See discussions, stats, and author profiles for this publication at: https://www.researchgate.net/publication/316601433

Adaptive avian responses to parasitism and predation View project

Population studies on tits in the Mediterranean region

Article · January 1987

CITATIONS 61	;	reads 37		
5 author	's , including:			
	Jacques Blondel French National Centre for Scientific Research 121 PUBLICATIONS 5,283 CITATIONS SEE PROFILE	٨	Alex Clamens Lycée Blaise Pascal-Clermont-Ferrand 17 PUBLICATIONS 162 CITATIONS SEE PROFILE	
Some of	the authors of this publication are also working on these related projects:			
Project	Nests in Paridae View project			

All content following this page was uploaded by Alex Clamens on 10 October 2018.

POPULATION STUDIES ON TITS IN THE MEDITERRANEAN REGION J. BLONDEL, A. CLAMENS, P. CRAMM, H. GAUBERT & P. ISENMANN

Centre Louis Emberger, CNRS, B.P. 5051, 34033 Montpellier Cédex, France

CONTENTS

2. Variation in clutch size of the Blue Tit	22
	22
in the Mediterranean region	
3. Breeding patterns of Blue and Great Tit in	
Holm and Downy Oak	23
4. Evolutionary significance of the differences	
in breeding patterns between an insular and	
a continental Blue Tit population	26
5. Conclusions	32
6. Acknowledgements	32
7. Summary	33
8. References	33
9. Samenvatting	34

1. INTRODUCTION

In 1976, when we started population studies on tits in southern France, we wished to extend toward the south the great amount of similar studies made in central and northern Europe. The paper by Kluijver (1951) on the Great Tit Parus major can be considered as the starting point of an impressive flow of publications which did not find any rest since that time. For example Perrins (1979) listed not less than 430 publications dealing more or less with tits. It is not surprising that so many papers, together with recent developments in life-history theories, gave rise to innumerable hypotheses and theoretical concepts. Our research is mainly justified by the fact that the breeding areas of the studied tit-species reach as far south as northern Africa (the Blue Tit Parus caeruleus even reaches the Canary Islands) and it is therefore worthwhile to know how these species behave outside the northern and central European limits. The Mediterranean climate is defined by its dry and hot summer and by a mild winter. The deciduous vegetation belt which characterizes central Europe is more and more replaced toward the south by an evergreen vegetation belt exhibiting a strong mosaical aspect stressed by a complicated orography. Moreover, forests are much more degraded (through fire, overgrazing and wood-cutting) than anywhere else in regions north of the Mediterranean area. The originali-



Fig. 1. Geographical location of the study sites. The numbers refer to code numbers in Table 1.

ty of our tit studies is to evaluate the influence of these specific environmental factors on lifehistory traits. In order to collect relevant sets of data we are working at various study sites in southern France and extended our investigations in 1981 to Morocco, in 1983 to Algeria and in 1985 to southern Spain (see Fig. 1). At the southern part of its range, an independent population study on the Blue Tit is in preparation by R. Alonso-Quecuty on Tenerife (Canary Islands).

Here we present a general overview of our work, most of which is still in progress. In all areas basic data on breeding biology are collected, and in areas 1, 3, 4 and 9 (see Table 1 and Fig. 1) studies are made (or planned) on population dynamics, interspecific relations and ecophysiology. According to the present state of knowledge on the population biology of tits in the Mediterranean area, our aim is more to raise questions from results of empirical studies and to propose further studies and experiments to be performed, than to try to explain and speculate on the basis of incomplete present knowledge.

In this context, three main questions are currently investigated:

Study sites	Location	Altitude	Dominant	Clutch size			Years	
		(m)	tree species	$\overline{X(S.D.)}$	Range	п		
1. Ventoux	44°08'N, 05°11'E	800-1050	Cedrus, Pinus, Quercus	8.7 (1.5)	6-12	110	1976-1985	
2. Ste Baume	43°22'N, 05°47'E	700-750	Fagus sylvatica	7.7 (1.9)	3-11	46	1976-1980	
3. Quissac	43°54'N, 04°00'E	100	Ouercus ilex	8.2 (1.5)	6-14	116	1979-1985	
4. Liouc	43°53'N, 04°01'E	100	Õuercus pubescens	10.8(1.7)	6-14	60	1982-1985	
El Pedroso/Sevilla	37°50'N, 05°45'W	500	Õuercus ilex	7.5 (0.8)	6-9	19	1985	
Mamora/Rabat	34°02'N, 07°00'W	50	Õuercus suber	6.8 (1.1)	5 9	42	1981-1983	
Ifrane/Middle Atlas	33°02'N, 05°15'W	1650	Ĉedrus atlantica	6.7 (1.3)	4-11	34	1981-1983	
Tikida/Kabylia	36°22'N, 03°55'E	1500	Cedrus atlantica	Data will b	e published	separately		
9. Fango/Haute Corse	42°24′N, 08°44′E	100 - 150	Ouercus ilex	6.3(1.0)	4-10	183	1976-1985	
10. Ghisoni:			~ '	× ,				
Vezzani/Haute Corse	42°10'N, 09°15'E	900 - 1000	Pinus laricio	No data av	ailable			
11. Tenerife	28°20'N, 16°20'W	800-1450	<i>Pinus canariensis</i> , Laurisilva	3.5 (1.0)	2-6	20	1983–1984	

Table 1. Location of study sites, characteristics of the habitats and geographical variation of clutch size in the Blue Tit.

- 1) How do habitat quality, latitude and altitude affect demographic parameters? As an example, Isenmann discusses the variation in clutch size of the Blue Tit (Ch. 2).
- 2) Is such an effect on demographic parameters different for the two common species, the Great Tit and the Blue Tit? Clamens & Cramm compare the breeding patterns of the two species in two oak habitats (Ch. 3).
- 3) To what extent do differences in community structure between an island (Corsica) and the mainland, in similar habitats, affect life-history traits (see Blondel 1979, 1981, 1985)? This subject will be treated by Blondel & Gaubert in Ch. 4.

