

## BREEDING PERFORMANCE OF THE BLUE TIT *PARUS CAERULEUS* IN A PATCHY MEDITERRANEAN LANDSCAPE

R. MAÍCAS CATALAN & J. FERNÁNDEZ HAEGER\*

### RÉSUMÉ

Cette étude compare la stratégie et le succès reproducteur de la Mésange bleue *Parus caeruleus* dans une forêt de chênes-lièges *Quercus rotundifolia* et une plantation de pins (*Pinus pinea* et *P. pinaster*) dans le sud de la péninsule Ibérique. Pendant la période de reproduction, un flux asymétrique d'individus se produit de la subéraie vers la pinède. Le flux est favorisé par les nichoirs où la Mésange bleue peut pondre. Pendant l'hiver, une grande partie de la population émigre de la pinède vers la forêt de chênes-lièges.

La densité de couples reproducteurs fut plus grande dans les chênes-lièges que dans la plantation de pins. Ce résultat pourrait s'expliquer par la qualité inférieure des ressources disponibles dans la plantation que les oiseaux compenseraient par des territoires plus grands. La densité de reproduction et la plupart des traits du cycle vital examinés (chronologie de la reproduction, taille de la ponte, taille des oeufs, succès reproducteur et poids des jeunes à l'envol) furent similaires dans les deux habitats traduisant un effet de la plasticité phénotypique de l'espèce. Bien que le succès reproducteur des couples ait été similaire dans les deux habitats, le recrutement de nouveaux individus par unité de surface fut plus élevé dans la forêt de chênes-lièges.

Nous discutons les conséquences sur la conservation des espèces des plantations de pins comme type de gestion de la végétation.

### SUMMARY

This study compares reproductive strategy and breeding success of *Parus caeruleus* in a holm-oak (*Quercus rotundifolia*) forest and a pine plantation (*Pinus pinea* and *P. pinaster*) in the southern Iberian Peninsula. During the breeding period, an asymmetric flow of individuals takes place from the holm-oak forest to the pine plantation. This flow is favoured by nestboxes where Blue tits can lay their eggs. During the winter, a large part of the population moves back from the pine plantation to the holm-oak forest.

Breeding pair density was much higher in the holm-oak forest than in the pine plantation. This may be accounted for by the poorer quality of the resources available in the pine plantation which birds try to compensate for with larger breeding territories. Breeding density and most life-history traits examined (timing of breeding, clutch size, egg size, number of fledglings and fledgling weight) were similar in both habitats, as a result of the phenotypic plasticity of this species. Although breeding success was similar in both habitats, recruitment of new individuals per unit area was higher in the holm-oak forest.

The consequences of pine plantations, as a form of forestry management, on species conservation is discussed.

---

\* Departamento de Biología Vegetal y Ecología. Facultad de Ciencias. Universidad de Córdoba 14071 - Córdoba. Spain. Fax (957) 218606. (E-mail: BV1FEHAJ@UCO.ES).

## INTRODUCTION

In the southern Iberian Peninsula, human management of natural vegetation over the centuries has given rise to an agro-silvo-pastoral system on a single space named *dehesa* (Joffe *et al.*, 1988). This human management, consisting essentially in clearing the original holm-oak (*Quercus rotundifolia*) forest to produce pastureland for sheep and pig grazing, involved selection of trees for their fruit quality and production. Hence, *Q. rotundifolia* has been favoured over other less productive, non-evergreen species such as *Q. faginea* and *Q. pyrenaica* (see González Bernáldez *et al.*, 1976 for more details about the history of this area). The result of this management is a mosaic of connected units of grassland and scrub under a canopy of large evergreens distributed at a low to medium density.

However, economic changes during recent decades have led to this traditional management being abandoned and, as a result, not only have grasslands been gradually invaded by scrub, but also huge areas of ancient “*dehesas*” have been turned into pine plantations for timber production. Such changes in land practice must have affected the quality of habitats for the animal populations exploiting them, and may be reflected in some population parameters.

One species that might be affected by land-practice changes is *Parus caeruleus*. Pine plantations (*Pinus pinea* and *P. pinaster*) offer a new type of habitat that differs from holm-oak forests in terms of a number of structural and functional characteristics. One significant feature of pine plantations for the species under study is the absence of hollows for nesting purposes.

In short, human management has given rise to two different adjacent habitats in this area: one is the traditional seminatural *dehesa*, the result of human management over centuries, to which Blue Tits should by now be well adapted; the other habitat consists in pine plantations developed over the last forty years, which the Blue Tit colonizes from its former habitat.

Spatial heterogeneity of habitats is one of the key factors influencing most attributes of populations. Differences in vegetation, resource structure, availability in time, productivity, etc. determine, to a great extent, habitat selection by birds, and thence the specialization and life-history traits of the populations that inhabit them over part or the whole of their life cycle (Cody, 1981; Blondel & Dias, 1994; Hanski, 1994; Hastings & Harrison, 1994).

Long-term studies of population biology in the Blue Tit (*Parus caeruleus*) in Mediterranean habitats have reported differences in breeding traits between different habitat types (Blondel, 1985; Blondel *et al.*, 1987; 1993). Since this species occurs in many forest types and has been extensively studied across its range, it affords a good model for evaluating the extent to which life-history traits are adapted to local environments. In southern Spain, the Blue Tit is very common in evergreen forests where *Q. rotundifolia* predominates.

According to predictions from habitat-selection models (Fretwell & Lucas, 1970), Blue Tits breeding in pine plantations (a recently-colonized habitat) would retain life-history traits adapted to holm-oak forest (the original habitat); failure to adapt to the characteristics of the new habitat would lead to a lower rate of breeding success than that achieved in the older and locally more abundant holm-oak habitat, to which the birds would be well-adapted. Thus, mismatching in certain life-history traits of the Blue Tit, such as clutch size, egg size, laying date and breeding success, might be expected in pine plantations.

The purpose of this study was to detect the Blue Tit's response (mismatching or phenotypic plasticity) to the recently-colonized habitat (pine plantation). This was achieved through comparison of population abundance and reproductive patterns (timing of breeding, reproductive effort and breeding success) of Blue Tits breeding in nestboxes in both habitats.

## MATERIAL AND METHODS

The study area is located in Sierra Morena (38° 02' N; 5° 7' W), southern Spain, at an average height of 550 to 650 m.a.s.l.

The original vegetation of the area is a Mediterranean holm-oak forest with tall trees scattered over connected patches of grassland and scrub. Alongside this vegetation is a plantation of *P. pinea* and *P. pinaster*, introduced in about 1950 and now spreading over huge areas; the two species occur in monospecific patches on the Southern and Northern slopes respectively.

The vegetation structure of these types of habitat depends to a great extent on forestry management, mainly scrub clearing and thinning. Essentially, tree density in the holm-oak forest is lower, and the trees are larger than in the pine plantation: 116.7 and 302 trees/ha respectively for tree density; 51 and 29.4 m<sup>2</sup> respectively for average cover per tree canopy. Canopy cover is larger in the pine plantation (87 %) than in the holm-oak forest (59 %), whereas ground cover by scrub in the holm-oak forest is twice that of the pine plantation (35.1 % and 16.5 % respectively) (Maícas, 1994).

The most abundant scrub species in the holm-oak forest are *Cistus monspe-liensis*, *C. ladanifer* and *C. albidus* and in the pine plantation *C. ladanifer*, *Genista hirsuta*, *Rosmarinus officinalis* and *Lavandula stoechas* (Maícas, 1994; Maícas & Fernández Haeger, 1996).

Blue Tit density data were obtained using the linear transect method, taking a main band 60 metres wide on either side of the census transect, subdivided into six 10-metres sub-bands to which birds sighted or heard were then assigned. Within these limits, the method used enabled estimation of a Blue Tit detectability coefficient (CD), subsequently used to calculate absolute species density (Emlen, 1971; Shields, 1979).

