

Do harlequin mediterranean environments function as source sink for Blue Tits (*Parus caeruleus* L.)?

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Abstract

We investigate whether a mosaic of habitats of different quality functions as a source-sink system for the Blue Tit *Parus caeruleus* L. Breeding parameters, especially laying date, clutch size and breeding success have been studied in relation to the food supply in three habitats: two habitats, one rich and one poor, next to each other on the mainland (southern France) and one poor habitat on the island of Corsica. Food resources are more abundant and are available earlier in the season in the rich habitat than in both the mainland and the island poor habitats. The timing of breeding is nicely timed on the food peak of abundance in the rich mainland habitat and in the poor insular one but tits are mistimed in the poor mainland habitat because they start to breed too early in relation to food availability. Such patterns strongly suggest that the rich mainland habitat where birds produce many fledglings functions as a source from which birds emigrate in the poor habitat which functions as a sink. These birds which are genetically programmed to breed in the source habitat become mistimed in the sink. Tits on Corsica which are isolated from any mainland population have adjusted their breeding traits on the local patterns of food availability and abundance. This hypothesis is supported by the existence of a strong genetic component of laying date which has been experimentally proved.

Introduction

For several decades, population ecologists have mainly focused on local mechanisms of population dynamics in small areas of homogeneous habitat. Their approach was based upon the assumption that animal numbers and population regulation are mainly determined through local factors (Lack 1966), which led to the misleading concept of a more or less constant carrying capacity. Most ecologists agree today that local processes are not independent from those occurring on larger scales of space (Den Boer 1968; Ricklefs *et al.* 1984; Wiens 1986, 1989; Ricklefs 1987; Blondel 1987; Soule 1987) so that ecological processes which determine

species assemblages and population regulation operate on spatial and temporal scales far larger than those usually utilized in field studies (Wiens 1986; Ricklefs 1987; Blondel 1986, 1987, 1990). Most species can regularly be found in a variety of habitats of different quality. Assuming that a local habitat patch, say of a few hectares, demographically interact with other habitat patches, investigations should focus on geographical movements of individuals between habitats, each of them becoming a part of a larger region (Rosenzweig 1985). More precisely, the problem is to identify which individuals participate to these geographical movements and whether emigrating or immigrating individuals differ in some phenotypic and genotypic