2. VARIATION IN CLUTCH SIZE OF THE BLUE TIT IN THE MEDITERRANEAN REGION

The main points investigated were factors governing the onset of breeding, clutch size and breeding success. We possess as yet only sufficient data to analyze clutch size variation. A publication on this topic is in preparation. The variation in the mean value registered at 9 studied sites (from southern France to the Canary Islands) is strikingly high (Table 1): the highest mean value (10.8) is about 3 times as large as the lowest one (3.5). The highest value (more than 10 eggs) comes from a habitat with pure deciduous oak stands. Intermediate values (between 7.0 and 10.0) were found in the following habitats: evergreen Quercus ilex as the dominant tree, Cedar Cedrus atlanticus with a few Quercus pubescens and Beech Fagus sylvatica. The lowest values (< 7.0) come from an evergreen habitat in Corsica, two habitats in Morocco and one on Tenerife at the southernmost fringe of the breeding range. It is not surprising that the largest clutches were laid in habitats with deciduous oaks, considered to be the most favourable for the Blue Tit (Snow 1954). These values are similar to those found in deciduous habitats north of the Mediterranean area. They do not agree with Lack's (1954) claim of a latitudinal cline in clutch size but agree with Neub (1977) and Slagsvold (1981). Where deciduous Downy Oaks are mixed with some evergreen Holm Oaks the clutch size begins to drop. This suggests that the Blue Tit is faced here with less good conditions than in pure Downy Oak stands. Such adverse conditions may occur either when the females collect the energy to produce their eggs, or during the feeding period of the young, or both. A relatively low clutch size comes from a Holm Oak habitat in southern Spain and a Cork Oak habitat in northern Morocco. These are probably the lowest values reached by lowland continental populations in the whole breeding range. We can presently only speculate on the factors responsible for such low values: pure evergreen oaks in the southern part of the Mediterranean region constitute probably poor habitats with weakly fluctuating feeding resources all the year round. Nevertheless, the lowest mean clutch size ever found for the Blue Tit is recorded on Tenerife (R. Alonso-Quecuty, unpubl. data). In this particular case insularity might play a major role. Without entering in a more thorough discussion, the geographical variation of clutch size seems to be much more related to habitat quality than to any other known factor playing a role in clutch size determination (Ricklefs 1980).

Table 2. Breeding data for first clutches of the Blue Tit and
the Great Tit in Liouc (Downy Oak) and Quissac (Holm
Oak) in 1982-1985, combined. For laying date, the first
number is the day and the second the month; S.D. in days.
m = mean, S.D. = standard deviation, $n = sample size$.

	Blu	e Tit	Gre	at Tit
	Liouc	Quissac	Liouc	Quissac
Laying date of 1st egg				
m	11/IV	19/IV	17/IV	24/IV
S.D.	6.0	4.3	5.6	7.4
n	60	88	31	85
Clutch size				
m	10.8	7.8	9.4	8.6
S.D.	1.7	1.5	1.3	1.6
n	60	85	31	84
Number fledged				
m	6.5	4.2	5.1	3.6
S.D.	4.4	3.0	4.2	3.4
n	60	85	31	84
Fledging weight				
m	11.1	10.8	16.0	16.7
S.D.	0.8	1.1	1.9	1.6
n	41	59	19	50

3. BREEDING PATTERNS OF BLUE AND GREAT TIT IN HOLM AND DOWNY OAK

3.1. INTRODUCTION

The results presented here concern some aspects of a comparison between two study sites from 1982 to 1985. The discussion will be limited to the effect of habitat on the breeding patterns. A more complete survey is in preparation by Cramm (see also Cramm 1982, Isenmann 1983a,b).

As compared with the Holm Oak (Quissac) the breeding patterns in the Downy Oak (Liouc) present three main differences (Table 2):

- earlier laying dates: 8 days on average for the Blue Tit (t-test, p < 0.001) and 7 days for the Great Tit (t-test, p < 0.001);

- higher clutch size, 3.0 eggs for the Blue Tit (t-test, p < 0.001) 0.8 egg for the Great Tit (t-test, p < 0.05);

- a higher number of young fledged: 2.3 more young for the Blue Tit (t-test, p < 0.001) and 1.5 for the Great Tit (n.s.).

Moreover, the fledging weight of the Blue Tit is slightly higher in the Downy than in the Holm Oak, the reverse is true for the Great Tit, but these differences are not significant.



Fig. 2. Upper part: comparative leafing phenology of Holm Oak and Downy Oak, and caterpillar frass fall data (histograms) in 1982. Lower part: seasonal trends in number of nestlings in the two sites in 1982.

3.2. TIMING OF THE BREEDING SEASON

As pointed out by many authors (Kluijver 1951, Perrins 1965, Van Balen 1973, Leclercq 1977. Schmidt 1984) the onset of laving is correlated with air temperature in two ways: firstly by the sum of the daily mean temperatures during a certain period preceding laying, and secondly by some peaks of temperature higher than 10 °C. The two study sites are so close geographically (4 km) that climate alone cannot account for the differences registered in the onset of laying between the two sites. Hence, we searched for factors more directly related to the kind of habitat, especially the nature of the foliage which is deciduous for Downy Oak and evergreen for Holm Oak. The leafing patterns of the two trees are different. We studied these patterns through a scale of fixed stages of leaf emergence and growth (adapted from Leclercq 1977 and Du Merle & Mazet 1983) running from 1 (bud closed as in winter) to 6 (full-grown leaves). At each visit, forty oaks were sampled at both study sites. Furthermore, as we wished to link the leafing with food availability we col-

20

10

85/84

lected and counted the caterpillar frass fall with forty paper plates placed during 24 hours once or twice each week. As shown for 1982 (Fig. 2), the measurements gave the following results:

- the opening of buds (stage 3.5, see Fig. 2) in Downy Oak occurs on average 19 days earlier than in the Holm Oak:

- the period of leaf emergence and growth (stages 2 to 5) is shorter for the Downy (70 days) than for the Holm Oak (108 days);

- the peak of frass abundance is earlier by about 32 days in Downy Oak as compared to Holm Oak.

The two first differences between Downy Oak and Holm Oak should explain why laying dates are earlier in the former. This suggests that the major factor controlling the onset of laying is food availability for the females.

Because the phenology of the Downy Oak (leafing pattern and associated food resources) occurs earlier than that of the Holm Oak, this deciduous tree seems to play a major role in the onset of laying. It remains however to be proved whether the correlations found between leafing and laying reflect a relation between food availability in the Downy Oak and requirements of the females to produce their eggs.

3.3. VARIATION IN CLUTCH SIZE

Clutch size is higher in Downy Oak than in Holm Oak (Table 2). It is obvious that habitat plays a major role in clutch size determination (Lack 1966, Klomp 1970, Van Balen 1973).

