What are the consequences of being a downy oak (*Quercus pubescens*) or a holm oak (*Q. ilex*) for breeding blue tits (*Parus caeruleus*)?

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Abstract

By comparison with deciduous oaks, the lower yearly production of new leaves in sclerophyllous oaks is hypothesized to have several consequences on animal communities. In particular, the production of arthropod communities that feed upon the leaves should be lower in sclerophyllous than in deciduous oaks, this causing changes in breeding patterns and the demographic balance in insectivorous birds. Studies in both deciduous and sclerophyllous habitats in southern France have shown that: 1) the spring development of new leaves occurs later and more slowly in sclerophyllous than in deciduous oaks, 2) the biomass of caterpillars is much lower in sclerophyllous oak forests, and 3) there is a large variation in life history traits of the Blue Tit depending in which type of habitat they breed. Laying date occurs later and clutch size is lower in sclerophyllous habitats than in deciduous habitats. The evolution of life history traits is discussed according to whether poor sclerophyllous habitats are isolated (e.g. on Corsica) or are parts of landscapes including both habitat types.

Introduction

Depending on soils and land use patterns, many forest landscapes in the Mediterranean region are mosaics of habitats dominated either by deciduous oaks such as the downy oak *Quercus pubescens* or by sclerophyllous oaks such as the holm oak *Q. ilex*, or by a combination of both. The ability of evergreen plants to retain within their tissues nutrients that may be in short supply and reduce the loss of minerals by year-round leaf fall (Monk 1966; Harper 1977) involves the yearly renewal of only a fraction of the foliage (ca. 30%) since leaves are photosynthetically active for several years. For example, holm oak trees shed their leaves in their third year (Floret *et al.* 1989). By comparison with that of deciduous oaks, which renew their whole foliage each year, this pattern of foliage renewal must have important consequences for animal communities and populations that feed upon the leaves. In the context of a food chain approach, evergreenness indicates the following hypotheses:

1. Since most of the photosynthetic system is present and active in early spring, the production of new leaves should occur later and eventually more slowly in sclerophyllous than in deciduous trees, i.e. the spring bloom of the vegetation should be less conspicuous in the former than in the latter.

2. Given that leaves older than one year are no longer edible for most phyllophagous insects (e.g. caterpillars) because they are too hard and contain tannins and other biochemical repellents (Varley 1967; Lebreton 1982; Feeny 1975), insect production should be lower in sclerophyllous forests, in which all the leaves produced in spring are available for insects. In sclerophyllous forests however, the higher production of male catkins, which are eaten by caterpillars, partially compensates for the lower production of new leaves (Du Merle, pers. comm.).

3. Provided that 1) and 2) are true, such differences should result in changes in the feeding and breeding habits of insectivorous birds.

It must be recognized, however, that the lack of studies on the comparative biology of sclerophyllous and deciduous oaks, as well as on their associated arthropod communities make such hypotheses difficult to test (Du Merle, pers. comm.). Furthermore, in view of the enormous year-to-year variation in arthropod communities, the results of this study are not generalizable without precaution.

The purpose of this study has been to test the above hypotheses using data on the phenology of trees, insect abundance and breeding patterns of the Blue Tit *Parus caeruleus* in four mediterranean habitats.

Material and methods

The study areas comprise 1) a habitat dominated by the deciduous downy oak near Montpellier, in southern France, denoted as QPM; 2) two habitats (QIM1 and QIM2) a few kilometers from QPM; 3) a habitat dominated by the sclerophyllous holm oak on the island of Corsica (QIC) (see Blondel 1985; Blondel *et al.* 1987; Cramm 1982; Isenmann *et al.* 1987 for more details on the habitats). The three mainland habitats are at a similar altitude on a calcareous substrate, and only differ in the dominant tree species. The island habitat is on a siliceous substrate.