Blue Tit density, expressed as individuals/10 ha, was calculated according to the following equation:  $D = 10 (N/K)/12 CD$ , where *D* is species density, *N* the number of individuals recorded in one month, *K* the number of kilometres travelled in that period, and *CD* the specific detectability coefficient: 0.333 in holm-oak forest (*n* = 340 individuals) and 0.273 in pine plantation (*n* = 167) over an annual cycle of censuses; the census covered 12 ha per km travelled, for a total band width of 120 m.

Three to four censuses were carried out in each of the two habitats every month over the period from March 1989 to February 1991. Adults were not distinguished from juveniles, all birds being considered together for census purposes. In the pine plantation, census transects were made along 1 150 m and 1 700 m in the first and second years respectively. The length of census transects in the holm-oak forest was 1 125 m and 1 650 m respectively. The distance between census points was 3 km.

In order to monitor breeding, we used nestboxes previously erected (1975) in the area as well as new ones. The new boxes were erected in winter before each

breeding season (1989, 1990 and 1991) in a regular pattern and at different densities (20, 40 and 80 boxes/10 ha) (Table I). A further 300 nestboxes had previously been examined in the pine plantation for the 1988 breeding season. These boxes had been erected at random by the local forestry management agency. Altogether, 788 nestboxes were monitored from 1988 to 1991.

TABLE I

*Number of nestboxes monitored in the plots of the pine plantation and holm oak forest. Monitoring years in brackets.*

<b>Plots Plot surface Year</b>	Plot 20/10 ha 20 ha (1990)	Plot 40/10 ha 29 ha (1989)	Plot 80/10 ha 5 ha (1990)	Plot 80/10 ha (see below) (1991)
<b>Nest-boxes in Pine plantation</b>	42	116	42	48 (5,7 ha)
<b>Nest-boxes in Holm Oak</b>	42	116	42	42 (5 ha)

Nestboxes were inspected weekly throughout the breeding season until every fledgling had left the nest. The variables recorded were clutch size, egg volume and number of young raised to fledging; egg volume was calculated using the equation developed by Hoyt (1979). Although eggs were measured individually, all analyses and comparisons were made using mean clutch volume. Nestlings were weighed at day 15. This weight estimate was deemed to represent the definitive weight of nestlings on leaving the nest (Perrins, 1965; Garnet, 1981).

In order to analyse the reproductive cycle in both habitats, we calculated the barycentre 'g' from the equation developed by Blondel, 1985. This parameter is considered more suitable than the average laying date, since values are weighted to reflect total offspring throughout the breeding season. In this case, dates refer to weekly periods. The overall laying-date barycentre was calculated by combining values for the different years under study. Layings made up to and including the barycentre date are considered 'early layings', while those taking place subsequently are considered 'late layings'.

The choice of statistical tests used for comparisons was governed by the type of data distribution involved. Student's t test was used for normal distributions; elsewhere, different non-parametric tests were used, depending on the data: Spearman's correlation coefficient, the Kruskal-Wallis test, and the Mann-Whitney test.

## RESULTS

### ABUNDANCE

Pooling data from all censuses, mean Blue Tit abundance was higher, in both years, in the holm-oak forest ( $\bar{x} = 20.4 \pm 10.6$  indiv/10 ha,  $n = 20$ ) than in the pine

plantation ( $\bar{x} = 8.9 \pm 9.2$  indiv/10 ha,  $n = 20$ ) (Student:  $t_{38} = 3.650$ ,  $p < 0.001$ ). Despite the apparently random fluctuation of density over the two study years, two different trends could be discerned (Fig. 1): a) during the breeding season (February to June) in both years, Blue Tits tended to become less abundant in the holm-oak forest and more abundant in the pine plantation (Spearman correlation,  $r_s = -0.551$ ,  $p < 0.05$ ,  $n = 10$ ); b) during the winter (November to January), when the southern Iberian peninsula receives a considerable number of overwintering individuals migrating from northern areas, Blue Tits were much more abundant in the holm-oak forest ( $\bar{x} = 18.4 \pm 8.9$ ,  $n = 7$  versus  $\bar{x} = 3.34 \pm 3.8$ ,  $n = 7$ ). These results suggest that, during the winter, both overwintering and resident individuals exploit habitat resources mainly in the holm-oak forest, whereas in the breeding season many pairs move to the pine plantation in order to breed in the nestboxes.

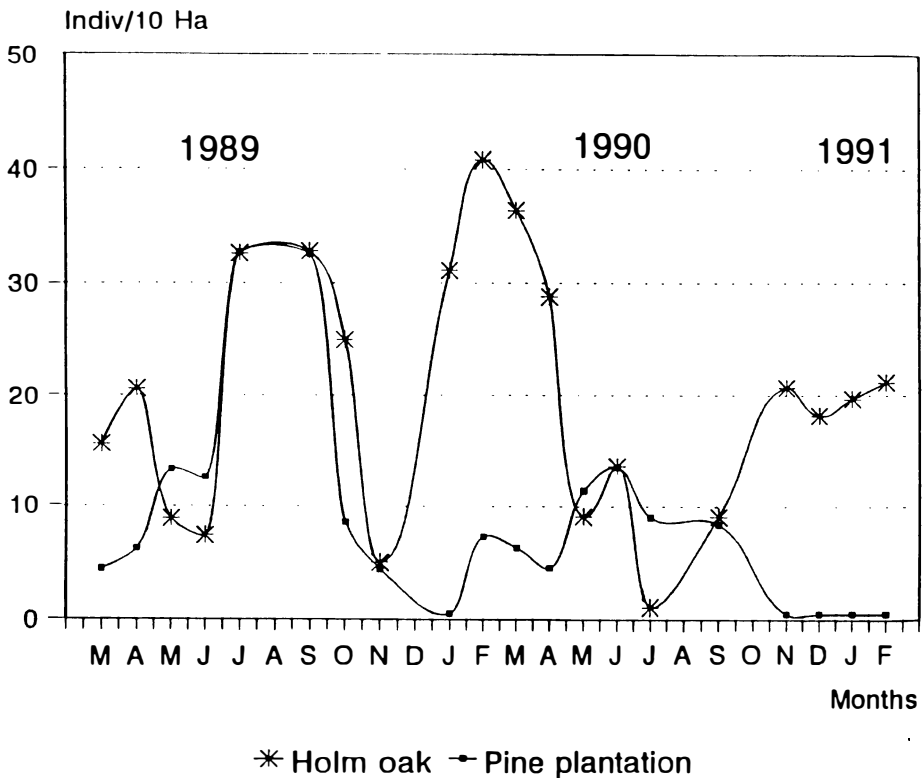


Figure 1. — Monthly variation of Blue Tit density (individuals/10 ha) in the holm oak forest and the pine plantation during the two year study.