Nevertheless, part of the difference observed in the Blue Tit can be attributed to the breeding density: when we increased the density of breeding tits by increasing the number of nest boxes in the Holm Oak site, the Blue Tit's clutch size dropped from 10.0 eggs at a breeding density of 7.5 pairs/10 ha to 7.5 eggs at a density of 15.0 pairs/10 ha. In other words, clutch size decreases by 10 per cent as the density increases by ca. 30 per cent (Fig. 3). Such a direct effect of density has not been found in the Great Tit: though its density increased from 6.5 to 13.5 pairs/10 ha, clutch size remained unchanged. The fact that clutch size decreases as density increases in a poor habitat suggests that food availability for the female influences clutch size of the Blue Tit. An alternative explanation



r=-0,888

 $\rho < 0.05$

variation (in per cent) for the Blue Tit in the Holm Oak study site. Each data represents the variation between two consecutive years.

could be that it is the food for the young which determines clutch size ultimately. In this case there are two possibilities: 1) it is a phenotypic adaptation to breeding in Holm Oak, but we can hardly imagine how the female could be informed of the feeding resources to come for the brood; 2) it is a genetic adaptation, but this seems unrealistic because dispersion between the two habitats is too large to allow for an emergence of local adaptations either to Holm Oak or to Downy Oak.

3.4. BREEDING SUCCESS AND FLEDGING WEIGHT

Breeding success is higher in Downy Oak than in Holm Oak for both species (60% instead of 54% for the Blue Tit, and 54% instead of 42% for the Great Tit, Table 2), but the differences are not significant (Kolmogorov- test with classes of breeding success per family). Since brood size is higher in Downy than in Holm Oak, especially for the Blue Tit, this enhances the trend of better breeding performance in the deciduous habitat. If we consider now the synchronization between food requirements of Blue Tit nestlings and food availability, we notice that in Downy Oak (Liouc), the maximum of food requirements by the nestlings occurs shortly after the peak of resources, whereas in Holm Oak (Quissac) it occurs shortly before (Fig. 2). For this comparison it is assumed that the caterpillar frass fall is a good measure of food availability. In the case of the Great Tit, which lays later than the Blue Tit, the synchronization is worse in the Downy Oak, but

	Territe	Territories with Downy Oak			Territories without Downy Oak		
	m	S.D.	n	m	S.D.	n	
Laying date of 1st egg	18/IV	3	7	22/IV	2	8	
Clutch size	8.3	1.1	7	8.9	2.2	8	
Number fledged	5.7	1.6	7	6.1	2.3	7	
Mean fledging weight	10.6	1.2	7	11.7	1.0	7	

Table 3. Breeding data from territories of Blue Tits, with and without Downy Oaks, in the Holm Oak habitat of Quissac in 1985.

better in the Holm Oak. This would explain why fledging weights of the Blue Tit are higher in Downy Oak and those of the Great Tit higher in Holm Oak (Table 2).

To sum up, habitats have a crucial influence on breeding patterns at two stages: when the females have to produce and lay their eggs and during the nestling period.

3.5. EFFECT OF PRESENCE OF DOWNY OAKS ON BREEDING PARAMETERS OF THE BLUE TIT

In order to evaluate the particular influence of a few Downy Oaks scattered within a Holm Oak study site, we compared in 1985 the territories of Blue Tits with and without deciduous trees. Table 3 shows that:

- 1) pairs which have Downy Oaks in their territory lay on average their first egg 4 days earlier than those which have not (Kolmogorov test, p < 0.05);
- 2) no significant difference is observed in clutch size and number of young raised;
- 3) the mean fledging weight is slightly higher in territories without Downy Oaks but the difference is not significant.

These data are important to understand some characteristics of the reproduction of the Blue Tit in Holm Oak. We assume that with the presence of Downy Oaks in their territories, female Blue Tits find enough food to form the eggs at an earlier date than where Downy Oaks are absent. This enhancement, however, does not go as far as to increase their clutch size owing to the numerical dominance of the Holm Oaks. On the other hand, these early breeders seem to produce young with lower fledging weights because the peak of food resources in Holm Oak stands occurs after the maximum of the food requirements for the young due to the later development of the vegetation in this kind of habitat (own obs.).

Theoretically a Blue Tit inhabiting a Holm

Oak forest faces the dilemma of starting egg laying either early or late. Although we do not precisely know the criterion for territory choice, except that nest boxes exert a strong attraction, we assume that a pair that settles early in the breeding season is in the position to choose the best territory. But such an early settlement could be followed by an early laying date, with the consequences that the food requirements of young are at their maximum before the maximum of food resources. If such an early pair has Downy Oaks in its territory, the time lag is increased because of the early laying date, and hence the fledging weight is reduced. Let us now consider a pair that settles late in the season. The conspecifics which already hold territories may hinder this pair to find a good territory (one with a nestbox for instance). Such a pair will lay late, except if it has Downy Oaks in its territory. The young will have a higher fledging weight because their nutritional requirements coincide with the period of good feeding resources which appear late in the Holm Oaks. The disadvantage of late settlement is counterbalanced by a higher probability of survival.

To sum up, in a Holm Oak forest, the best strategy would be to settle as early as possible and to postpone laying. No pair shows such a behaviour which should be an optimization of breeding strategies obviously beyond the capacities of the birds. To go further in this problem would need data on recruitment rates of fledglings that are produced early or late.

3.6. PROSPECTS

At this stage of our study, some hypotheses have to be tested by experimental verification of the various correlations found. By providing supplementary food in winter (seeds, fat and proteinic complements) and in spring (mealworms), we hope to advance the laying date in order to test whether the food supply for the female plays a major role in the onset of breeding. In this way we shall examine to which extent territories near the feeding places are held by older birds. A study of the utilisation of Downy Oaks by tits all the year round will show to which extent this tree is really attractive for the birds and at which time of the breeding cycle.

A way to examine the adaptive significance of the low clutch size in Holm Oak will be to check the number and quality of offspring from experimentally enlarged broods. One hypothesis is that a delayed laying date would be advantageous in Holm Oak because of the late peak in feeding resources. A way to assess the limiting factors for a late laying date should be to delay the hatching date by taking out eggs before the start of incubation and then to study the breeding success.

4. EVOLUTIONARY SIGNIFICANCE OF THE DIFFERENCES IN BREEDING PATTERNS BETWEEN AN INSULAR AND A CONTINENTAL POPULATION OF THE BLUE TIT

4.1. INTRODUCTION

These studies are conducted in Mont-Ventoux (Provence) and in Corsica; see Table 1, Fig. 1 and Blondel (1985) for a description of the habitats. Since many results and preliminary interpretations were recently published (Blondel & Isenmann 1979, Isenmann 1982, Blondel 1985, Blondel *et al.* 1985, Gaubert 1985) we shall only present here some new results and reinterpretations. More important, we shall address a series of questions relevant to further studies and experiments, to be performed in the scope of this long-term programme.