The spring development of the leaves of the

oaks has been checked using a procedure described by Du Merle and Mazet (1983). In each habitat of 5 areas, 5 trees were sampled during 4 consecutive years. Samples of branches were taken randomly every 3–4 days at different heights above the ground (from 2 to 20 m) and 6 apical buds were sampled for each branch. Bud burst and the development of the leaves were scaled over 7 stages from stage 1 when the bud is completely closed to stage 7 when the new leaf is fully developed (see Fig. 1). For each date in each habitat the number of buds at each stage was multiplied by the number of the stage and expressed as a proportion so that the final figure gave the average stage of the leafing process over time. The raw data fitted to a logistic model.

Sampling insects in the foliage of the trees for assessing the amount of food available for insectivorous birds is extremely difficult (Newton 1980). However, the most preferred food for tits is caterpillars (Perrins 1965; van Balen 1973; Zandt *et al.* 1990), which are also by far the most important on a biomass basis. The diet of tits may include other prey than caterpillars although a high proportion of such other prey is an indication of food shortage. Food supply has therefore been estimated in three habitats, the mainland deciduous habitat (QPM), one mainland sclerophyllous habitat (QIM1) and the Corsican sclerophyllous habitat (QIC) using the procedure devised by Tinbergen (1960; see Zandt *et al.* 1990). The method consists in collecting the droppings of caterpillars falling from the foliage using 0.25 m^2 trays erected under the canopy of the trees (one tray per tree). This method, which has been utilized over a number of years in tit studies in Holland, provides a reliable estimate of the relative abundance of caterpillars and on their seasonal variation. Assuming that this method gives similar results in Mediterranean oakwoods, frass pellets have been sampled from 10 to 25 oaks twice a week during most of the breeding seasons of 1988 and 1989. They were then classified into two categories: (a) frass produced by caterpillars of the gypsy moth *Lymantria dispar*, which have not been included in the calculations because caterpillars of this species, which are eas-
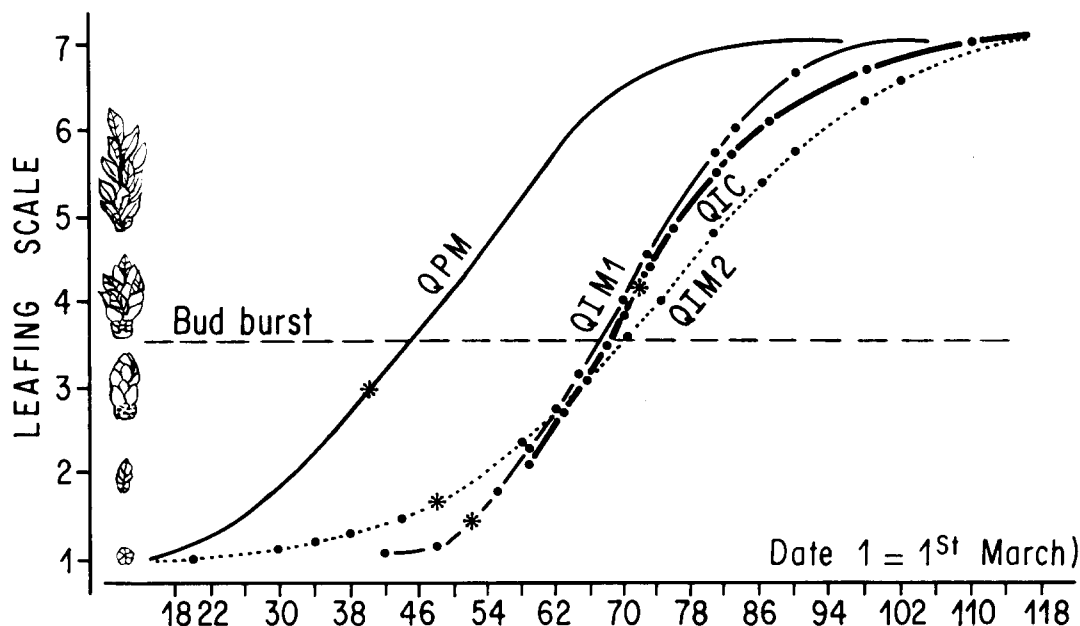
Fig. 1. Leafing process and bud burst of oaks in a deciduous oakwood (QPM), two sclerophyllous oakwoods on the mainland (QIM1, QIM2), and a sclerophyllous oakwood on Corsica (QIC). The leafing scale ranges from stage 1 to stage 7. The data for the years 1987–90 have been averaged and then fitted to a logistic model. Stars indicate the laying date of blue tits in each habitat. Dates from 1st of March (38 = 7 April).