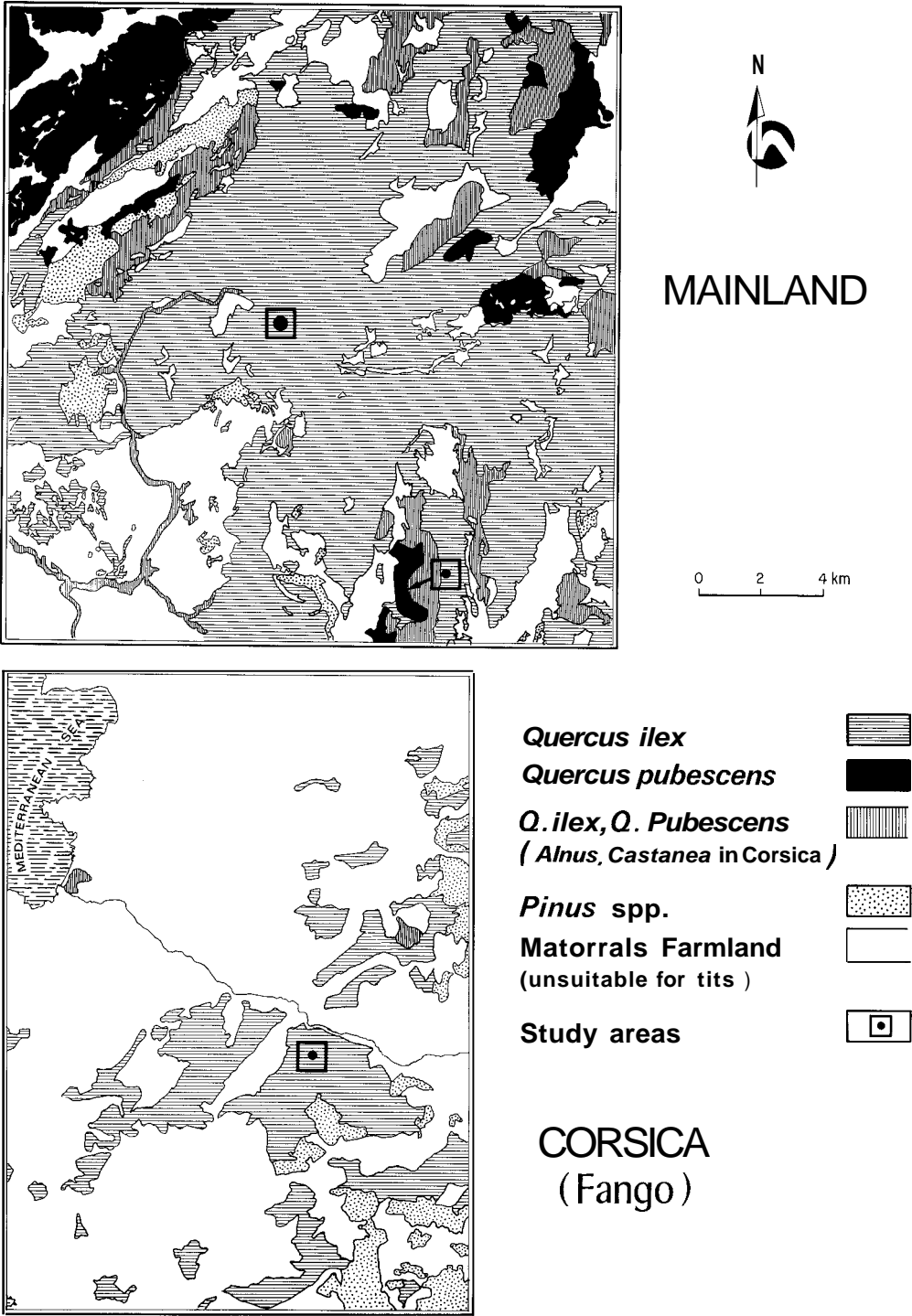


Fig. 1. Location of the study areas on the mainland, southern France near Montpellier (mosaic of deciduous and sclerophyllous habitats) and on Corsica (only sclerophyllous habitats are suitable for tits).

attributes from those which do not move. Provided that exchanges of individuals between habitat patches are dissymmetric, *i.e.*, some habitat patches export more individuals than others, a distinction must be made between 'source' and 'sink' habitats (Lidicker 1975; van Horne 1983; Pulliam 1988). This paper is a preliminary approach to an application of the BIDE (Birth-Immigration-Death-Emigration) model of Cohen (1969, 1971) using the Blue Tit *Parus caeruleus* L. in Mediterranean habitats as a case study. Three reasons explain why the Blue Tit is a good model for such an approach: 1) This species is widespread and common in most woodland oakwoods (Snow 1954; Perrins 1979) but it is rather flexible in habitat choice and occurs in most types of forests including mixed, sclerophyllous and conifer forests. However densities are usually lower in non deciduous habitats which are poor habitats for this species. 2) The Mediterranean region is a patchwork of habitats where the vegetation is dominated by either deciduous trees (*e.g.*, the Downy oak *Quercus pubescens*) or sclerophyllous trees (*e.g.*, the Holm oak *Q. ilex*). Thus, from a tit's point of view there are side by side 'good' deciduous habitats (hypothesized as source) and 'poor' sclerophyllous habitats (hypothesized as sink). 3) Food is assumed to be the main factor determining habitat quality. Although the amount of food available for birds is usually extremely difficult to assess with some accuracy (Newton 1980), tits mostly prey upon caterpillars which, fortunately, are reasonably easy to sample through their frass falling from the canopy of the trees (Tinbergen 1960; Zandt *et al.* 1990).