This study was primarily based upon two assumptions:

1) the timing of the breeding season is related to the phenology of the environment in such a way that the period of greatest food demand by the nestlings coincides with the peak in food availability (Lack 1968), and 2) a variation in reproductive output is directly related to a parallel variation in the cost to the breeding individual. According to Williams (1966) a reciprocal relationship between fecundity and survival is advocated as an essential factor in the consideration of the evolution of breeding strategies (Cody 1971, Charnov & Krebs 1974, Stearns 1976, Ricklefs 1977, Bell 1980). Such a relationship has been demonstrated for holenesting birds by several authors (Askenmo 1979, Nur 1984a,b, Ekman & Askenmo 1987). Others have failed to find it (i.e. Tinbergen 1987). Van Noordwijk & De Jong (1986) have proposed a model explaining why a positive correlation between life history traits such as clutch size and survival can be found, where a negative correlation would be expected. Keeping in mind these assumptions, two main theories which are refinements of Lack's hypothesis on the regulation of bird populations deal with the evolutionary significance of the breeding effort and associated life-history parameters. The first hypothesis makes use of the principle of energy allocation and the concept of optimization of the reproductive effort in relation to adult survival. In this view, which was first suggested by Williams (1966) and which has been integrated by Cody (1966, 1971) in the model of r- and K-selection, there is a coevolution of life history traits in such a way that a low breeding effort is compensated by a high adult survival and vice versa. The mechanism which underlies such a coevolution is claimed to act through true density dependent selection, as was recently reassessed by Boyce (1984). Some authors have interpreted their results in the light of this hypothesis (Higuchi 1976, Blondel & Isenmann 1979, Crowell & Rothstein 1981). The second hypothesis stipulates that the effort of reproduction, hence clutch size, is determined by the differences in food resources between the breeding season and the non-breeding season, whatever the absolute amount of the food supplies. This is the socalled Ashmole's hypothesis (Ricklefs 1980). Both hypotheses rely upon environmental stability with a lower winter mortality in insular predictable environments than in continental ones, but they differ in the causality of the reduced clutch size. In Cody's model life history traits are coadapted in such a way that clutch size and survival are closely related to each other, while in Ashmole's view the reduction of clutch size and mortality are independent effects of the stable environment. Recent refinements of life history theory (Stearns 1976, 1980), new results and deeper analyses of the data lead us to believe that such broad theories are useful to

		Ventoux						Corsica		
	1st brood			2nd brood						
	m	S.D.	n	m	S.D.	n	m	S.D.	n	
Laying date of 1st egg	24/IV	7.6	110	30/V	9.7	16	14/V	8.9	187	
Clutch size	8.7	1.5	110	6.5	1.2	15	6.4	1.0	183	
Number fledged	4.4	3.5	109	3.2	2.2	15	3.2	2.8	181	
Fledging date	3/VI	7.9	76	3/VII	8.7	13	17/VI	16.3	115	

Table 4. Breeding data for the Blue Tit in Ventoux and in Corsica (1976–1985 combined). Further as in Table 2.

generate working hypotheses but cannot account *per se* for the extremely complicated network of interactions which exist in each local situation between environmental parameters and life history traits.

From the results obtained so far we shall try to identify some important points of this network and address relevant hypotheses and field experiments designed to test them.

4.2. RESULTS

The main differences between the breeding cycles of the Blue Tit in Provence (Ventoux) and in Corsica (Fango) are (Tables 4, 5 and Blondel 1985): 1) The onset of the breeding season is delayed by about three weeks in Corsica as compared with the mainland. At first sight this is surprising since the Corsican site is at a lower latitude and a lower altitude than the mainland one (Fig. 1, Table 1). The Blue Tit starts to lay later in Corsica than in any other continental habitat either in northern Africa or in Europe. The same is true for the Great Tit and the Coal Tit.

2) Clutch size is reduced by 27% in Corsica (6.35 eggs) as compared with the mainland (8.66 eggs). Actually the difference would have been even larger if a lowland mainland habitat had been chosen to match the insular one.

3) There are no second broods on the island whereas 15% of the pairs have second broods on Ventoux. Furthermore the proportion of repeat clutches in case of destruction of the first is lower in Corsica than on the mainland.

4) The breeding success of the two populations is rather low. The percentage of eggs giving fledgings is 50% in Corsica and 51% on the mainland. Taking into account the 15% of pairs raising second broods on the mainland, each pair raises on average 3.2 young in Corsica and 5.0 in Mont-Ventoux.

5) The age structure of the breeding population, expressed as the ratio of adults (more than one year old) to yearlings, does not differ significantly between the two populations (Table 5). There are slightly more adult birds in Corsica than on Ventoux. This is especially true for adult males which make up 86% of the male breeding population in Corsica instead of 75% in Ventoux. On the other hand there are slightly more adult females (59%) in Ventoux than in Corsica (54%). This quite unexpected result is in contradiction with the theory. As has been found earlier (Perrins 1979), males have a higher annual survival than females, and the proportion of old males is particularly high in these Mediterranean habitats.

4.3. DISCUSSION

This discussion is based on the following assumptions:

1) Breeding strategies result from a set of interactions between life history traits and characters of the environment in relation to which they have an adaptive value. These interactions are mediated by natural selection.

2) In evolutionary thinking all individuals of a population are not identical in terms of breeding

Table 5. Proportion of yearlings and adults of breeding Blue Tits in Ventoux and in Corsica (1976-1985 combined).

		Ventoux		Corsica			
	Yearlings	Adults	% Adults	Yearlings	Adults	% Adults	
Males	15	45	75	11	69	86	
Females	29	41	59	46	53	54	
Males + females	44	86	66	57	122	68	

performance and ability to transmit genetic material to the following generations. Thus differences between parents and among the same parents from year to year are crucial points to investigate in order to understand the evolutionary significance of life history traits (Drent & Daan 1980).

These assumptions urge us to focus attention on the balance between the benefits and costs of reproduction. This will be discussed below in the scope of three main questions which can be raised from our results.

1) Why is the breeding season so much delayed on the island?

Many authors have claimed that the availability of food for nestlings is the main ultimate factor in the evolution of breeding seasons in temperate zone birds (Lack 1968, Immelmann 1971) and that a variation in food availability is correlated with a variation in climatic factors, especially air temperature. A close relationship between the timing of the breeding season and air temperatures has been demonstrated by many authors (ref. in Van Balen 1973, Perrins 1979). The climatic patterns of the Ventoux and Corsican sites have been summarized by Blondel (1985) who showed that air temperatures are on average 5 °C higher in Corsica than in Ventoux during the months February–June. But more important than the absolute values, it has been demonstrated that the predictability of both temperature and rainfall is much better on the island than on the mainland. Thus the insular bioclimate is considered to be much more stable than the continental one. We found a correlation between air temperatures and the onset of breeding in Ventoux for both the Blue Tit and the Coal Tit (Michelland 1982, Blondel 1985), but we failed to find any such correlation in Corsica, neither for the Blue Tit nor for the Coal Tit. Although the climate is more severe on the mainland than in Corsica, the breeding cycle starts earlier and comes to end later in the former than in the latter habitat. Such a discrepancy is not easy to explain and needs clarification.