ily distinguishable (Liebhold & Elkinton 1988), are not eaten by tits, and (b) frass of all other caterpillars. Caterpillar abundance has been arithmetically scaled over 5 levels of abundance (Fig. 2).

The breeding biology of the blue tit has been studied using nestboxes evenly distributed in the habitats at a density of 2 nestboxes ha^{-1}. Life history traits, especially laying date (mean of the dates on which each pair laid its first egg) and clutch size (the mean number of progeny in completed clutches laid by each female) were checked by routine weekly inspection of the nestboxes over the breeding season. Only first clutches are considered in this paper.

Finally the diet of tits was studied based on the food items brought to the nestlings using automatic camera nestboxes (see Blondel *et al.* 1991 for the description of the system). The study was carried out in the holm oak habitat on Corsica and in a mainland habitat (Mont-Ventoux) where tits mostly forage on downy oak trees. The data set included 6 nests (totaling 20 full days filming

and 1,662 successful pictures) on the mainland and 7 nests (35 days and 2,138 pictures) on Corsica. Prey items were identified as far as possible in the taxonomic hierarchy (Blondel *et al.* 1991).

Results

The process of bud development and the growth of young leaves in the two species of oaks is illustrated in Figure 1. This process began 3 weeks earlier in the downy oak than in the holm oak (opening of buds (stage 3.5, see Fig. 1) = May 8 in the holm oak and April 14 in the downy oak). The leafing process of the holm oak was similar on the island and on the mainland despite higher spring temperatures and rainfall in the former (mean daily temperature = 9.32 °C, rainfall = 378.1 mm for the months January–April, 1980–1989 combined) than in the latter (7.9 °C and 241.3 mm).

The timing of caterpillar abundance paralleled that of the leafing process (Fig. 2): frass collectors began receiving caterpillar droppings in the first
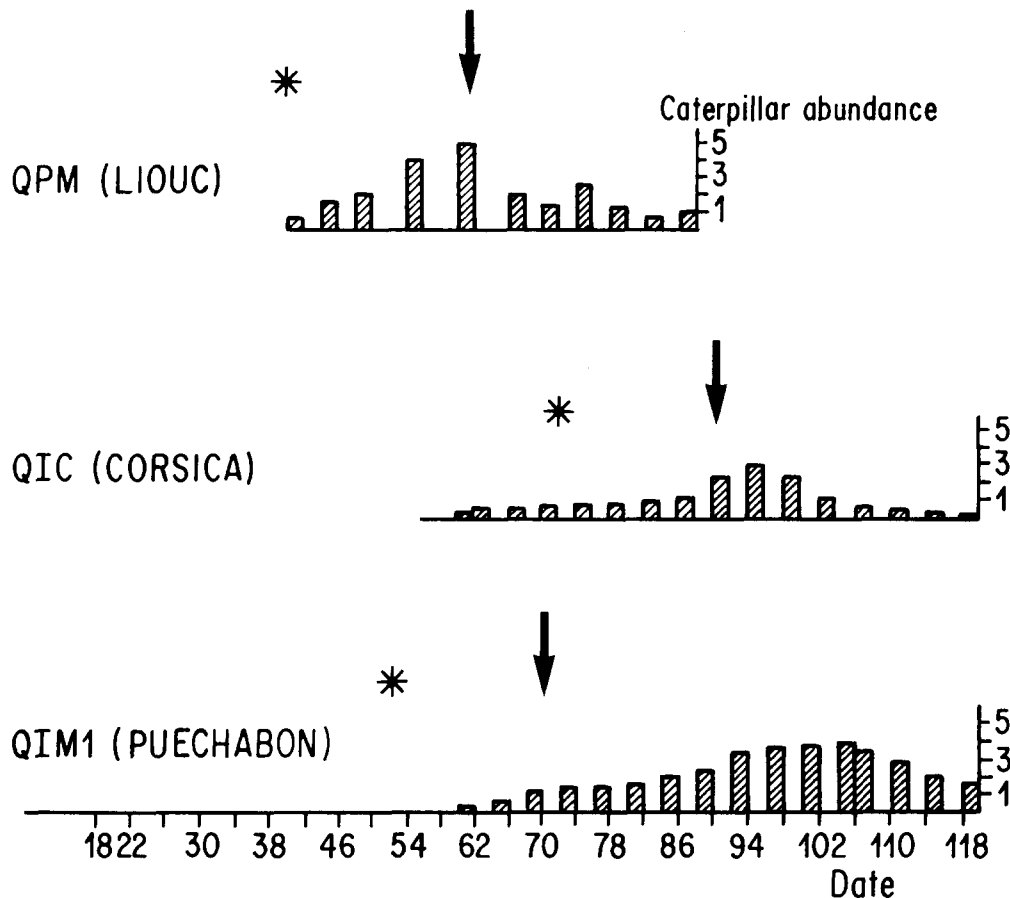
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Fig. 2. Seasonal variation of the caterpillar abundance in the three habitats (classes of abundance on the vertical axis). Stars indicate the laying date and arrows the hatching date of blue tits. The hatching date coincides with the peak of caterpillar abundance in the deciduous mainland habitat (Liouc) and on Corsica but it occurs much earlier in the sclerophyllous mainland habitat. See text.