There is a large variation of clutch size over the distributional range of the Blue Tit: clutch size is high with a small between-habitat variation in temperate and northern Europe ($X = 10.9 \text{ eggs} \pm \text{sd} = 0.47$, $n = 12$), but much lower with a high variability in the Mediterranean region ($X = 7.7 \pm \text{sd} = 1.88$, $n = 11$). Such a large variation in clutch size and associated life history traits such as laying date in Mediterranean habitats is hypothesized to be related to differences in the quality of habitat patches. We will investigate to which extent between-habitat differences in such factors as food resources explain these patterns of variation of life

history traits and may result in a sink-source system resulting in geographical movements of birds between habitat patches.

Material and methods

Populations of Blue Tit have been studied in three habitats which differ by their dominant trees species and degree of isolation (Fig. 1): 1) A habitat dominated by the deciduous Downy oak *Quercus pubescens* near Montpellier, southern France (Isenmann *et al.* 1987), 2) A habitat dominated by the sclerophyllous Holm oak *Q. ilex* a few kilometers from the first, and 3) A habitat dominated by the sclerophyllous Holm oak on the island of Corsica where most of the vegetation is sclerophyllous (see Blonde1 1985; Blonde1 *et al.* 1987; Isenmann *et al.* 1987 for more details on the habitats and the experimental design). The breeding biology of the bird has been studied using nestboxes evenly distributed in the habitats at a density of 2 nestboxes ha^{-1} . Life history traits, especially laying date, clutch size and breeding success have been checked through weekly routine inspection of the nestboxes over the breeding season. Meteorological data have been collected from official stations within or at close proximity of the study sites. The phenology and the amount of food available for tits have been measured during three consecutive years (1986–1988) by putting frass collectors (trays of 0.25 m^2) under the canopy of the trees (see Zandt *et al.* 1990 for more details).

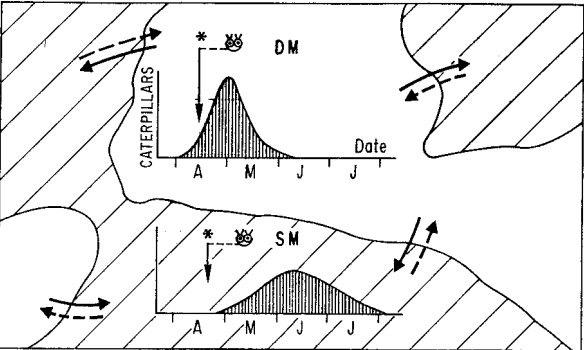
Results

Table 1 and Fig. 2. summarize some results relevant to this study, *i.e.*, the breeding parameters of the Blue Tit (first clutches), the correlations between laying date and spring temperatures, and the peak-date of caterpillar abundance. Tits start to lay on average the 11th April in the deciduous mainland habitat, then 9 days later in the sclerophyllous mainland habitat, and much later in the sclerophyllous insular habitat. There is a trend of decreasing clutch size in the three habitats, clutch size on Cor-

Table 1. Laying date, clutch size and average number of fledglings produced per pair of Blue Tit, correlation between spring temperatures (WS) and laying date (LD), and caterpillar peakdate in the three habitats. Data ± 1 SD, ** = P < 0.01, * = P < 0.05, NS = non significant.

	Mainland' deciduous	Mainland sclerophyllous	Island sclerophyllous
Laying date:	11 April ± 6.0	20 April ± 4.2	11 May ± 7.0
Clutch size:	10.8 ± 1.7	8.5 ± 1.5	6.5 ± 1.1
Nb of fledglings:	6.5	4.7	3.2
Correlation WS-LD:	- 0.80 (**)	- 0.57 (*)	0.14 (NS)
Caterpillar peakdate:	30 April	13 June	6 June
'Data' from Isenmann <i>eta/.</i> (1987)			

