els quals volaren en una millor condició que aquells nascuts al pinar. Dits resultats s'ajustaren al fet de què al Carrascar hi havia molt més menjar (Capítol IV). Per altra banda, a nivell de microhàbitat vàrem mesurar algunes variables relacionades amb l'estructura de la vegetació al voltant de cada caixa niu (Capítol VII). L'èxit reproductiu fou major en aquells nius localitzats a zones de vegetació inmadura, caracteritzades per una vegetació densa, degut a una menor taxa de predació (Capítols VII i VIII). Aquestos resultats recolzaren la hipòtesi del "total-foliage" que prediu una disminució del risc de predació segons augmenta la vegetació total al voltant del niu. El mecanisme proposat és que una major densitat del fullatge inhibix entre altres, la transmissió de senyals visuals de la presa (Martin 1993). Per tant, sembla que diferents factors estan operant a diferents nivells: disponibilitat d'aliment a nivell de macrohàbitat, i predació de nius a nivell de microhàbitat. Aquestes restriccions contribuixen a explicar les diferències en l'èxit reproductiu de les Mallerengues Carboneres al Mediterrani entre i dins d'un mateix bosc.*

Emprant diferents escales espacials permitix també conèixer perquè algunes espècies atípiques d'un lloc hi poden aparèixer (veure més al Capítol IX). Per tant, nosaltres vam emprar un anàlisi a dos escales per tal de respondre per què les Mallerengues Emplomallades Lophophanes cristatus*, una espècie típica de pinars, estaven reproduint-se en un bosc no comú per a l'especie, un Carrascar (veure Capítol IX). A més, nosaltres estàvem interessats en conèixer cóm les diferències en el tipus de vegetació dominant podrien influir en alguns trets reproductors i en l'ecologia tròfica (dieta dels polls, tamany de presa i freqüència* *d'aprovisionament d'aliment) d'aquesta espècie. Trobàrem que les Mallerengues Emplomallades es reproduiren en aquells territoris dins del Carrascar on la coberta de pins fou del 5% com a mínim. Per altra banda, la dieta dels polls fou semblant entre poblacions reproductores al Carrascar i al pinar, i estigué composta principalment per orugues. A més, tant el tamany de presa, comprés entre 1 i 2 cm, com l'èxit reproductiu (tamany de posta, nombre i pes dels volantons) foren semblants als dos boscos. Finalment, els adults visitaren les caixes niu a una taxa prou semblant. Per tant, hem demostrat que les Mallerengues Emplomallades al Carrascar, es van reproduir sorprenentment bé malgrat ser un hàbitat poc usual per a l'espècie, sempre i quan hi hagués pins al voltant de la caixa niu. Aquest estudi ha sigut el primer en descriure la dieta dels polls d'aquesta espècie al Carrascar, i a més oferix més informació sobre la dieta dels polls als pinars (Cramp and Perrins 1993). A més, aquesta tesi també destaca la importància de les aproximacions multinivell en les relacions espècie-hàbitat, mostrant la importància dels pins per a la presència de les Mallerengues Emplomallades a un bosc que no siga de coníferes.*

Les aus són un dels millors grups animals estudiats en termes de selecció sexual per mig de colors vistosos i altres signes visuals (p.ex. Andersson 1994). Una de les qüestions més rellevants en estudis de selecció sexual és per què els individus s'emparellen selectivament. Dit tipus d'emparellament ocurrix quan la coloració del mascle assenyala algun benefici a l'èxit reproductiu de la femella (veure Capítol VIII). Segons el que coneixem, la majoria d'estudis han investigat i trobat emparellament selectiu emprant la coloració del plomatge a les Mallerengues Carboneres i a altres espècies (Andersson 1994; per a una excepció, veure Hegyi et al. 2007). Malgrat això, pocs estudis han introduït la qualitat de l'hàbitat com a una variable potencialment rellevant. Per exemple, Alatalo et al. (1986a) va *mostrar que els Mastegatatxes no s'emparellaven selectivament. En aquesta població, la coloració del mascle no informava o assenyalava cap benefici per a l'èxit reproductor de la femella, i aquestes prestaren més atenció a les característiques de l'hàbitat que a la coloració del mascle.*