week of April in the downy oak but not before the end of April, i.e. three weeks later, in the holm oak sites on the mainland and on Corsica. Caterpillar abundance increased faster and was much higher in the downy oak than in the two holm oak stands and it has been higher in the mainland holm oak population than on Corsica. Assuming that tits are food-limited, these differences in caterpillar abundance between deciduous and sclerophyllous oakwoods make the former 'good' habitats for tits and the latter 'poor' habitats.

The two most important breeding traits of the blue tit in relation to food supply are laying date and clutch size. Laying date was earliest in the downy oak, QPM (11 April), and latest in the

Corsican holm oak, QIC (11 May) with intermediate values in the two mainland holm oak habitats (21 April and 17 April in QIM1 and QIM2 respectively, Table 1). Similarly, clutch size was highest in the downy oak site (10.8 eggs), and lowest in the Corsican holm oak stand (6.5 eggs) with intermediate values in the two mainland holm oak habitats (8.6 eggs in QIM1 and 8.4 eggs in QIM2, Table 1).

Food items brought to tits' nestlings differed greatly between the mainland habitats and Corsica (Table 2, Blondel *et al.* 1991). In the former, the bulk of the diet consisted of caterpillars (57.7%) while on Corsica, the diet was more diverse with a large range of arthropods other than

Table 1. Breeding traits of the blue tit (standard deviation in brackets) and habitat characteristics (bud opening of oaks and peak dates of caterpillar abundance) in a deciduous habitat on the mainland (QPM), two holm oak habitats on the mainland (QIM1, QIM2) and a holm oak habitat on Corsica (QIC) (mean values for 1985–1990 combined). Roman numbers = months (IV = April)

	QPM	QIM1	QIM2	QIC
Laying date:	11/IV (6.7)	21/IV (4.9)	17/IV (6.9)	11/V (6.8)
Clutch size:	10.8 (1.7)	8.6 (1.5)	8.4 (1.4)	6.5 (1.1)
Hatching date:	4 May	11 May	7 May	30 May
Bud opening:	14 April	6 May	9 May	7 May
Caterpillar peak date:	30 April	13 June	no data	6 June

caterpillars. The second most important prey was spiders (26.3%), then grasshoppers (17.3%) and prey from many other insect families. The more diverse diet on Corsica is expressed by the values of the Shannon diversity index: $H' = 4.18$ on Corsica compared with 3.72 on the mainland (Blondel *et al.* 1991).