We must reason in terms of limits of the breeding season, viz. the 'starting limit' which determines the onset of breeding and the 'end limit' beyond which the probability of success is very low. The problem is to determine which environmental factor makes each individual female tit to take the decision to start to breed how she does. For instance, for laying date there is a large variation between females since this date is rather scattered around the mean (S.D. = 7.6 days in Ventoux and 8.9 days inCorsica, Table 4). In Corsica this variation is considerable, considering that all nestboxes are roughly at the same altitude and the climate is very stable from year to year. Van Noordwijk et al. (1981) have shown that a large part of the variation, up to 40%, is genetically determined, which implies large differences between females. Controls of ringed females in Ventoux and in Corsica show that there is a constancy of laying in individual females, even if they do not breed in the same nestbox from year to year (Blondel own obs.).

In Provence the starting limit is clearly determined, as elsewhere in Europe, by climatic conditions and their effects on the vegetation and associated food supply for the tits. The climate is thought to act as a proximate factor in such a way that the period when the young are in the nest coincides with the period of maximum food supply. But in Corsica the starting limit is certainly not proximately determined by the climate since air temperatures are more than 10 °C higher than those when the birds start to breed in continental Europe. On the other hand, it must be acknowledged that the leafing of the vegetation possibly occurs later on the island than on the mainland, even for the same species of trees, so that feeding conditions might be better later in the season than on the mainland. This means that although the climatic pattern and the food availability on the island appear to be much more stable and predictable than on the mainland there should be nevertheless a threshold of food quantity and/or quality. One hypothesis could be that although sufficient for the maintenance of a high population of tits, food quality does not allow the female to form her eggs because it is too dry and/or too poor in protein (R.H. Drent pers. com.). Thus, although the climate could allow the birds to breed much earlier than they do, they have to wait for some spring flush of insects even if this

flush is delayed on the island and much less pronounced than on the mainland.

The only way to test this hypothesis is to try to move experimentally the starting limit by providing the birds with supplementary food rich in water and protein. Such an experiment is planned for the years to come.

Most studies on population dynamics of tits focus attention on the climatic conditions prevailing at the beginning of the breeding season. In fact, on the mainland the end limit is probably not a crucial point. But in the southern part of their range, as in Mediterranean habitats, the birds could also be limited by climatic factors prevailing at the end of the breeding season when very high temperatures can be harmful to the birds. Thus we must investigate whether or not the severe heat and dryness in summer act as limiting factors for breeding. The end limit could be directly and indirectly set by the very hot climate in June. Circumstantial evidence suggests that there could be a direct effect of high temperatures through hyperthermia of the young in the nest. Preliminary observations suggest that very high temperatures in June and early July can kill the young in the nest. We cannot explain otherwise why so many young die at once in the nest when ambient temperatures exceed 32 to 34 °C and are probably higher inside the nestbox. For instance, in 1981 four broods died on the same day at 34 °C while the parents tried unsuccessfully to feed them. However, it would be important to compare simultaneously temperatures inside nest boxes and in natural cavities to be sure that temperatures in nest boxes are not biased. Here again experiments are needed to clarify this point, e.g. by cooling nestboxes in very hot situations.

In addition to the direct effect of high temperatures, there occurs in Corsica severe parasitism by blood sucking larvae of the fly *Trypocalliphora lindneri*. These larvae hang on the legs and the bill commissures of the chicks and suck blood until these die. The flies probably lay eggs in the nest material during the incubation period and these eggs probably do not hatch until the air temperature has reached a certain value. In years in which this threshold occurs in mid June, most of the nests are parasitized. Up to 50–56% of the young Blue Tits died from parasitism in the very hot seasons of 1977, 1979 and 1981, but none in the cooler seasons of 1978, 1980, 1982 and 1983. Thus there seems to be a relation between average spring temperatures and the action of this parasite which must be acknowledged as an important factor of environmental unpredictability. Early broods of the Blue Tit and most broods of the Coal Tit, which breeds earlier, are not injured by this insect. This cause of mortality does not occur in Ventoux.

2) Why is the clutch size so low on the island? We first interpreted the reduction of clutch size in Corsica in the frame of theories claiming that there is a close relationship between clutch size and survival. We thought that in the stable and predictable environment of Corsica there was a low adult mortality and hence a high density of birds which should compete for food. In order to test whether or not adult tits have difficulties in foraging we made experiments by enlarging broods in Corsica (Blondel et al. 1985, Gaubert 1985). In 1984 and 1985 we enlarged broods so that the number of young in the nest was the same as those of continental broods. On average two to three young were added one day after hatching. Each was individually marked and weighed to the nearest 0.05 g every two days from hatching up to fledging. Five broods have been enlarged: 1 to 9 young, 3 to 10 young and 1 to 11 young. Results have shown that all nestlings from enlarged broods have normally fledged. This result confirms that the observed clutch size is not necessarily the most productive one (see Nur 1984a,b).

Fledging weights and growth rates of the young have been measured for two enlarged broods in 1984. Table 6 shows that these parameters are not signicantly different from those of natural broods, but the sample is so small that

Table 6. Clutch size, number of young fledged per clutch, fledging weight and growth rate of 2 control and 2 enlarged broods, in Corsica. Differences in fledging weight and growth rate are not significant.

	Control	broods	Enlarged broods		
Clutch size	6	7	9	10	
Number fledged	6	7	9	91)	
Fledging weight Growth rate	10.1 0.46	10.20 g 0.46 j ⁻¹		95 g 7 j ⁻¹	

1) One nestling was accidently killed when it was ten days old.



Fig. 4. Feeding frequencies (number of visits per h and per nestling) in relation to the age of the nestlings of an enlarged brood of 10 young and of a natural brood of 7 young in 1985 in Corsica.

conclusions drawn from these results are only tentative.

In order to test the surplus of energy required from the parents to feed enlarged broods we measured by direct observation and automatic recorder the feeding frequencies of both control and enlarged broods. It was shown that the number of visits/brood increases with brood size but that feeding frequencies (number of items/ chick/hour) are slightly less for broods of 10 than for broods of 7 (Mann-Whitney, p <0.002, Fig. 4). As was shown by several authors (see Klomp 1970, Nur 1984a,b), the frequency of feeding per nestling decreases as brood size increases. Since fledging weights are not lower for nestlings from enlarged broods than for those from normal broods this result does not support the contention of Lack (1954) that the decline in the number of visits/nestling as brood size increases reflects the inability of the parents to sustain high feeding frequencies. It suggests that there is some compensation for this smaller amount of food per young when the brood is larger. This could be related to the so-called Royama effect: nestlings from larger broods are fed relatively less often because energetic requirements are lower for nestlings from larger broods than for nestlings from smaller broods. Actually such an effect should be true only for temperatures below the lower limit of the thermoneutral zone (12-15 °C). Since ambient temperatures are above these values in Corsica when the tits feed their young, this effect probably does not occur in this case (see later).