MAINLAND



CORSICA

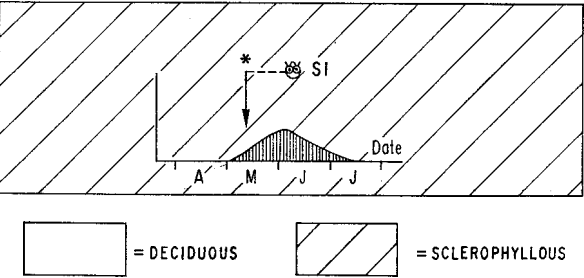


Fig. 2. Laying date (stars) of the Blue Tit in relation to food supply (caterpillar abundance) in a mosaic of deciduous and sclerophyllous Mediterranean habitats near Montpellier (upper) and in Corsica (below). DM = deciduous mainland, SM = sclerophyllous mainland, SI = sclerophyllous island. Months on the horizontal axis. Arrows indicate the postulated exchanges of individuals between habitat patches. More individuals should move from deciduous into sclerophyllous habitats than the reverse. See text.

giving fledglings) is the highest in the deciduous mainland site and the lowest in the sclerophyllous island habitat. Compared to the two others, all the parameters in the sclerophyllous mainland site have intermediate values except the caterpillar peakdate.

Many studies in temperate Europe have shown that the onset of breeding of tits is proximately affected by spring temperatures. More precisely the sum of the maximum daily temperatures over a period of 50 days before laying ('temperature warmth-sum', WS) seems to have a major effect on laying date (Perrins and McCleery 1989). Such correlations are significant in the two mainland habitats but not on Corsica. Finally, the pattern of food availability much differs between the deciduous and the two sclerophyllous habitats (Table 1, Fig. 2). In the former, the emergence of caterpillars starts at the beginning of April, caterpillar abundance increases very fast and culminates at a high level of abundance at the end of April. On the other hand, food availability starts three weeks later, lasts longer but with a much lower peak of abundance in the sclerophyllous Holm oak. The pattern is roughly the same in both the mainland and the island except that the peakdate of caterpillars occurs slightly earlier and the total amount of food is lower in Corsica. These patterns of variation in food availability parallel those of the leafing development of oaks which starts about three weeks earlier and goes faster in the deciduous than in the sclerophyllous oaks. The leafing process and caterpillar development are closely related because caterpillars are dependent of the leaves upon which they feed.

sica being the lowest so far recorded in Mediterranean habitats. Breeding success (proportion of eggs

Discussion

Many studies (*e.g.*, Drent and Daan 1980; Ricklefs 1983; Martin 1987) have shown that the availability of food is the most important ultimate and proximate factor in the timing of breeding in birds. Positive correlations have been found between the peak-date of caterpillar abundance and laying date in British and Dutch Blue Tits; Spearman rank coefficients of correlation are respectively $r_s = 0.85$ and $r_s = 0.63$ (Zandt *et al.* 1990). Tits start to lay at such a time that young are raised when food availability reaches a maximum level (Perrins 1965; van Balen 1973). The mainland population in the deciduous habitat (DM on Fig. 2) is rightly timed on the food supply and the pattern of food availability parallels that of the leafing development which is itself correlated to an increase in spring temperature, hence a good correlation between laying date and the latter. This early breeding in a good habitat is associated with a high clutch size and a good breeding success. The insular population (SI) is also rightly timed on the food supply. Because the spring development of trees and of its associated arthropod fauna occurs much later in sclerophyllous trees than in deciduous ones, tits also start to breed much later at a date when temperatures have no more proximate effect on laying date, hence the absence of correlation between laying date and spring temperatures. The combination of a late initiation of breeding and of a low amount of food explains why clutch size is so low (but see Blondel 1985, 1990 for a more detailed analysis). Breeding traits of the Corsican population strongly support the view according to which food is the most important proximate and ultimate factor in explaining breeding parameters. The sclerophyllous mainland population (SM) shows intermediate values in the three breeding traits considered. Since patterns of food availability are similar to those on the island, birds are obviously mistimed because young are raised long before the caterpillar peakdate. Many pairs fail to produce any fledgling from their first brood and the rate of repeat and second broods (up to 58%) as well as the fledging success of these late broods (78%) are exceptionally high for this usually single-brood species (Perrins 1979). This is because