Discussion

It is commonly argued that food is the main ultimate factor in the evolution of both laying date and clutch size in birds (Lack 1950; Perrins 1970; Drent & Daan 1980; Martin 1987). To be successful in producing young requires: 1) to begin breeding at such a time that the greatest food demand by both the parents and the young coincides with the peak of food availability in the habitat (Lack 1954; Perrins 1965; van Balen 1973), and 2) to raise broods of such a size that parents optimize their breeding commitment in terms of number and survival probabilities of the young produced. Within the limits set by these two requirements, the most successful birds are those which lay as early as possible and which have the largest clutch size.

Concerning laying date, two of the four populations of this study show an appropriate behaviour in relation to food supply: the population in the mainland downy oak stand (QPM on Fig. 1 and 2 and Table 1) which starts to lay several days before bud opening, and the population in the Corsican holm oak stand (QIC) which starts to lay several days after bud opening. In these habitats, birds start to breed, on average, at such

Table 2. Composition of the diet (in percent) of nestling blue tits in a mixed habitat on the mainland (Mont-Ventoux) and in a holm oak habitat on Corsica; diversity index H' from the Shannon function. Sample sizes: 1,662 on the mainland, 2,138 on corsica (after Blondel *et al.* 1991).

Prey categories	Mainland	Corsica
Caterpillars:	57.7	17.4
Beetles:	2.5	3.4
Dipterans:	2.4	1.2
Grasshoppers:	0.2	17.3
Hymenopterans:	0.5	0.1
Hemipterans:	0.0	5.7
Dermapterans:	0.0	1.6
Homopterans:	0.0	0.8
Other insects:	6.1	7.7
Spiders:	16.8	26.3
Unidentified prey:	13.8	18.5
Diversity (H')	3.72	4.18

a time that young hatch around the date of maximum caterpillar abundance (Fig. 2, Table 1). It may be surprising that Corsican tits are synchronized on caterpillars since this prey category constitutes only 17.4% of the diet of the nestlings (Table 2). In fact, caterpillars are more important than suggested from this figure for two reasons. First, caterpillars brought to tit nestlings are much larger (60.3% larger) on Corsica than on the mainland, and, second, this prey category is much richer in water (around 85%, Edney 1977) than other prey such as spiders (73%) and grasshoppers (70%). This is an important factor in Mediterranean ecosystems which are water limited (see Blondel *et al.* 1991).

In all studies published to date on the relationships between breeding patterns of tits and their

food supply, caterpillars have always been the key prey on which tits are synchronized (Perrins 1979). Mediterranean tits do not depart from this rule. In the mainland downy oak habitat, the laying date is correlated with bud opening (Clamens 1990) which coincides with the time when first instars of caterpillars become available and start to grow rapidly. On Corsica, the spring development of the ecosystem, i.e. the emergence of new leaves and that of caterpillars, occurs 3 weeks later but, here again, tits lay at such a time that young hatch around the peak of caterpillar abundance (Table 1). In contrast, the two mainland holm oak populations (QIM1 and QIM2) start to lay when oak buds are still closed and far from opening. Hence they are mistimed because young hatch long before the caterpillar peak in abundance.

Assuming that tits on Corsican are well synchronized with food resources, why then do tits in the mainland holm oak stands not breed later since patterns of food availability are similar to those on the island? Tits in the mainland holm oak stands would have been well timed to food availability had they bred in surrounding deciduous oaks. Actually, the laying date of blue tits in these mainland holm oak habitats is correlated with bud opening in downy oak stands (Clamens 1990). 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 (holm oak) and good deciduous (downy oak) oakwoods.