BREEDING DENSITY

The density of breeding pairs of Blue Tits tended to increase with nestbox density in both habitats (Fig. 2 upper). However, relative nestbox occupancy was

lower at higher nestbox densities (Fig. 2 lower). Breeding pair density was always much higher in the holm oak forest plots, although in both habitats it increased notably when nestbox density doubled from 20 to 40/10 ha (from 4 to 18 breeding pairs in holm-oak forest and from 0.5 to 5 pairs/10 ha in pine plantation); however,

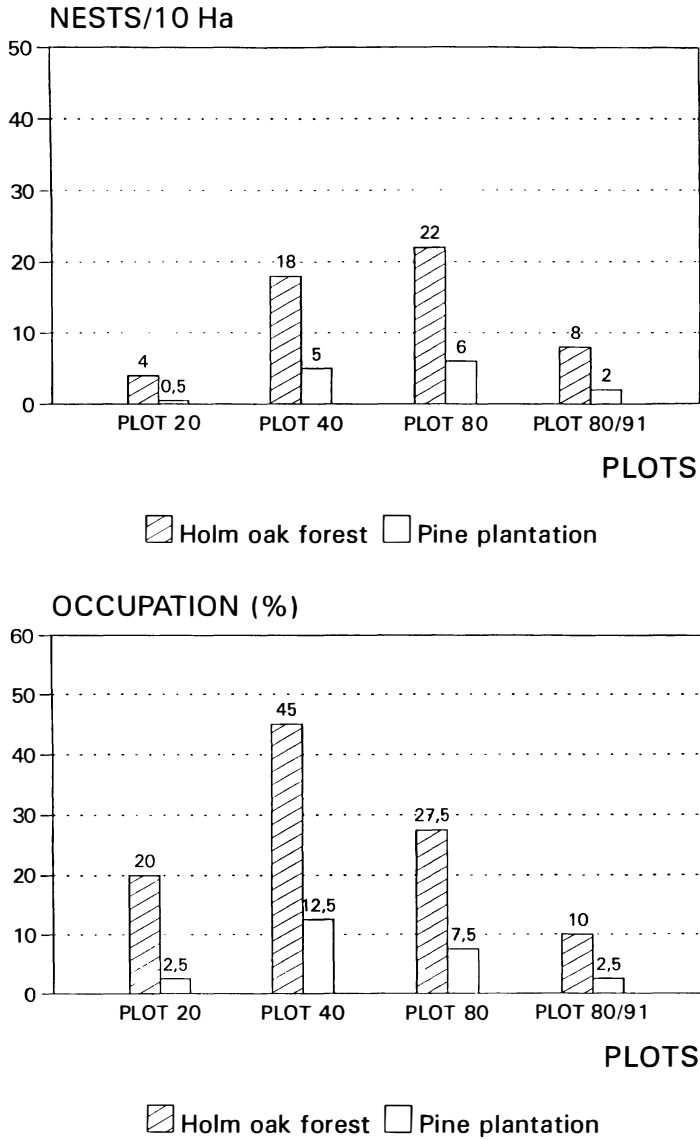


Figure 2. — Upper) Density of Blue Tit nests in the holm oak forest and the pine plantation in plots with 20, 40 and 80 nestboxes per 10 ha. Lower) Nestbox occupancy of Blue Tit in the holm oak forest and the pine plantation in plots with 20, 40 and 80 nestboxes per 10 ha. Plot 80/91 = Plot with 80 nestboxes/10 ha for year 1991.

when nestbox density doubled from 40 to 80/10 ha, the increase in breeding-pair density was only slight (from 18 to 22 pairs/10 ha in holm-oak forest and from 5 to 6 pairs/10 ha in pine plantation).

In the plot containing 80 nest-boxes/10 ha, the only plot studied in 1991, breeding-pair density was much lower than in 1990, probably due to unusual and highly unfavourable climate conditions for the area during February 1991. Pooling the data from all nestboxes over both years, mean density was 3.4 pairs/10 ha and 13.0 pairs/10 ha in the pine plantation and holm oak forest, respectively.

The average distance to the nearest conspecific nest was significantly higher in the pine plantation than in the holm-oak forest ( $x = 111.4 \pm 44.3$  m,  $n = 132$  vs.  $\bar{x} = 67.5 \pm 32.8$  m,  $n = 65$ , respectively; Kruskal-Wallis test  $H = 15,348$ ,  $p < 0.001$ ). Hence, breeding pairs maintained a larger theoretical territory (*sensu* Ripley, 1985) in the pine plantation than in the holm-oak forest (0.97 ha vs. 0.35 ha, respectively).

Additionally, since Great and Blue Tits compete for nestboxes, we calculated the average distance between the nearest nests of both species in both habitats. Distances proved similar in both habitats ( $\bar{x} = 62.6 \pm 17.4$  m,  $n = 18$ , in the pine plantation;  $\bar{x} = 60.5 \pm 20.3$  m,  $n = 65$  in the holm-oak forest; Kruskal-Wallis test:  $H = 1.248$ ,  $p > 0.05$ ).

#### BREEDING PHENOLOGY: VARIATION BETWEEN HABITATS

Egg laying started in the same week in both habitats: between 12 and 19 of March (Fig. 3). Nevertheless, it lasted longer (until the end of May) in the holm-oak forest. Considering the cycle as a whole, late layings (repeat clutches or second broods) were unlikely to produce a bimodal curve of egg presence in the nest in the holm-oak forest, whereas in the pine plantation the proportion of late layings from mid-April onwards actually moved the barycentre two weeks forward with respect to the holm-oak forest.

At the barycentre, the percentage of total laid eggs was 65 % ( $\bar{x} = 27.6 \pm 23.5$  % for the whole cycle) in the holm-oak forest and 50 % ( $\bar{x} = 34.1 \pm 17.9$  %) in the pine plantation. This suggested better clutch synchronization in the holm-oak forest, since most layings took place over a shorter period than in the pine plantation.

Although egg laying started on the same date in both habitats, nestlings were detected two weeks earlier in the holm-oak forest. Hence, hatching took place later in the pine plantation. In addition, the breeding period was shorter in the pine plantation (7 weeks) than in the holm-oak forest (11 weeks).

Nestling food demand in the holm-oak forest peaked between 16 and 23 April, when 40 % of nestlings were being raised; in the pine plantation, it peaked four weeks later, between 14 and 21 May, when 45 % of nestlings were being raised (Fig. 3). These results suggest phenologic differences in breeding conditions between the two habitats.

Nevertheless, no differences were recorded between habitats for average breeding length in nestboxes (Kruskal-Wallis test:  $H = 0.515$ , n.s.). Including only successful layings in both habitats, average breeding length (from first egg laid to fledgling leaving nest) was six weeks ( $\pm 1.12$ ,  $n = 45$  and  $\pm 0.61$ ,  $n = 25$ , respectively).

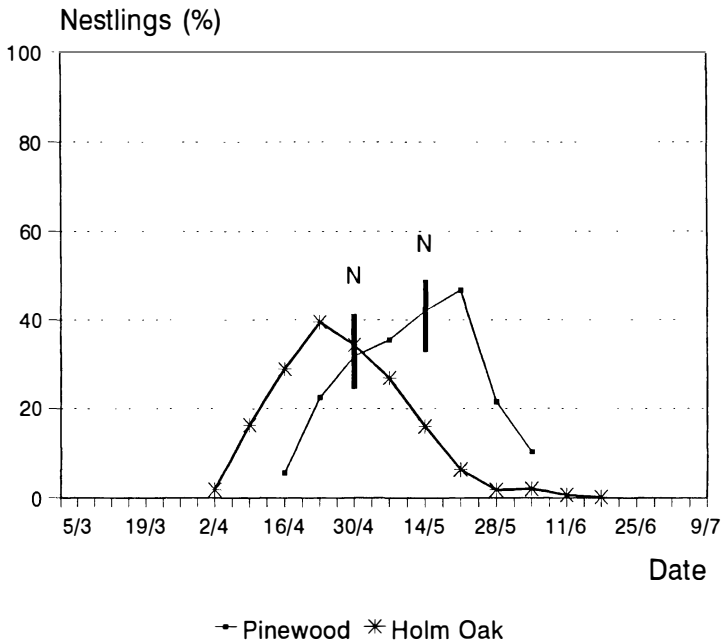
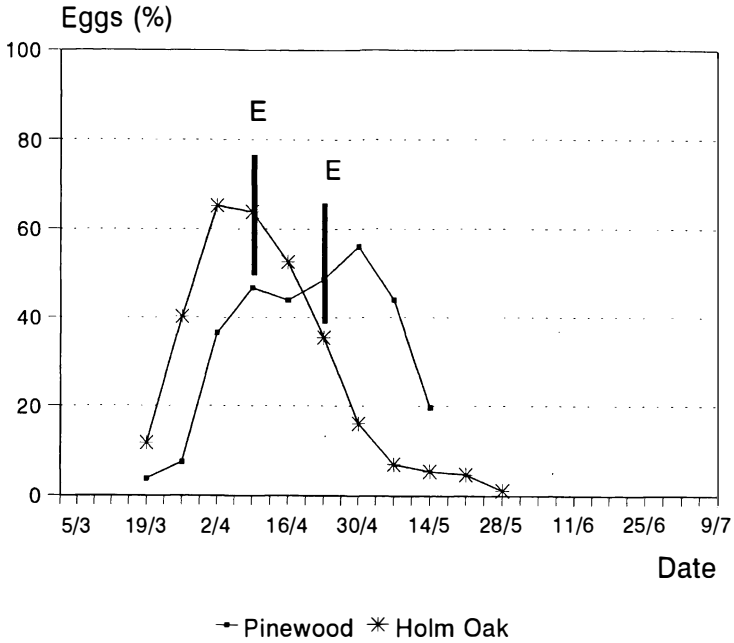


