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Geographical variation in clutch-size: the example of the Blue Tit *(Parus caeruleus)* in the Mediterranean area

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1. Introduction

The Blue Tit *(Parus caeruleus)* has one of the highest clutch-sizes of the passerines. Up to 12 eggs are frequently laid by a single female. This species also shows a very impressive geographical variation in clutch-size as has been reported by SNOW (1956). In this article which is the result of a team work of the ornithological group at the Centre L. Emberger (Centre National de la Recherche Scientifique) in Montpellier, I present new data on this topic from the western Mediterranean which is situated at the southwestern corner of its breeding range. These data are compared with those collected in Central and Northern Europe where the species extends its range northward to South Scandinavia and Finland. From these comparisons, I propose that factors associated with the quality of the habitat play a major role in the geographic variation of clutch-size in tit-species.

2. Material and methods

Data were collected with Schwegler nest-boxes except in the Canary Islands. The nest-boxes were visited once a week during the whole breeding season (mid-March to mid-July). I only use records from first clutches. The study sites were the following (see Fig.):

Southern continental France: Mont-Ventoux/Vaucluse (44° 07′ N / 05° 10′ E). Cedar *(Cedrus atlantica)* largely predominant. Altitude between 750 and 1050 m. 1976–1984. – Saint-Baume/Var (43° 22′ N / 05° 47′ E). Beech *(Fagus sylvatica)*. Altitude 700 to 750 m. 1976–1980. – Quissac/Gard (43° 54′ N / 04° 00′ E). Evergreen Holm Oak *(Quercus ilex)*. Altitude: 100 m. 1979–1984. – La Fage/Gard (43° 58′ N / 03° 51′ E). Downy Oak *(Quercus pubescens)*. Altitude: 350 to 400 m. 1979–1981. – Liouc/Gard

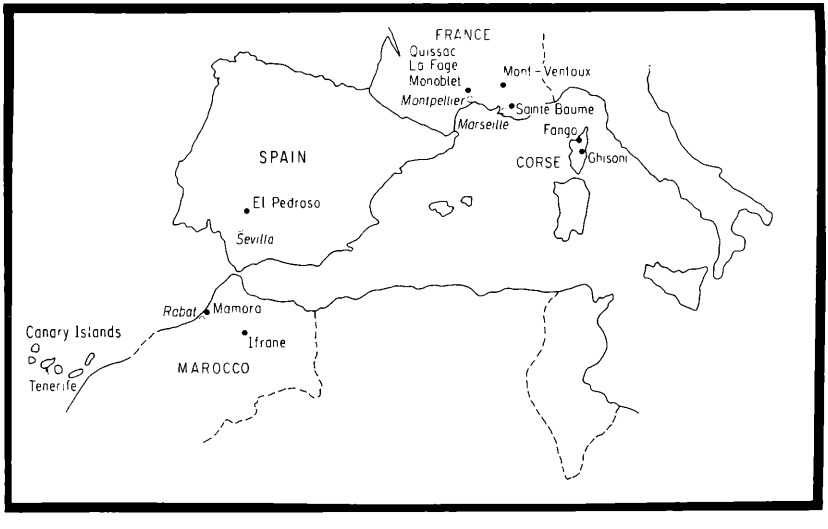

Fig. 1: Location of the different study sites.
Abb. 1: Geographische Lage der verschiedenen Untersuchungsstellen.

(43° 53′ N / 04° 01′ E). Downy Oak. Altitude: 100 m 1982–1984. – Monoblet/Gard (43° 58′ N / 03° 53′ E). Mixed wood: ⅓ Downy Oak and ⅔ Holm Oak. Altitude: 200 m. 1980–1984.

Corsica: Fango/Haute Corse (42° 34′ N / 08° 44′ E). Holm Oak. Altitude: 100 to 150 m. 1976–1984. – Ghisoni/Haute Corse (42° 10′ N / 09° 15′ E). Mixed wood *(Pinus laricio* and *Fagus sylvatica)*. Altitude: 900 to 1000 m. 1981 and 1982.