These results suggest that competition for food is not a causal factor in the evolution of clutch size in Corsica. Actually as it is recognized in modern life history theory, we must also take into account for assessing the reproductive effort the probability of survival of the female (Williams 1966, Charnov & Krebs 1974). Nur (1984a,b) has shown that female weight loss increases linearly as the feeding frequency of the brood increases. Assuming that there is a relation between the weight of the female and her probability to survive to the following year, which has not been proved as yet in these populations, we must take into account this weight variation in order to interpret the evolutionary significance of the observed brood size. Such data on female weights are needed especially to test the model of Nur (1984b) which assumes that parents optimize the investment in their young by a compromise between the cost of reproduction (egg formation, food for young) and its benefit (number and survival of offspring, survival of female). Such an optimization could be achieved by adult birds by monitoring the energy balance of both parents and young through the breeding period (Nur 1984b, Drent & Daan 1980). As Nur points out natural selection should favour those breeding individuals that optimize the ratio between costs and benefits. Since the amount of food fluctuates from year to year, the optimal clutch size is determined by the mean feeding conditions. In some years these conditions may be much better than average (Van Noordwijk pers. com.).

Even more interesting are the comparisons of feeding frequencies between Corsica and Ventoux. Fig. 5 shows that for the same number of young, feeding frequencies are much lower in Corsica than in Ventoux. Although mainland tits are slightly heavier than Corsican ones (Blondel 1985), this cannot account for the difference in feeding frequencies. An explanation could be that prey sizes are larger on the island. Van Balen (1973) has shown for the Great Tit that feeding frequencies decrease as prey size increases. Preliminary observations by automatic photography inside the nestbox show that the mean prey size is not larger in Corsica than on the mainland, although the range of prey sizes is wider. Another explanation could be that the



Fig. 5. Above: mean daily air temperatures during the nestling period of an enlarged brood of 9 young in Corsica (dots) and of a natural brood of 9 young in Ventoux (triangles). Below: feeding frequencies (number of visits per h and per nestling) in relation to the age of nestlings of these broods.

quality of the food is different in the two habitats. However, this is highly improbable because growth rates as well as the length of nestbox occupancy by the nestlings are nearly the same in the two populations (Blondel et al. 1985, Gaubert 1985). The most likely explanation for this difference is that air temperatures, which are on average 10-15 °C higher in Corsica than in Ventoux when the tits feed their young (Fig. 5), reduce the energy requirements of both parents and young on the island. Van Balen (1973) has shown for the Great Tit that above a critical threshold of 12 °C feeding frequencies decrease. Haftorn & Reinertsen (1985) have demonstrated for the Blue Tit that below a critical lower temperature of 15 °C energy expenditure increases above the resting metabolism. Since ambient temperatures are much higher in Corsica than in Ventoux when the tits feed their young, we hypothesize that differences in feeding frequencies between the two habitats are determined by the difference in energy expenditure and energy requirements of the young and the parents.

In order to test this effect of temperature on investment of the parents to feed their young, we plan to manipulate some continental broods by monitoring the temperatures inside the nestbox using the method of Mertens (1980). Feeding frequencies will be recorded simultaneously. Such experiments do not exclude further analyses of the food (caloric value, prey size) for which our data are still scanty.

3) Is there a relation between reproductive effort and survival?

An assumption accepted until recently in life history theory is that fecundity and adult survival are negatively correlated (Snow 1956, Cody 1971, Crowell & Rothstein 1981). Since each breeding pair raises on average 5.0 young on the mainland and 3.2 in Corsica, adult survival should be much higher on the island than on the mainland. If such is the case, the ratio adult/ yearling breeders should be much higher in Corsica than in Ventoux. Obviously this is not the case since there are on the whole 66% adult breeding birds in Ventoux whereas this proportion is 68% in Corsica (Table 5). This difference between the two habitats is not significant. Assuming that dispersion rates are roughly the same in the two habitats and that the proportion of adults and yearlings breeding in the nestboxes is the same, which is acceptable, this means that survival of the juveniles is higher on the island than on the mainland. About 0.32 of the breeding birds in Corsica are yearling birds, that is 0.64 yearlings per breeding pair. Since each pair raises on average only 3.2 young, this means that local survival of juveniles from fledging to breeding is about 0.64/3.2 = 0.20. In Ventoux the figures are 0.68/5 = 0.14. These values are very high, especially the ones from Corsica, when compared to local survival rates of 0.01 to 0.15 given by Perrins (1979) for populations of temperate Europe. A higher survival of juveniles in Corsica is especially true for females since the ratio adults/yearlings breeding in the nestboxes is 54/46 instead of 59/41 in Ventoux (Table 5). Such figures do not support either the general assumption of a direct relationship between fecundity and survival or the view that adult birds survive better in the predictable climate of an island than in the unpredictable climate of the mainland. A preliminary analysis of capture-recapture data using the basic model of Cormack (1964), recently revised by Clobert *et al.* (1985), shows that adult survival rates are 0.55 in Corsica and 0.60 in Ventoux. The difference is not significant (Clobert *in litt.*). These results support the view of Ricklefs (1973, 1980 and pers. comm.) that the general trade-off of life history parameters has only little to do with the actual clutch size.

Whatever future studies, three conclusions emerge from these results:

1) In order to assess the reproductive effort, we must think in terms of a compromise between costs and benefits. Benefits must be measured not only by the number of offspring, but also by the survival of parents. Several authors think that body condition is a predictor of subsequent survival and hence of future contribution to following generations, but this is not certain for tits (Van Balen pers. comm.). Measurements of body weight must be taken in order to have sound data on reproductive benefits.

2) Ecophysiological studies involving manipulation of temperatures inside the nestbox are needed in order to evaluate the energy requirements of the nestlings and the role of temperature in the cost of reproduction, which appears to be much lower on the island than on the mainland. Since the mean air temperature when the tits feed their young is on average 11 °C in Ventoux and as high as 20.3 °C in Corsica, the energetic requirements of the two populations are very different.