A la present tesi, nosaltres ens vam interessar en conèixer si dos poblacions de Mallerengues Carboneres al Mediterrani s'emparellaven selectivament sota la restricció d'un elevat nivell de predació emprant la coloració del plomatge, la llargària del tars i el pes corporal. Els mascles foren més colorits que les femelles. Malgrat això, no hi hagué emparellament selectiu per cap dels trets analitzats (veure Capítol VIII). La coloració dels mascles no va estar relacionada ni amb la productivitat ni amb la freqüència d'aprovisionament d'aliment al niu. Per tant, no hi hagué una contribució per part del mascle a l'èxit reproductor de la femella. Per altra banda, la coloració de la femella fou relacionada amb la productivitat del niu mitjançant les característiques de la vegetació: les femelles vistoses mostraren una major productivitat als territoris amb vegetació inmadura. La productivitat a les femelles menys colorides no va estar relacionada amb les característiques de la vegetació. La predació de nius fou menor als territoris amb vegetació inmadura (Capítols VII i VIII). Per tant, hi sembla que als ambients on la predació de nius és elevada, les femelles colorides prestaren més atenció a les característiques de l'hàbitat més que a les del mascle. Pocs estudis a dia d'avui han demostrat de manera convincent que les femelles volien en realitat les característiques del territori més que les dels mascles (veure Capítol VIII). Hem demostrat que la predació és una restricció que afecta no sols a l'èxit reproductiu sinó també a l'elecció de la parella per part de la femella.

Alguns mecanismes han evolucionat per tal de permetre la coexistència entre grans competidors que viuen al mateix lloc. Aquestos mecanismes en aus paseriformes menudes s'han analitzat durant l'hivern, quan el menjar es suposa que és escàs (Alatalo 1982 per a una revisió). Poc estudis s'han fixat en fer-ho durant el període reproductor (veure Capítol X). A la present tesi, ens vàrem centrar en analitzar alguns mecanismes que potencialment podrien permetre la coexistència de tres espècies de mallerengues, la Mallerenga Carbonera, l'Emplomallada i la Petita Periparus ater *a un bosc de pi al Mediterrani. Vàrem demostrar que les Mallerengues Petites diferien de les Mallerengues Carboneres (el millor competidor) en el tipus de presa, tamany de presa i en les característiques de la vegetació al voltant dels nius. Les Mallerengues Petites menjaren orugues més menudes i niuaren en zones de vegetació madura, mentre que les Mallerengues Carboneres ho feren en zones de vegetació inmadura, alimentant-se d'orugues més grans. Per tant, el solapament de níntxol entre aquestes dues espècies fou baix. Hi va haver un solapament relativament alt en relació als seus cicles reproductors. Per altra banda, les Mallerengues Emplomallades s'alimentaren de tipus de presa i tamanys de presa semblants als de les Mallerengues Carboneres, i ambdúes espècies niuaren majoritàriament en territoris de vegetació inmadura. Malgrat això, les Mallerengues Emplomallades es reproduiren més prompte que les Mallerengues Carboneres, per tant evitant el solapament dels períodes de màxima demanda d'aliment per part dels polls de ambdúes espècies. Amb el present estudi hem destacat la importància d'una mena de combinació complexa de les dimensions del níntxol per tal d'explicar la coexistència de grans competidors.*

L'objectiu general de la present tesi fou estudiar com els organismes s'havien d'enfrontar simultàniament amb diversos aspectes del seu medi (fenologia *de l'aliment, medi físic, predació, competència intra i interespecífica…), i per tant, en moltes situacions s'havien d'enfrontar a trade-offs entre demandes conflictives. Nosaltres hem demostrat que les aus utilitzen la temperatura ambiental per tal d'enfrontar-se i solventar els problemes relacionats amb la fenologia de l'aliment, o l'ús que fan de les característiques de la vegetació per reduir la predació. Les aus també s'enfrontaren i solventaren alguns factors ambientals i intrínsics durant el procés d'alimentació dels polls al niu, disminuint o augmentant el seu esforç. També hem demostrat cóm solventaren demandes conflictives, per exemple, entre la coloració del plomatge i la predació de nius. Les femelles colorides evitaren la predació de nius elegint zones amb molta vegetació per fer-los críptics. A més, hem demostrat com les Mallerengues Emplomallades reproduïnt-se a un bosc atípic solventaren de manera exitosa les noves condicions ambientals mitjançant l'ubicació dels nius en zones amb presència d'alguns pins. Finalment, les tres espècies de mallerengues emprades ací solventaren el problema de la coexistència al mateix hàbitat gràcies a les diferències existents en tamany de presa, característiques de la vegetació al voltant del niu o al moment de la reproducció.*

Finalment, és important ressaltar que els resultats obtesos i detallats al llarg de la present tesi foren obtesos mitjançant l'ús de caixes niu. Per tant, els resultats podrien no servir en casos en els que les aus es reprodueixin en forats naturals degut a les diferències, per exemple, en pressió per predació. A més, les pressions podrien també diferir depenent de si l'au niua en una caixa niu o en un forat natural.