Morocco: Mamora/near Rabat (34° 02′ N / 07° 00′ W). Cork Oak *(Quercus suber)*. Altitude: 50m (Data from BAOUAB 1983). – Ifrane/Middle Atlas (33° 02′ N / 05° 15′ W). Cedar *(Cedrus atlas)*. Altitude: 1650 m (Data from BAOUAB 1983).

Canary Islands: Tenerife (28° 20′ N / 16° 20′ W). Mostly *Pinus canariensis* and *laurisilva*. Altitude: 800 to 1450 m.

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3. Results

There ist a striking variation in the mean value of the clutch-sizes recorded at the eleven study sites (Table 1). The highest value (10.9 eggs) ist about three times higher than the lowest one (3.5 eggs). The two highest values (>10.0 eggs) come from the two habitats (La Fage and Liouc) with pure deciduous oaks *(Quercus pubescens)*. It is only at Liouc that we recorded clutches with more than twelve eggs (up to fourteen eggs). An intermediate set of values (>7.0 and <10.0 eggs) was found in the following four habitats: two with evergreen Holm Oak, exclusively (Quissac) or predominantly (Monoblet), one with cedars mixed with a few Downy Oaks (Mont-Ventoux) and one with beeches, the two latter at a relatively high altitude. The lowest values (<7.0 eggs) come from a Holm-Oak habitat on a continental island (Fango/Corsica), the two study areas in Morocco and one on Tenerife/Canary Islands. For a better understanding of this rather high variation in clutch-size throughout the western Mediterranean, it is necessary to give some additional details.

It is not surprising that the highest clutch-sizes were laid in habitats with deciduous oaks. These are considered to constitute the optimal habitat for the Blue Tit (SNOW 1954). Both at La Fage and Liouc, this species is the most abundant breeding bird-species. When Downy Oaks are progressively replaced by Holm Oaks the clutch-size begins to diminish (Monoblet and Quissac). In the Holm Oaks at Quissac, the Blue Tit nevertheless had a rather high clutch-size at the beginning of the study in 1979 (10.0 eggs) and in 1980 (9.3 eggs). In 1981, when we increased the density of breeding birds by supplementary nest-boxes, the mean clutch-size dropped significantly to lower values (a reduction of 1.4–2.1 eggs occured; t-Test, $p<0.01$). In this case, the breeding density was magnified by two or three. This factor was as important as the quality of habitat in inducing a reduction of 0.9 to 1.6 eggs, in comparison to the mean value from the nearby Downy Oaks of Liouc. This suggests that the species is then faced with less favourable conditions than in pure deciduous Downy Oaks. The clutch-size recorded at Mont-Ventoux remains relatively high if we consider the altitude (750 to 1050 m; increased altitude reduces clutch-size, see ZANG 1982) and the predominant tree-species. Although conifers are largely avoided by the Blue Tit, cedars are probably an exception (e.g. this species regularly lives in cedar woods in Northern Africa). The southern French study site with the lowest recorded clutch-size is the beech wood at La Sainte-Baume. Both altitude (700–750 m) and probable poor feeding resources may have lead to smaller clutch-sizes. Clutch-sizes with less than seven eggs come from: 1) a Holm Oak habitat on an island (Corsica). This striking reduction has been extensively discussed elsewhere (BLONDEL 1985, BLONDEL et al. 1987, ISENMANN 1982). It fits with a general reduction in fecundity observed in isolated island populations. It is noteworthy that the mountainous birds of Ghisoni do not show a supplementary reduction due to altitude (but our sample is very small; see Table 1). 2) Two study

Table 1: Mean clutch-size of the Blue Tit at the different mediterranean study sites. First row: mean (range), second row: S.D. (n).