Figure 3. — Phenology of the breeding cycles of Blue Tit in the holm oak forest and the pine plantation. Upper) Percentage of eggs throughout the cycle. Lower) Percentage of nestlings throughout the cycle. Solid bars show barycentre of eggs and nestlings respectively.



REPRODUCTIVE EFFORT

*Clutch size*

Frequency distribution of clutch size in the pine plantation did not fit a normal distribution ( $X^2 = 5.405$ ,  $df = 1$ ,  $p < 0.05$ ) (Fig. 4).

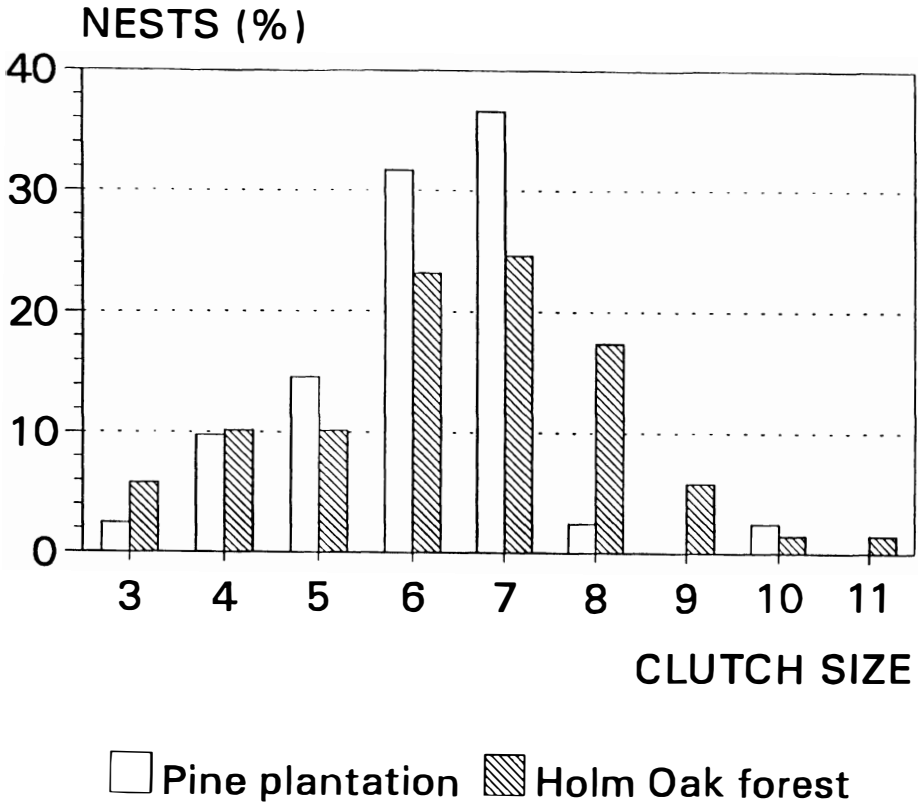


Figure 4. — Frequency of Blue Tit nests in the pine plantation and the holm oak forest with different clutch sizes.

In both habitats most clutches had 6 or 7 eggs (32 and 36 % respectively in the pine plantation; 23 and 24 % respectively in the holm-oak forest). The pine plantation recorded a much lower frequency (4.8 %) of larger clutches compared to the holm oak forest, where 26 % of clutches had more than 7 eggs.

No significant difference in mean clutch size was recorded between the two habitats (Mann-Whitney test:  $Z = 1.235$ , n.s.) (see samples sizes in Table II). Inter-habitat differences were significant for early clutches ( $Z = 2.264$ ,  $p < 0.05$ ) but not for late clutches (Mann-Whitney test:  $U = 69$ , n.s.). Mean clutch size was

TABLE II

*Effect of type of habitat and seasonality on reproductive parameters of Blue Tit. Mean and standard deviation are given; sample size is shown in brackets.  $p < 0.05$  (\*);  $p < 0.01$  (\*\*);  $p < 0.001$  (\*\*\*) ;  $p > 0.05$  (NS).*

Variation source	Reproductive parameters	Pine plantation	Holm oak forest	P
HABITAT	Clutch size	6.1 ± 1.28 (n = 41)	6.42 ± 1.72 (n = 69)	NS
	Egg volume (cm <sup>3</sup> )	1.0 ± 0.05 (n = 17)	1.0 ± 0.11 (n = 59)	NS
	Fledglings	5.03 ± 0.98 (n = 29)	5.00 ± 0.98 (n = 45)	NS
	Fledglings weight (g)	3.56 ± 2.46 <sup>(1)</sup> (n = 41)	3.31 ± 2.83 (n = 68)	NS
SEASONALITY	Clutch size	9.80 ± 0.97 (n = 47)	9.82 ± 0.85 (n = 143)	NS
	----- Early <sup>(2)</sup>	6.17 ± 1.31 (n = 29)	6.87 ± 1.69 (n = 47)	*
	----- Late	5.5 ± 1.38 (n = 6)	5.45 ± 1.37 (n = 22)	NS
		NS	***	
	Egg volume (cm <sup>3</sup> )			
	----- Early	1.01 ± 0.10 (n = 11)	1.00 ± 0.10 (n = 44)	NS
	----- Late	1.00 ± 0.10 (n = 6)	1.00 ± 0.11 (n = 15)	NS
		NS	NS	
	Fledglings			
	----- Early	4.91 ± 0.89 (n = 21)	5.52 ± 1.79 (n = 31)	NS
	----- Late	5.00 ± 1.41 (n = 4)	3.86 ± 1.61 (n = 14)	NS
		NS	**	
Fledglings weight				
----- Early	9.72 ± 0.59 <sup>(3)</sup> (n = 30)	9.73 ± 0.73 (n = 89)	NS	
----- Late	9.94 ± 1.44 (n = 17)	9.96 ± 1.00 (n = 54)	NS	
	NS	P = 0.05		

(1) Taking account all clutches (with and without breeding success). (2) Early clutches in pine plantation: clutches laid before April 23; Early clutches in holm oak forest: clutches laid before April 9. (3) n = number of fledglings.

larger in the holm-oak forest for layings taking place in the first part of the reproductive cycle, i.e. before 9 April and 23 April, respectively. These results suggest that laying date exerts a stronger effect than habitat on clutch size.

In the holm-oak forest, late clutches were considerably smaller than earlier ones (1.42 eggs/clutch;  $t_{67} = 3.4$ ,  $p < 0.001$ ). In the pine plantation, late clutches were also smaller, but did not differ significantly from early clutches (Kruskal-Wallis test:  $H = 1.156$ ,  $p < 0.05$ ), probably due to the very few late clutches found in this habitat.