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PUBLICATIONS

The chapters of the present thesis have led to the following manuscripts which have been published, are in press, or have been submitted to different scientific journals:

Barba, E., **Atiénzar, F.**, Marín, M., Monrós, J.S. and Gil-Delgado, J.A. 2009. Patterns of nestling provisioning by a single-prey loader bird, Great Tit *Parus major*. *Bird Study* 56: 187-197. (Chapter V)

Atiénzar, F., Andreu, J., Álvarez, E. and Barba, E. 2009. An improved wire cage for the study of parental feeding behaviour of hole-nesting passerines. *Catalan Journal of Ornithology*, in press. (Chapter III)

Atiénzar, F., Barba, E., Holleman L.J.M. and Belda, E.J. Nesting habitat requirements and chick diet in Mediterranean Crested Tits *Lophophanes cristatus*. *Submitted* (Chapter IX)

Atiénzar, F., Visser, M.E., Greño, J.L., Holleman, L.J.M., Belda, E.J. and Barba, E. Across and within-forest effects on breeding success in Mediterranean Great Tits. *Submitted* (Chapter VII)

Atiénzar, F., Visser, M.E., Greño, J.L., Holleman, L.J.M., Belda, E.J. and Barba, E. Bright Great Tit females go for safety, not for sexy males. *Submitted* (Chapter VIII)

Barba, E., **Atiénzar, F.**, Marín, M., Monrós, J.S. and Gil-Delgado, J.A. Evidences for individual optimization of clutch size in Mediterranean Great Tits *Parus major*. *Submitted* (Chapter VI)

Atiénzar, F., Barba, E. and Belda, E.J. Mechanisms of coexistence in Mediterranean tits. *Submitted* (Chapter X)

Atiénzar, F., Barba, E. and Belda, E.J. Fitness consequences of mistiming reproduction to food phenology in Mediterranean forests. *Submitted* (Chapter IV)

APPENDIX

As indicated in the previous section, most chapters of this thesis have been transformed into manuscripts which have been sumitted to scientific journals. Some of them are already published or are in press or under review. Several co-authors have contributed to different manuscripts. We detail below the contribution of the PhD student to the different chapters. Depending on the chapters, co-authors have contributed to data collection, analyses and writing, though the PhD student produced the first draft and lead the writing and review process. :

Chapter III. The PhD student (F. Atiénzar) was who had the idea to make the wire structure for filming. F. Atiénzar helped in the breeding data collection with other people involved in the same project. Writing and analyses were also done by FA under the supervision of director and co-director.

Chapter IV. The idea was shared among the PhD student, director and co-director. F. Atiénzar helped in the breeding data collection with other people involved in the same project. Writing and analyses were also done by FA under the supervision of director and co-director.

Chapter V. Data were collected by the director and other co-authors of the manuscript. Writing and analyses were done by F. Atiénzar under the supervision of director and co-director.

Chapter VI. Data were collected by the director and other co-authors of the manuscript. Writing and analyses were done by F. Atiénzar under the supervision of director and co-director.

Chapter VII. F. Atiénzar and the director were who had the idea. Vegetation data were collected by FA, and he helped in the breeding data collection with other people involved in the same project. Writing and analyses were done by F. Atiénzar under the supervision of director and co-director.

Chapter VIII. F. Atiénzar was who had the idea. Vegetation data were collected by FA, and he helped in the breeding data collection with other people involved in the same project. Writing and analyses were done by F. Atiénzar under the supervision of director and co-director.

Chapter IX. F. Atiénzar was who had the idea. Vegetation data were collected by FA, and he helped in the breeding data collection with other people involved in the same project. Writing and analyses were done by F. Atiénzar under the supervision of director and co-director.

Chapter X. The idea was shared among the PhD student, director and co-director. Vegetation data were collected by FA, and he helped in the breeding data collection with other people involved in the same project. Writing and analyses were done by F. Atiénzar under the supervision of director and co-director.

To date, data showed in all chapters of the present thesis have not been used for any other thesis explicitly or implicitly. This thesis has been reviewed by three external referees: Francisco Valera(Estación Experimental de Zonas Áridas –CSIC-), Tomasz Wesołowski (University of Wrocław) and Paula Dias (Centre National de la Recherche Scientifique).

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