Tab 1: Durchschnittliche Gelegestärke der Blaumeise an den verschiedenen Untersuchungsstellen im westlichen Mittelmeer. Erste Reihe: Durchschnittswert (Amplitude Eizahl), zweite Reihe: Standardabweichung (Anzahl der Gelege).

Study Sites	1976	1977	1978	1979	1980
Mont Ventoux	8.6(8—9) 0.6(3)	9.2(8—11) 1.2(8)	8.4(6—10) 1.3(10)	9.6(7—12) 1.5(9)	8.6(6—11) 1.9(10)
Sainte Baume	8.8(7—11) 2.0(5)	7.3(3—10) 2.1(12)	8.0(6—10) 1.5(7)	8.7(7—10) 1.0(8)	7.8(4—10) 1.5(14)
Quissac	— —	— —	— —	10.0(9—12) 1.1(6)	9.3(8—11) 1.2(9)
La Fage	— —	— —	— —	9.7(7—12) 1.6(12)	10.1(9—12) 1.2(12)
Liouc	— —	— —	— —	— —	— —
Monoblet	— —	— —	— —	— —	11.0(10—12) 0.8(4)
Fango	6.3(5—8) 0.9(8)	6.1(4—10) 1.4(16)	5.9(4—8) 1.0(17)	6.1(4—8) 1.3(14)	5.8(4—7) 1.0(16)
Ghisoni	— —	— —	— —	— —	— —
Mamora	— —	— —	— —	— —	— —
Ifrane	— —	— —	— —	— —	— —
Tenerife	— —	— —	— —	— —	— —

Study Sites	1981	1982	1983	1984	average
Mont Ventoux	8.7(7—10) 1.1(14)	8.9(6—11) 1.3(13)	8.7(7—11) 1.3(14)	8.5(6—10) 1.0(13)	8.8(6—12) 1.3(94)
Sainte Baume	— —	— —	— —	— —	7.7(3—11) 1.9(46)
Quissac	8.6(7—11) 1.2(16)	7.5(6—10) 1.4(24)	7.7(6—12) 1.5(21)	7.9(6—11) 1.3(21)	8.1(6—12) 1.5(97)
La Fage	10.4(9—2) 1.1(14)	— —	— —	— —	10.0(7—12) 1.3(38)
Liouc	— —	11.5(9—14) 1.5(12)	10.4(9—13) 1.2(9)	11.0(8—14) 1.8(20)	10.9(7—14) 1.8(41)
Monoblet	9.4(8—12) 1.4(7)	10.1(9—11) 0.8(6)	8.4(7—10) 1.0(7)	9.3(8—11) 1.5(6)	9.5(7—12) 1.4(30)
Fango	6.3(5—8) 0.9(18)	6.0(5—8) 0.9(16)	6.4(4—8) 1.1(24)	6—7(5—8) 0.7(21)	6.2(4—8) 1.0(151)
Ghisoni	6.0(6) 0.0(3)	6.6(6—7) 0.6(3)	— —	— —	6.3(6—7) 0.5(6)
Mamora	6.9(5—9) 1.1(17)	6.3(5—8) 1.6(15)	7.2(6—8) 0.6(10)	— —	6.8(5—9) 1.1(42)
Ifrane	5.7(4—8) 1.1(13)	7.7(6—10) 1.3(8)	7.6(5—11) 1.7(13)	— —	6.7(4—11) 1.3(34)
Tenerife	— —	— —	3.3(2—5) 0.8(10)	3.8(2—6) 1.1(10)	3.5(2—6) 1.0(20)

Table 2: Mean clutch-size of the Blue Tit in some north-western european oakwoods.
Tab 1: Durchschnittliche Gelegestärke der Blaumeise in einigen nordwesteuropäischen Eichenwäldern.