### *Egg volume*

Frequency distribution of mean egg volume of clutches fits a normal distribution pattern in both habitats (Kolmogorov-Smirnov test:  $D_{17} = 0.194$ , n.s. for pine plantation;  $\chi^2 = 5.331$ ,  $df = 6$ , n.s. for holm-oak forest).

Mean egg volume (Table II) was similar in both habitats ( $t_{74} = 0.087$ , n.s.), and no inter-habitat difference was recorded with regard to egg size at early and late layings (Mann-Whitney test:  $Z = -0.537$ , n.s. for early layings; Mann-Whitney test:  $U = 47$ , n.s. for late layings).

No intra-habitat difference in egg size between early and late clutches was found for either habitat (Mann-Whitney test:  $U = 36$ , n.s. for pine plantation;  $Z = 0.218$ , n.s. for holm-oak forest).

Thus, unlike clutch size, mean clutch volume was unaffected by either habitat or laying date.

## BREEDING SUCCESS

The number of fledglings raised per clutch ranged from 3 to 7 in the pine plantation and 2 to 8 in the holm-oak forest (Fig. 5). Broods with 4 to 6 nestlings accounted for 63.4 % in the pine plantation and only 32.4 % in the holm-oak forest, while broods with 6 to 8 nestlings accounted for 5 % and 16 %, respectively. These results suggest fewer variations in brood size in the pine plantation than in holm-oak forest.

In the pine plantation, 146 fledglings were raised from 250 eggs laid (58 %) compared to 225 fledglings raised from 443 eggs laid (51 %) in the holm-oak forest. This difference accounts for the average survival rate in both habitats: 3.56 and 3.31 fledglings per clutch respectively (Table II).

When failing clutches were excluded from the analysis, there was no inter-habitat difference in average breeding success: 5.03 fledglings/clutch in the pine plantation; 5.00 fledglings/clutch in the holm oak forest ( $t_{89} = 0.091$ , n.s.). Neither early ( $t_{50} = 1.448$ , n.s.) nor late clutches (Mann-Whitney test:  $U = 40$ , n.s.) showed any significant inter-habitat difference in breeding success. The lack of significance in the comparison between late clutches may, as reported earlier, be due to the very low number of clutches in the pine plantation ( $n = 4$ ) since, on average, the four clutches in the pine plantation yielded 1.14 fledglings/clutch more than the fourteen late clutches in the holm-oak forest.

There was no significant difference in the number of young raised per clutch in early and late clutches in the pine plantation, whereas in the holm-oak forest late broods yielded considerably fewer fledglings raised than early clutches. This reduction in the number of fledglings from late clutches is associated with a lower hatching success in late clutches (Kruskal-Wallis test:  $H = 5.246$ , n.s.). Average hatching success in late clutches was  $4.46 \pm 1.83$  ( $n = 14$ ), i.e. 1.53 fewer

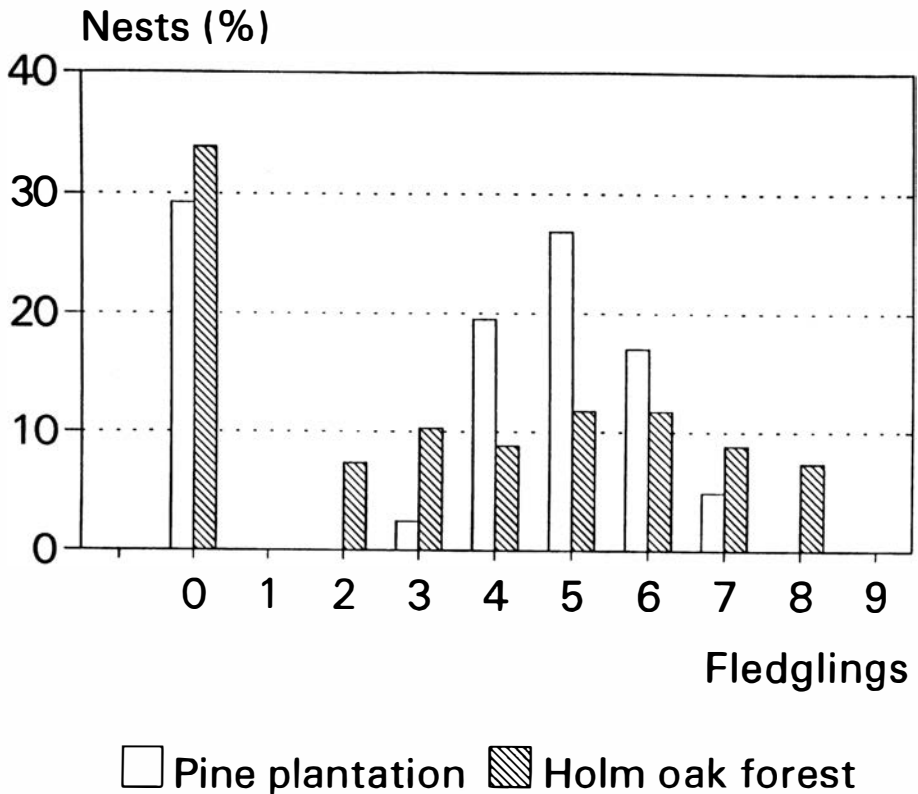


Figure 5. — Frequency of fledglings raised by Blue Tit in the pine plantation and the holm oak forest.

eggs/clutch than in early clutches ( $5.96 \pm 2.1$ ,  $n = 31$ ). Variation in this parameter may thus account for variations in breeding success over the last part of the breeding cycle.

In the pine plantation, hatching success remained constant over the breeding season (Kruskal-Wallis test:  $H = 0.038$ , n.s., early clutches vs. late clutches). In early clutches, average hatching success was  $5.24 \pm 0.94$  eggs/clutch ( $n = 21$ ), compared with  $5.25 \pm 1.71$  ( $n = 4$ ) eggs/clutch in late clutches.

In the pine plantation clutches of more than seven eggs were very rare (2%); similarly, breeding success was considerably reduced in broods from clutches of that size. Only two (5%) out of seventeen (41.4%) broods with seven eggs and over yielded seven fledglings, and none yielded more (Fig. 5).

The same pattern was found in the holm-oak forest, where 50.6% of clutches had seven eggs or over, and only 16.1% yielded seven fledglings or over.

These results suggest that a clutch size of seven eggs or over represents in both habitats a breeding effort contributing poorly to the number of fledglings raised. Hence, this species would obtain little reproductive advantage by increasing clutch size over six eggs.

Differences were recorded in intra-habitat productivity between early and late clutches in the holm-oak forest: in late clutches, an average of 1.66 fewer nestlings were raised to fledglings compared to early clutches ( $t_{43} = 2.969$ ,  $p < 0.01$ ). No significant differences were found in this respect for the pine plantation (Mann-Whitney test:  $U = 50$ , n.s.) (Table II).

In both habitats, brood size depended on clutch size. However, regression analysis shows a stronger relationship in the holm-oak forest than in the pine plantation (Fig. 6). In the former, 51.9 % of the variation in fledgling numbers can be accounted for by clutch size ( $r^2 = 51.9$ ) whereas in the latter clutch size accounts for up to 25 % ( $r^2 = 24.9$ ) of this variation.