the later they breed, the closer they are to the maximum food availability. First broods of these mainland tits in sclerophyllous trees would have been well timed had they bred in deciduous oaks of the surroundings. Interpreting this mistiming needs to consider a landscape including both good (*i.e.*, deciduous) and poor (*i.e.*, sclerophyllous) habitats. Contrary to Corsica where all the habitats within the dispersal range of the population are 'poor' for tits because the vegetation is entirely sclerophyllous, the mainland vegetation is a patchwork of both poor sclerophyllous and good deciduous oakwoods.

One hypothesis to explain the mistiming of Blue Tit breeding in sclerophyllous mainland habitats is that the birds are primarily adapted on the mainland to the best habitat where they produce many fledglings. Since density dependent processes set an upper limit to population size, a number of birds must emigrate to settle elsewhere. Those individuals that breed in poor sclerophyllous oakwoods where the food supply is low and occurs late in the season breed there nearly as if they were in good habitats. Hence they are mistimed probably because asymmetric gene flow from deciduous oakwoods prevents them to become adapted to sclerophyllous trees. On the other hand the absence of deciduous forests on Corsica, where tits are isolated from any mainland population (the Corsican population belongs to the subspecies *Parus c. ogliastreae* Hartert), has allowed the birds to evolve life history traits fairly well adjusted to local sclerophyllous habitats.

Such an hypothesis would be supported if 1) there is a strong genetic component for laying date and 2) directional selection may adjust this trait to local environmental conditions. Therefore, two samples of birds, one from the late-laying Corsican population and one from an early-laying mainland population, have been experimentally hand-raised in the same environment in aviaries at Montpellier. Corsican birds have bred during three consecutive years at the same date and in the same way as did natural populations from which they came (Blondel *et al.* 1990). This is a demonstration that the timing of breeding is genetically determined and a confirmation of previous studies on the heritability of laying date in the Great Tit *Parus major* (van Noord-

wijk *et al.* 1980; van Noordwijk 1987). Moreover these authors have shown that natural selection can operate very rapidly, within a few generations, to adjust ecologically important life history traits to local environmental conditions. However a delay of 9 days in the laying date of the sclerophyllous mainland population as well as a lower clutch size suggest that while the laying date is under tight genetic control, some tuning is achieved through a phenotypic response of both laying date and clutch size to food availability.

The mosaic of habitat patches of different quality for tits is hypothesized to operate as a source-sink system (Wiens and Rotenberry 1981; Pulliam 1988). Sink habitats, where birds are misadapted because they immigrate from source habitats to which they are adjusted, probably produce few recruits so that reproduction cannot balance local mortality. Populations in such habitats may persist provided that they are permanently restocked with immigrants from more productive source habitats. On Corsica where there is no more productive habitat within the normal range of dispersal of the population, gene flow must be small and the population could have become adapted to its environment (Fig. 2). The demonstration of asymmetric exchanges of individuals between habitat patches on the mainland is still lacking, however, but the mistiming of some populations as well as their lower breeding output predict that such processes should occur (Pulliam 1988). Additional studies are needed to document the balance as well as dispersal patterns of the birds at the between-habitat scale.

This case study is an example of the necessity to extend studies of populations (and communities) on a larger scale than just one habitat. How would one have interpreted the functioning of the mistimed mainland population without a reference to the two others? Such mechanisms may affect biodiversity on a regional scale by maintaining species in local areas, where they cannot persist, by an influx of individuals from other areas where high productivity balances local losses (Lidicker 1975; Van Horne 1983; Morris 1988; Pulliam 1988). Local assemblages of species which are of primary concern for ecologists and conservationists have clear geographic extents because habitat selection, dispersal

of individuals among populations and genetic responses to differences in habitat quality are a natural part of the ecology of most species.

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