One hypothesis to explain the mismatching between the breeding season and food resources in sclerophyllous mainland habitats is that the birds on the mainland are primarily adapted to the best habitat where they produce many fledglings. Those individuals that breed in poor sclerophyllous oakwoods where the food supply is low and occurs late in the season breed as if they were in good habitats. They are mistimed probably because asymmetric gene flow from deciduous oakwoods prevents them from becoming adapted to sclerophyllous trees, i.e. more individuals immigrate from deciduous oakwoods to sclerophyllous

oakwoods than the reverse. Such an hypothesis is consistent with the demonstration of a high genetic component of laying date (van Noordwijk 1987; Blondel *et al.* 1990) which prevents tits to evolve life history traits adapted to local habitat characteristics of the holm oak. A similar situation has been found by van Balen (1973) in great tits breeding in a poor scots pine (*Pinus sylvestris*) plantation close to rich oakwoods in the Netherlands. The demonstration of asymmetric dispersal between such habitats of different quality may be achieved either directly by data on the dispersal of ringed birds or indirectly through demographic or genetic approaches. Such studies are currently in progress.

Thus, the mosaic of habitat patches of different quality for tits is hypothesized to operate as a source-sink system (Wiens & 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 not more productive habitat within the normal range of dispersal of the population, gene flow is necessarily small because tits are isolated from any mainland population, this allowing birds to adapt their laying date and clutch size to the local environment.

The second most important breeding trait in relation to food resources is clutch size which is widely recognized to ultimately depend on food resources (Lack 1950; Perrins 1970). Clutch size in the downy oak population is nearly as high as that in the most productive oakwoods in temperate Europe (Perrins 1979) and is associated with an early and abundant food supply. In contrast, clutch size on Corsica is the lowest so far recorded in Mediterranean habitats and is associated with a very low and late-occurring food supply.

Compared with those in deciduous oaks, arthropod communities in evergreen oaks such as the holm oak are characterized by a high species

richness (Favard 1962; Dajoz 1980) but probably low average population densities. The huge year-to-year variation of caterpillar abundance makes generalization from such trends difficult (Du Merle comm. pers.). This low abundance of insects is presumably related to the low amount of new leaves (30% of the foliage) which are edible by caterpillars before the development of tannins (Varley 1967; Lebreton 1982; Feeny 1975). Assuming that varying the diet is much less advantageous than collecting as much as possible of a same type of food (Royama 1970; Owen 1977; Perrins 1965), feeding conditions are certainly far from optimal in sclerophyllous oakwoods. The best indication that tits on Corsica are constrained by food is the extremely diverse diet of the nestlings (Table 2). A poor food supply thus sets an upper limit on fecundity.

The intermediate size of clutches in the two mainland holm oak habitats is more difficult to interpret. It might be related to either a proximate adjustment of clutch size to the amount of food which is intermediate between that on Corsica and that in the downy oak population or by a genetical component from downy oak-adapted birds, or by a combination of both through phenotypic plasticity. Whatever the case, clutch size variation in these four habitats parallels that of the timing and abundance of food.

Conclusion

For insectivorous birds, differences in leafing habits between deciduous and sclerophyllous oaks have consequences at both the population and community level. At the population level, living in habitats of different quality may result in such changes in the breeding season, fecundity, survival, and dispersal patterns that trade-offs between traits are completely different depending on habitat quality. This may be an important issue in species conservation because population studies in poor (sink) habitats may yield weak information on the factors regulating population size if population size in such habitats largely depends on the source populations of neighbouring rich habitats (Pulliam 1988). In turn, such changes may have consequences at the community level. Most bird species are more sensitive to the structure of the vegetation than to the identity of plant species (Cody 1981), hence they can be found in a variety of habitats. If the dispersal range of a species is larger than the size of habitat patches, then those individuals that settle in poor habitats may produce very few offspring and eventually become genetically 'dead'. The persistence of populations in patchy environments, and as a result certain components of community diversity, may depend on habitat-specific population dynamics. In addition, a habitat may be rich for one species but poor for another species, making communities mixtures of populations, only some of which are self-sustaining. Thus, to understand community structure, neighbouring habitats must be considered because the diversity of any given habitat may depend on both the regional diversity of habitats and the diversity and abundance of resources in each local habitat.

Acknowledgements

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