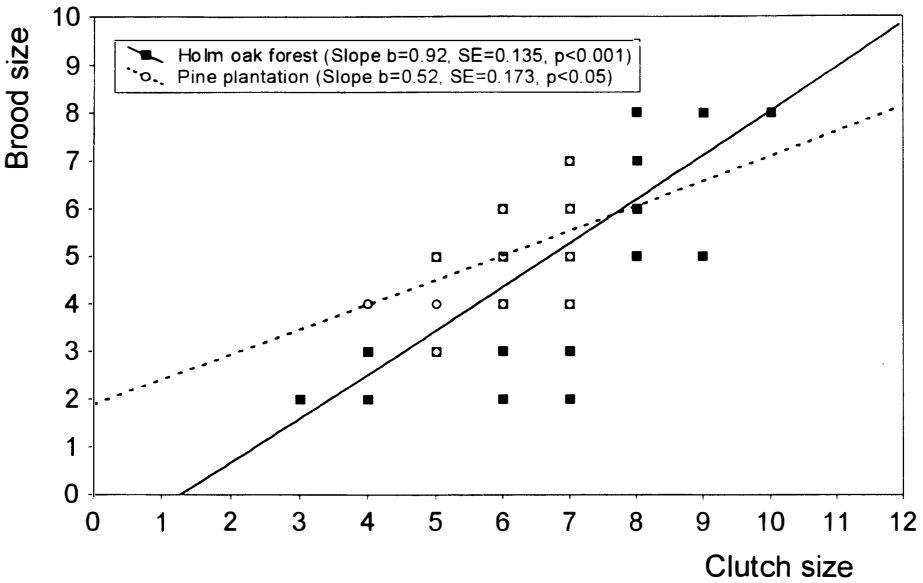


Figure 6. — Relationship (Linear Regression Analysis) between brood size and clutch size.

Another parameter used to assess breeding success was fledgling body size measured as weight in grams. Mean weight of fledglings when leaving the nest was similar in both habitats (Kruskal-Wallis test:  $H = 0.259$ , n.s.) (Table II). Inter-habitat differences in body size as a function of laying date were not significant. Therefore, fledgling weight does not depend on habitat type.

Intra-habitat variation in fledgling weight between early and late clutches was significantly different in holm-oak forest ( $H = 3.703$ ,  $p = 0.05$ ) but not in the pine plantation ( $H = 0.078$ , n.s.). Nevertheless the difference detected in the holm-oak forest could be considered trivial and related to a sample size effect.

## BREEDING FAILURE

Of all breeding pairs (N = 110), 38 % completely failed to breed; twelve (11 %) in the pine plantation and 30 (27 %) in the holm-oak forest (Table III).

TABLE III

*Relative importance of causes of breeding failure of Blue Tit in pine plantation and holm oak forest nests in stages of egg and nestling; percentages of the nests in each forest are given in brackets. OPD = one of the parents was found dead in the nest; EP = egg predation; ED = egg desertion; I = reproduction interference by other species through displacing from the nestbox; NP = nestling predation; ND = nestling desertion; A = ants; E = presence of ectoparasites; HUM = humidity by rain.*

CAUSE	EGG STAGE		NESTLING STAGE	
	Pine plantation	Holm oak	Pine plantation	Holm oak
OPD	—	1 (1)	—	—
EP	1 (2)	3 (4)	—	—
ED	4 (10)	11 (16)	—	—
I	—	—	—	1 (1)
NP	—	—	2 (5)	3 (4)
ND	—	—	5 (12)	4 (6)
A	—	—	—	2 (3)
E	—	—	—	4 (6)
HUM	—	1 (1)	—	—
TOTAL	5 (12)	16 (22)	7 (17)	14 (20)

No fledglings were produced in 29 % of nests in the pine plantation and 34 % in the holm-oak forest (Fig. 5). Results show not only higher breeding failure in the latter, but also a wider number of causative factors, such as ectoparasites (E), ants (A) of *Crematogaster* sp. and inter-specific interference (I). These factors were not present in the pine plantation.

During the egg stage, laying loss in the holm-oak forest was almost double that of the pine plantation (22 % and 12 %, respectively). However, during the nestling stage, the proportion of broods yielding no fledglings was similar in both habitats (20 % and 17 %, respectively). Breeding failure in the pine plantation was largely due to clutch and brood desertion. These factors were also found in the holm-oak forest alongside ectoparasites.

## DISCUSSION

The present study of breeding pairs of *P. caeruleus* revealed certain distinctive features of the pine plantation in contrast to the holm-oak forest: 1) Breeding-pair density was lower, and territory larger; 2) Early clutches were smaller; and 3) very few seven-egg clutches were laid.

In the pine plantation, there is greater uniformity of tree size and shape than in the holm-oak forest (Fernández Haeger & Rodríguez, 1982; Maícas, 1994), where these features vary widely and the distance between trees is longer. The greater canopy cover afforded by pines gives rise to an environment affecting both richness and relative abundance of species (Fernández Haeger & Rodríguez, 1982; Maícas, 1994), as well as prompting phenological variations in plants and associated insects (Jordano *et al.*, 1989; Jordano *et al.*, 1990).

In addition, since pines are both shorter and younger than oaks (around 40 years compared, in some cases, to centuries), pine plantations afford no hollows in which to breed; nestboxes erected in the pine plantation attempt to compensate for this. These features may account for the lower mean abundance of Blue Tits in the pine plantation, which further decreases during the winter months.

During the breeding season (March-June), the number of individuals increases in the pine plantation and decreases in the holm-oak forest. This variation suggests an asymmetrical flow of individuals from holm-oak to pine forest, probably associated with settling breeding territories. In any case, there were fewer breeding pairs in the pine plantation than in the holm-oak forest: at different nestbox densities, occupancy rate was always below 30 % of that recorded in the holm-oak forest. This difference in breeding density may be considered conservative for two reasons. First, if no nestboxes were erected in the pine plantation, breeding pairs could not settle there; second, only pairs in nestboxes were included in the analysis, whereas in the holm-oak forest many pairs nested in tree holes; thus, breeding density is probably even higher than that recorded here in the holm-oak forest.

These results suggest that breeding conditions are more favourable in the holm-oak forest (preferred habitat). For this reason, dominant individuals would settle their territories in this type of habitat whereas subordinates would be displaced to the less preferred habitat in the pine plantation (Fretwell, 1992; Dhondt *et al.*, 1982; Westman, 1990; Blondel *et al.*, 1993). Thus the Blue Tit habitat occupancy pattern would follow the 'ideal despotic distribution model'.

Although Blue Tit habitat selection during the breeding season is density-dependent, breeding results do not fit the 'ideal despotic distribution' model that predicts a lower breeding success in the less preferred habitat (Fretwell & Lucas, 1970); breeding success was similar in the two habitats. This result differs from findings reported in other studies of inter-habitat differences in breeding success with regard to density and habitat quality (Lundberg *et al.*, 1981; van Balen, 1973; Ulfstrand *et al.*, 1981; Lemel, 1989; Riddington & Gosler, 1995; Dias & Blondel, 1996).

Lower breeding-pair density and a greater distance between nests yield larger breeding territories, probably associated with a poor quality of food resources necessary for breeding. The different size of territories is a mechanism regulating population size in each habitat during the breeding period (Dhondt *et al.*, 1982; Clamens, 1987).

Although inter-habitat difference in mean clutch size was not significant, clutches of over seven eggs were very rare in the pine plantation (4.8 % of the total), but fairly frequent (26 %) in the holm-oak forest. Clutch size is associated with the number of fledglings raised (Cody, 1966; Lack, 1968; Balen, 1973; Martin, 1987; Nur, 1988; Slagsvold & Lifjeld, 1988). The different slopes of regression equations for both habitats suggest that clutches of over 7 eggs would yield a lower breeding success in the pine plantation than in the holm-oak forest;

this difference, however, is not significant. Individuals displaced to the pine plantation are likely to have low breeding success from extremely large clutches. This suggests that it would be more advantageous not to increase clutch size over six eggs and instead devote greater effort to exploiting a wider territory.