3) Survival rates of juveniles and adults in Corsica and in Ventoux are very interesting to consider. Juvenile mortality appears to be higher in Ventoux than in Corsica, since there is a higher proportion of juvenile females breeding in the nestboxes on the island. Adult mortality rates are about the same in the two populations. This is in contradiction with the widely accepted contention, that adult survival is higher in buffered insular bioclimates than in more contrasted continental ones. Should there be less intraspecific competition between a smaller number of juveniles on the island? Is the higher than expected mortality of adults in Corsica linked with the severe heat and dryness of the Mediterranean summer which would be a strong limiting factor

on birds tired just after their breeding effort? Answers to such questions are our main center of interest for the years to come.

5. CONCLUSIONS

Our main conclusion is that each local population-environment system is a particular case, *i.e.* breeding biology more reflects local conditions than the overall demography of the population. Thus, the problem is to explain in each habitat how life-history traits respond to each local set of environmental factors. A major problem for a bird is to adjust his reproductive investment to environmental factors. Such an adjustment has to be achieved by a balance between the cost of reproduction and its benefit. Drent & Daan (1980) emphasize that energetics of reproduction are a crucial point for this adjustment. Quality of parents, especially body weight that could be a good predictor for future survival. must be measured in order to assess the decisions each female has to take for her breeding (laying time, clutch size) in relation to her energetic investment. Most of the questions currently raised by the different populations under study, especially the mechanisms of reproductive adjustment, should be answered through experiments designed to modify energetic investment in order to test whether or not the foraging capacity of the parents is optimized in natural conditions. Such experiments should produce either a decrease of the energetic cost of reproduction (supplementary food, decrease of brood size, increase of temperatures inside the nestbox, etc.), or an increase of this cost.

6. ACKNOWLEDGEMENTS

We greatly benefited from many stimulating discussions with all participants of the workshop, especially Dr. J. H. van Balen. We are particularly indebted to Prof. Dr. R. H. Drent, who gave us much of his time in Wageningen, the Camargue and Montpellier to discuss our programme. Our warmest thanks go to Dr. J. H. van Balen, J. L. Martin, Dr. A. J. van Noordwijk, Prof. Dr. S. Stearns, Dr. J. M. Tinbergen and Dr. J. W. Woldendorp, who greatly improved a first draft of the manuscript. O. Moreno, Enrique E. Alès and R. M. Alonso-Quecuty provided unpublished data from Spain. A. Dervieux, H. Kowalski, M. Maistre and Ph. Perret actively participated in the field work. Drawings were made by J. Vilanova and his colleagues. This work is supported by GRECO/CNRS 82, ATP/CNRS 'Biologie des Populations' and the 'Basler Stiftung für biologische Forschung'.

7. SUMMARY

In the first part of this paper emphasis is given on the large variation in clutch size of the Blue Tit within the Western Mediterranean area. This between-habitat variation is due to the heterogeneity of many patchily distributed habitats of different quality (evergreen oak woodland, deciduous oak woodland, conifers) as well as to the physiographic diversity of the region. Comparative studies in progress on the breeding patterns of the Blue and the Great Tit in evergreen oak woodland (Quercus ilex) and in deciduous oak woodland (Q. pubescens) show that there are important differences between these two kinds of habitats for such parameters as the onset of breeding, clutch size and breeding success. Experiments are in progress in order to assess the role of the food supply in these differences, especially in the timing and the length of food availability as well as the quantity of the food supply. Detailed population studies are conducted mostly on the Blue Tit between an insular site (Corsica) and a continental one (Mont-Ventoux). Striking differences in the functioning of these populations cannot be explained in the light of theories of island biogeography. Paradoxally there seem to be on the island environmental constraints which limit the breeding time between two fixed limits. Suppose that the relation between laying date and local survival of the juveniles is steeper in Corsica than on the mainland. This would imply a strong competition and a greater investment for young to increase their chance of survival. This would lead to a smaller clutch size. Anyway there is on the island a reduced breeding productivity without a reduction in adult mortality which is as high as on the mainland. Actual clutch size cannot be interpreted in the light of a trade-off between fecundity and survival.

8. REFERENCES

- Askenmo, C. 1979. Effects of addition and removal of nestlings on nestling weight, nestling survival and female weight loss in the Pied Flycatcher Ficedula hypoleuca. Orn. Scand. 8: 1–18.
- Balen, J. H. van. 1973. A comparative study of the breeding ecology of the Great Tit *Parus major* in different habitats. Ardea 61: 1–93.
- Bell, G. 1980. The costs of reproduction and their consequences. Am. Nat. 116: 45-76.
- Blondel, J. 1979. Biogéographie et écologie. Masson, Paris.
- Blondel, J. 1981. Structure and dynamics of bird communities in Mediterranean habitats. In: F. di Castri, D.W. Goodall & R.L. Specht, (eds.). Maquis and Chaparrals. Coll. Ecosystems of the World, UN-ESCO. Elsevier, Amsterdam.
- Blondel, J. 1985. Comparative breeding ecology of the Blue Tit and the Coal Tit in mainland and island Mediterranean habitats. J. Anim. Ecol. 54: 531–556.
- Blondel, J., H. Gaubert, & A. Corman. 1985. Sur les mécanismes régulateurs de l'investissement dans la reproduction chez la Mésange bleue *Parus caeruleus* (Aves). C. R. Acad. Sci. Paris Ser. III, 18: 673–678.
- Blondel, J. & P. Isenmann. 1979. Insularité et démographie des Mésanges du genre *Parus* (Aves). C.R. Acad. Sci. Paris Ser. D, t. 289: 161–164.
- Boyce, M. S. 1984. Restitution of r- and k-selection as a model of density-dependent natural selection. Ann. Rev. Ecol. Syst. 15: 427–447.