On average, late clutches had fewer eggs than early ones in both habitats (Blondel *et al.*, 1987; Potti *et al.*, 1988; Dervieux *et al.*, 1990; Hilden, 1990; Verhulst & Tinbergen, 1991). Smaller clutch sizes suggest more severe conditions as the breeding season progresses. In this area of Southern Spain, high temperatures and lack of rain from the start of summer give rise to plant growth periods in winter and spring, with insect abundance peaking in May (Jordano *et al.*, 1989; Rodríguez *et al.* 1994).

Constant mean egg volume throughout the breeding season in both habitats would increase the probability of nestling survival by the end of breeding season, when clutches have fewer eggs but volumes remains the same (Schifferli, 1973; O'Connor, 1979; Howe, 1976). This strategy may favour nestling survival at a time when conditions are becoming severe, with a lack of suitable food for nestlings and risk of hyperthermia (Mertens, 1988).

However the number of fledglings from late clutches was significantly lower in the holm-oak forest. This confirms the above hypothesis, and was especially evident in this habitat, where the breeding season lasts longer (until the end of spring).

Fledgling weight is a predictor of Blue Tit survival rate. Thus, there is a significant correlation between fledgling weight and recruitment rate the following year (see Cichon & Linden, 1995). From the results obtained here, equal survival and recruitment rates can be predicted for fledglings in both habitats.

The proportion of clutch desertion is greater in the holm-oak forest during the egg stage, and is probably associated with higher breeding-pair and egg densities, possibly suggesting a mechanism for regulating breeding-pair density after settling territories. During the egg stage, clutch loss rates were closer and any difference can be accounted for by differing predator and parasite pressure between the two habitats.

Adaptation to the pine plantation affords the Blue Tit a similar breeding success to that attained in holm-oak forest. However, while certain life-history traits with an important genetic component, such as egg volume (Nilsson & Svensson, 1993) and laying date (Blondel *et al.*, 1990, Lambrechts & Dias, 1993) remain remarkably constant, others display great phenotypic plasticity and enable the Blue Tit to adapt to the conditions of the new habitat. Adaptations include a greater distance between breeding pairs (and consequently larger breeding territories) and fewer large clutches, enabling the Blue Tits to raise a similar number of fledglings with a weight close to that achieved in the holm-oak forest.

These results provide no data on species mortality rates. Nevertheless, it is very clear that a large proportion of the population leaves the pine plantation after breeding, probably to avoid scarcity of resources and high mortality during the winter, and concentrates in the oak forest. So the contribution of pine plantation to overall population recruitment is relatively low, due to the low density of breeding pairs. Therefore, the density of Blue Tits in the pine forest is maintained by migration of individuals from the adjoining habitat, in which the recruitment rate should be greater than the mortality rate.

From the conservation stand point, the replacement of original holm-oak forests by pine plantations is a forestry management policy with major implica-



tions for the Blue Tit. Although individual density is similar in the two habitats at some times of year, species persistence cannot be guaranteed. Artificial nestboxes favour the breeding of this species in the pine plantation, where breeding success is similar to that achieved in the holm-oak forest. However, pair density is much lower, giving rise to a lower recruitment rate per unit area. In addition, net flow to the holm-oak forest in winter may be interpreted as a strategy to avoid mortality associated with the poor quality of food resources available at that time of year. Hence, replacement of oak forests by exotic plantations involves extending areas where Blue Tits maintain low population densities through migration from adjacent habitats.

The quality of different habitats for a given species is not easy to assess. Although it may be inferred from the difference between birth- and death-rates, that difference can vary widely over time. Long term studies are therefore essential for the analysis of population attributes (Clutton-Brock, 1988; Newton, 1989; Newton, 1995; Dias, 1996). Moreover, other population parameters, such as density and its fluctuations, turnover, etc. could be valuable in detecting qualitative differences between habitats.

Differences between birth- and death-rates in different types of habitat within a heterogeneous environment are essential in order to distinguish source from sink habitats. Obviously, sink habitats, where mortality exceeds natality, are maintained by immigration of individuals from source habitats. Several categories have been described for sink habitats, including black hole sinks (no back migration) and leaky sinks (some back dispersal) (Morris, 1991; Holt & Gaines, 1992; Dias, 1996). In the case of Blue Tits studied here, the return of a substantial proportion of the population from pine plantation to holm-oak forest after the breeding season, evident in the census data, may be interpreted as a strategy for avoiding high mortality due to resource scarcity. This suggests that pine plantations may be a "leaky sink", in which the birth-rate is favoured by the provision of nestboxes and mortality is avoided by the return of part of the population to the original habitat.

## ACKNOWLEDGEMENTS

We wish to thank Raquel Martinez and Francisco Conde for their intensive and valuable help with the field work. The advice of our colleagues Fernando, Diego, Joaquín and Emilio has been equally important. We also wish to thank the owners of the estates *El Villarejo* and *Cortijo las Cañas* for their cooperation in allowing us to carry out part of this work on their land. The rest of the fieldwork was performed in pine plantations owned by the regional government. This work was supported by the Instituto Andaluz de Reforma Agraria (I.A.R.A.), a branch of the Andalusian Regional Government. Two anonymous referees made valuable comments on previous drafts of this paper.

## REFERENCES

- BALEN J.H.V. (1973). — A comparative study of the breeding ecology of the Great Tit *P. major* in different habitats. *Ardea*, 61: 1-93.
- BLONDEL, J. (1985). — Breeding strategies of the Blue Tit and Coal Tit (*Parus*) in mainland and island mediterranean habitats: a comparison. *J. Anim. Ecol.*, 54: 531-556.
- BLONDEL, J., CLAMENS, A., CRAMM, P., GAUBERT, H. & ISENMANN, P. (1987). — Population studies on tits in the mediterranean region. *Ardea*, 75: 21-34.

- BLONDEL, J. & DIAS, P.C. (1994). — Summergreenness, evergreenness and life history variation in mediterranean Blue Tits. Pp. 25-36, in: M. Arianoutsou & R.H. Groves (Eds). *Plant-Animal interactions in mediterranean-type ecosystems*. Kluwer Academic Publishers. Netherlands.
- BLONDEL, J., DIAS, P.C., MAISTRE, M. & PERRET, P. (1993). — Habitat heterogeneity and life-history variation of mediterranean Blue Tits (*Parus caeruleus*). *Auk*, 110: 511-520.
- BLONDEL, J., PERRET, P. & MAISTRE, M. (1990). — On the genetical basis of the laying-date in an island population of Blue Tits. *J. Evol. Biol.*, 3: 469-475.
- CICHON, M. & LINDEN, M. (1995). — The timing of breeding and offspring size in Great Tit *Parus major*. *Ibis*, 137: 364-370.
- CLAMENS, A. (1987). — Importance de la territorialité dans la reproduction de la Mésange bleue *P. caeruleus* en chênaie de chênes verts. *Rev. Ecol. (Terre et Vie)*, 42: 311-320.
- CLUTTON-BROCK, T. (1988). — *Reproductive success*. Chicago University Press. Chicago.
- CODY, M.L. (1966). — A general theory of clutch size. *Evolution*, 20: 174-184.
- CODY, M.L. (1981). — Habitat selection in birds: the role of vegetation structure, competitors and productivity. *BioScience*, 31: 107-113.
- DERVIEUX, A., ISENMANN, P., CLAMENS, A. & CRAMM, P. (1990). — Breeding time and breeding performance of the Blue Tit *Parus caeruleus* in two Mediterranean habitats. Pp. 77-87, in: J. Blondel et al., (eds). *Population Biology of passerine birds*. Springer-Verlag. Berlin Heidelberg.
- DHONDT, A.A., SCHILLEMANS, J. & DE LAET, J. (1982). — Blue Tits territories in populations at different density levels. *Ardea*, 70: 185-188.
- DIAS, P.C. (1996). — Sources and sinks in population biology. *Trend. Ecol. Evol.*, 11: 326-330.
- EMLEN, J.T. (1971). — Population densities of birds derived from transect counts. *Auk*, 88: 323-341.
- FERNÁNDEZ HAEGER, J. & RODRÍGUEZ, A. (1982). — Les peuplements de fourmis dans la Sierra Morena centrale (Espagne). Rapports avec l'exposition et la végétation. *Insectes Sociaux*, 29: 358-368.
- FRETWELL, S.D. (1992). — *Populations on a seasonal environment*. Princeton University Press. Princeton, N.J.
- FRETWELL, S.D. & LUCAS, H.L. (1970). — On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.*, 19: 16-36.
- GARNET, M.C. (1981). — Body size, its heritability and influence on juvenile survival among Great Tits, *Parus major*. *Ibis*, 23: 31-41.
- GONZÁLEZ BERNÁLDEZ, F., POU, A., RAMÍREZ, L., SANCHO, F., MERINO, J., GARCIA NOVO, F., COTA, H., TOJA, J., FERNÁNDEZ HAEGER, J. & LEVASSOR, C. (1976). — *Estudios ecológicos en Sierra Morena*. Servicio de Publicaciones del Ministerio de Agricultura. Madrid.
- HANSKI, I. (1994). — Spatial scale, patchiness and population dynamics on land. *Philos. Trans. Roy. Soc. London. Ser. B.*, 343: 306-308.
- HASTINGS, A. & HARRISON, S. (1994). — Metapopulation dynamics and genetics. *Ann. Rev. Ecol. Syst.*, 25: 167-188.
- HILDEN, O. (1990). — Long-term study of a northern population of the Blue Tit *Parus caeruleus*. In: J. Blondel et al. (eds). *Population biology of passerine birds*. Springer Verlag. Berlin Heidelberg.
- HOLT, R.D. & GAINES, M.S. (1992). — Analysis of adaptation in heterogeneous landscapes: implications for the evolution of fundamental niches. *Evol. Ecol.*, 6: 433-447.
- HOWE, H.F. (1976). — Egg size, hatching asynchrony, sex, and brood reduction in the Common Grackle. *Ecology*, 57: 1195-1207.
- HOYT, D.F. (1979). — Practical methods of estimating volume and fresh weight of bird eggs. *Auk*, 96: 73-77.
- JOFFRE, R., VACHER, J., DE LOS LLANOS, C. & LONG, C. (1988). — The *dehesa*: an agrosilvopastoral system of the Mediateranean region with special reference to the Sierra Morena area of Spain. *Agrofor. Systems*, 6: 71-96.
- JORDANO, D., FERNÁNDEZ HAEGER, J. & RODRÍGUEZ, J. (1989). — The life-history of *Tomares ballus* (Lepidoptera: Lycaenidae): phenology and host plant use in southern Spain. *J. Res. Lepidoptera*, 28: 112-122.
- JORDANO, D., FERNÁNDEZ HAEGER, J. & RODRÍGUEZ, J. (1990). — The effect of seed predation by *Tomares ballus* (Lep.: Lycaenidae) on *Astragalus lusitanicus* (Fabaceae): determinants of differences among patches. *Oikos*, 57: 250-256.
- LACK, D. (1968). — *Ecological adaptations for breeding in birds*. Methuen & Co. London.
- LEMEL, D. (1989). — Habitat distribution in the Great Tit (*Parus major*) in relation to reproductive success, dominance and hierarchy. *Ornis Scand.*, 20: 226-233.

- LAMBRECHTS, M.M. & DIAS, P.C. (1993). — Differences in the onset of laying between island and mainland mediterranean Blue Tits *Parus caeruleus*: phenotypic plasticity or genetic differences? *Ibis*, 135: 451-455.
- LUNDBERG, A., ALATALO, R.V., CARLSON, A. & ULFSTRAND, S. (1981). — Biometry, habitat distribution and breeding success in the Pied Flycatcher *Ficedula hypoleuca*. *Ornis. Scand.*, 12: 68-79.
- MAÍCAS, R. (1994). — *Estrategias reproductoras de P. major y P. caeruleus en nidales de una repoblación de coníferas y en un encinar mediterráneo*. Tesis doctoral. Facultad de Ciencias. Universidad de Córdoba.
- MAÍCAS, R. & FERNÁNDEZ HAEGER, J. (1996). — Breeding patterns of the Great Tit (*P. major*) in a coniferous plantation and a holm oak forest in a mediterranean region (southern Spain). *Rev. Ecol. (Terre et Vie)*, 51: 341-357.
- MARTIN, T.E. (1987). — Food as a limit on breeding birds: a life-history perspective. *Ann. Rev. Ecol. Syst.*, 18: 453-487.
- MERTENS, J.A.L. (1988). — Water balance of Blue Tits (*Parus caeruleus*) in Corsica. *Progress Report*: 13-18. Institute for Ecological Research.
- MORRIS, D.W. (1991). — On the evolutionary stability of dispersal to sink habitats. *Am. Nat.*, 137: 907-911.
- NEWTON, I. (1989). — *Lifetime reproduction in birds*. Academic Press. London.
- NEWTON, I. (1995). — The contribution of some recent research on birds to ecological understanding. *J. Anim. Ecol.*, 64: 675-696.
- NILSSON, J.A. & SVENSSON, E. (1993). — Causes and consequences of egg mass variation between and within Blue Tit clutches. *J. Zool. Lond.*, 230: 468-481.
- NUR, N. (1988). — The cost of reproduction in birds: an examination of evidence. *Ardea*, 76: 155-168.
- O'CONNOR, R.J. (1979). — Egg weights and brood reduction in the European Swift (*Apus apus*). *Condor*, 81: 133-145.
- PERRINS, C.M. (1965). — Population fluctuations and clutch-size in the Great Tit, *P. major* L. *J. Anim. Ecol.*, 34: 600-651.
- POTTI, J., MONTALVO, S., SANCHEZ-AGUADO, F.J. & BLANCO, D. (1988). — La reproducción del herrerillo común (*P. caeruleus*) en un robledal del centro de España. *Ardeola*, 35: 31-43.
- RIDDINGTON, R. & GOSLER, A.G. (1995). — Differences in reproductive success and parental qualities between habitats in the Great Tit *Parus major*. *Ibis*, 137: 371-378.
- RIPLEY, B.D. (1985). — Analyses of nest spacings. Pp. 151-158. In: Morgan B.J.T. & North, P.M. (Eds). *Statistics in Ornithology*. Springer-Verlag. Berlin.
- RODRÍGUEZ, J., JORDANO, D. & FERNÁNDEZ HAEGER, J. (1994). — Spatial heterogeneity in a butterfly-host plant interaction. *J. Anim. Ecol.*, 63: 31-38.
- SCHIFFERLI, L. (1973). — The effect of egg weight on the subsequent growth of nestling Great Tit *Parus major*. *Ibis*, 115: 549-558.
- SHIELDS, W.M. (1979). — Avian census techniques: an analytical review. Pp. 23-51, in: Dickson, J.G. et al. (Eds). *The role of insectivorous birds in forest ecosystems*. Academic Press. New York.
- SLAGSVOLD, T. & LIFJELD, J.T. (1988). — Ultimate adjustment of clutch size to parental feeding capacity in a passerine bird. *Ecology*, 69: 1918-1922.
- ULFSTRAND, S., ALATALO, R.V., CARLSON, A., & LUNDBERG, A. (1981). — Habitat distribution and body size of the Great Tit *Parus major*. *Ibis*, 123: 494-499.
- VERHULST, S. & TINBERGEN, J.M. (1991). — Experimental evidence for a casual relationship between timing and success of reproduction in the Great Tit *Parus m. major*. *J. Anim. Ecol.*, 60: 269-282.
- WESTMAN, B. (1990). — Environmental effect on dominance in young Great Tits *Parus major*: a cross-fostering experiment. *Ornis Scand.*, 21: 46-51.