- Charnov, E. L. & J. R. Krebs. 1974. On clutch-size and fitness. Ibis 116: 217–219.
- Clobert, J., J. D. Lebreton, M. Clobert-Gillet & H. Coquillart. 1985. The estimation of survival in bird populations by recaptures or sightings of marked individuals. In B. J. T. Morgan & P. M. North. (eds.). Statistics in Ornithology. Springer-Verlag, Berlin.
- Cody, M. L. 1966. A general theory of clutch-size. Evolution 20: 174-184.
- Cody, M. L. 1971. Ecological aspects of reproduction. In D. S. Farner & J. R. King. (eds.). Avian Biology, Vol. 1. Academic Press, New York.
- Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. Biometrika 51: 429–438.
- Cramm, P. 1982. La reproduction des Mésanges dans une chênaie verte du Languedoc. Oiseau 52: 347-360.
- Crowell, K. L. & S. I. Rothstein. 1981. Clutch-sizes and breeding strategies among Bermudan and North American passerines. Ibis 123: 42–50.
- Drent, R. H. & S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68: 225-252.
- Ekman, J. & C. Askenmo. 1986. Reproductive cost, agespecific survival and a comparison of the reproductive strategy in two European Tits (genus *Parus*). Evolution 40: 159–169.
- Gaubert, H. 1985. Etude comparée de la croissance pondérale des jeunes de deux populations de Mésange bleue *Parus caeruleus* en Corse et en Provence: augmentation expérimentale de la taille des nichées corses. Acta Oecologica/Oecol. gener. 6: 305-316.
- Haftorn, S. & R. E. Reinertsen. 1985. The effect of temperature and clutch size on the energetic cost of incubation in a free-living Blue Tit (*Parus caeruleus*). Auk 102: 470-478.
- Higuchi, H. 1971. Comparative study on the breeding of mainland and island subspecies of the Varied Tit, *Parus varius*. Tori 25: 11–20.
- Immelmann, K. 1971. Ecological aspects of periodic reproduction. In: D. S. Farner & J. R. King (eds.). Avian Biology, I. Acad. Press, New York.
- Isenmann, P. 1982. The influence of insularity on fecundity in tits (Aves, *Paridae*) in Corsica. Acta Oecologia/Oecol. gener. 3: 295–301.
- Isenmann, P. 1983a. Zur Brutbiologie einer Blaumeisen-Population Parus caeruleus in Süd-Frankreich. Vogelwelt 104: 142–148.
- Isenmann, P. 1983b. A case of higher clutch-size in second broods in Great Tit *Parus major* breeding in a Mediterranean evergreen habitat. Gerfaut 73: 123–126.
- Klomp, H. 1970. The determination of clutch size in birds: a review. Ardea 58: 1–124.
- Kluijver, H. N. 1951. The population ecology of the Great Tit, Parus m. major L. Ardea 39 : 1-135.
- Lack, D. 1966. Population studies of birds. Oxford.
- Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.
- Leclercq, B. 1977. Etude phénologique des paramètres de la reproduction des Mésanges en futaie de chênes. Rev. Ecol. (Terre et Vie) 31: 599-619.
- Merle, P. du & R. Mazet. 1983. Stades phénologiques et infestation par *Tortrix viridana* L. (Lep. Tortricidae)

des bourgeons du Chêne pubescent et du Chêne vert. Acta Oecologia/Oecol. Appl. 4: 47–53.

- Mertens, J. A. L. 1980. The energy requirements for incubation in Great Tits, Parus major L. Ardea 68: 185-192.
- Michelland, D. 1982. Survie en milieu insulaire: quelle stratégie? Le cas des Mésanges en Corse. Rev. Ecol. (Terre et Vie) 36: 187–210.
- Neub, M. 1977. Evolutionsökologische Aspekte zur Brutbiologie von Kohlmeise (*Parus major*) und Blaumeise (*Parus caeruleus*). Thesis, Univ. Freiburg.
- Noordwijk, A. J. van, J. H. van Balen & W. Scharloo. 1981. Genetic variation in the timing of reproduction in the Great Tit. Oecologia (Berl.) 49: 158–166.
- Noordwijk, A. J. van & G. de Jong. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. Am. Nat. 128: 137–142.
- Nur, N. 1984a. The consequences of brood size for breeding Blue Tits. I. Adult survival, weight change and the cost of reproduction. II. Nestling weight, offspring survival and optimal brood size. J. Anim. Ecol. 53: 479-496; 497-517.
- Nur, N. 1984b. Feeding frequencies of nestling Blue Tits (*Parus caeruleus*): costs, benefits and a model of optimal feeding frequency. Oecologia (Berl.) 65: 125–137.
- Perrins, C. M. 1965. Population fluctuations and clutch-size in the Great Tit Parus major. J. Anim. Ecol. 34: 601-647.

Perrins, C. M. 1979. British tits. Collins, London.

- Ricklefs, R. E. 1973. Fecundity, mortality and avian demography. In: D. S. Farner. (ed.). Breeding biology of birds. Nat. Acad. Sci., Washington D.C.
- Ricklefs, R. E. 1977. A note on the evolution of clutch-size in altricial birds. In: B. Stonehouse & C. M. Perrins. (eds.). Evolutionary ecology. MacMillan. London.
- Ricklefs, R. E. 1980. Geographical variation in clutch-size among passerine birds: Ashmole's hypothesis. Auk 97: 38–49.
- Schmidt, K.-H. 1984. Frühjahrstemperaturen und Legebeginn bei Meisen (*Parus*). J. Orn. 125: 321–331.

Slagsvold, T. 1981. Clutch-size and population stability in

birds: a test of hypotheses. Oecologia (Berl.) 49: 213–217.

- Snow, D. W. 1954. The habitats of Eurasian Tits Parus spp. Ibis 96: 565–585.
- Snow, D. W. 1956. The annual mortality of the Blue Tit in different parts of its range. Brit. Birds 49: 174–177.
- Stearns, S. C. 1976. Life history tactics: a review of the ideas. Quart. Rev. Biol. 51: 3-47.
- Stearns, S. C. 1980. A new view of life history evolution. Oikos 35: 266–281.
- Tinbergen, J. M. 1987. Cost of reproduction in Great Tits: intraseasonal costs associated with brood size. Ardea 75.
- Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. Am. Nat. 100: 687–690.

9. SAMENVATTING

In het eerste deel van dit artikel wordt de grote variatie in de legselgrootte van de Pimpelmees in het westelijke mediterrane gebied besproken. Deze heeft te maken met de heterogeniteit van de habitats (permanent groen eikenbos, loofverliezend eikenbos, naaldbos) en met de grote verschillen in hoogteligging en in isolatie van de populaties.

Vergelijkend onderzoek naar de broedbiologie van Koolen Pimpelmees in permanent groen en loofverliezend eikenbos (resp. *Quercus ilex* en *Q. pubescens*) in Zuid-Frankrijk heeft grote verschillen in legdatum, legselgrootte en broedsucces aan het licht gebracht. Nader onderzoek, o.a. met experimenten, zal moeten uitwijzen in hoeverre de beschikbaarheid van voedsel deze verschillen veroorzaakt.

Er bestaan grote verschillen in de broedbiologische parameters, zoals legdatum, legselgrootte, aantal uitgevlogen jongen en groei van de jongen, tussen de Pimpelmeespopulatie op Corsica en die van het vasteland (Mt. Ventoux). Deze verschillen kunnen niet verklaard worden met de in de literatuur geponeerde eilandtheorieën. De veel lagere productiviteit van de eilandpopulatie gaat niet gepaard met een hogere overleving van de oude vogels. Het lage niveau van de legselgrootte kan niet verklaard worden uit een afweging (op grond van kosten en baten) tussen reproductie en overleving.