Location	Clutch-Size	Range	S.D.	n	References
Southern Sweden					
55° 44′ N / 13° 18′ E	12.0	8—15	1.5	82	KÄLLANDER 1983
Northern Germany					BERNDT, WINKEL & ZANG
52° 20′ N / 10° 44′ E	11.5	—	—	260	1983
51° 13′ N / 11° 49′ E	10.1	3—17	2.6	65	SCHÖNFELD & BRAUER 1972
England					
51° 46′ N / 01° 15′ W	10.9	—	—	121	PERRINS 1965
Belgium					DELMÉE, DACHY & SIMON
50° 00′ N / 04° 38′ E	10.8	6—16	1.9	170	1972
Southern Germany					
48° 16′ N / 07° 45′ E	10.3	5—17	1.9	446	NEUB 1977
Northern France					
47° 10′ N / 05° 05′ E	11.0	—	2.5	112	LECLERCQ 1975
Southern France					
43° 53′ N / 04° 01′ E	10.9	8—14	1.7	41	This study

areas in Morocco. There are no differences between the lowland birds living in Cork Oaks (Mamora) and the mountainous one living in cedars (Ifrane). Compared to similar habitats at the same altitudes in continental Southern France, the reduction is of 2.1 eggs betwenn Mont Ventoux und Ifrane and of 2.7 eggs between Monoblet and Mamora or of only 1.3 eggs between Quissac and Mamora. The lowest value is recorded on Tenerife/Canary Islands where the sample is large enough to be relevant. SNOW (1956) reported a mean clutch-size of 4.3 eggs for the Canary Islands. The tenerifian Blue Tit lays as many as 3.2 eggs less than its montainous moroccan congener.

4. Discussion

The variation of clutch-size recorded for the Blue Tit from Southern France southward to the Canary Islands is much larger than that registered in that part of the breeding range situated north of the Mediterranean area (see Table 2 but also NEUB 1977 and HAFTORN & REINERTSEN 1985). In the deciduous oak habitats of Southern France (La Fage and Liouc) the clutch-size remains as high as in the deciduous oak woods in Central and Northern Europe with the exception of Southern Sweden (KÄLLANDER 1983). In the latter the clutch-size is significantly higher than that of Liouc (Kolmogorov-test; $p<0.05$). The clutch-size in the deciduous oak wood habitats ranges between ten and twelve eggs along a gradient of about 11° in geographical latitude. Thus, it seems inappropriate to speak of a latitudinal decrease in the clutch-size in this species concerning populations in lowland deciduous oak habitats. This view is in agreement with previous claims by NEUB (1977) and HAFTORN & REINERTSEN (1985) but contradicts LACK (1966) and BERNDT, WINKEL & ZANG (1983). ORELL & OJANEN (1983), in a review of the Great Tit *(Parus major)*, could not find any geographical clutch-size variation from Northern to Central Europe. For the Blue Tit, data show how closely clutch-size is related to habitat quality. The minor differences observed from one population or from

one year to another should be attributed to various other factors which are also known to pay a role in determining clutch-size such as nest-hole volume (LÖHRL 1977), density of breeding pairs, laying dates (LACK 1958 but also SCHMIDT & STEINBACH 1985), altitude (ZANG 1982), genetic characteristics of the breeders (van NOORDWIJK 1980). The exact influence of each of these factors remains difficult to determine in most cases and moreover their importance can vary spatially and temporarily (generally they are not given when clutch-size values are published). The importance of habitat quality is further emphasized when we compare the clutch-sizes from deciduous oak woods with those from Holm-Oaks (Quissac and also Monoblet). A slight initial decrease is then noticeable which probably continues throughout Spain (for 1985, some early informations from the El Pedroso Holm Oak wood near Sevilla in Southern Spain indicated an average clutch-size of 7.5 eggs for 19 pairs/S.D. = 0.7; range = 6–9; E. ALES and O. MORENO in litt.). In Morocco, the clutch-size drops to 6.8 eggs (it must be remembered here that in Northern Africa as well as in the Canary Islands the birds form a distinct subspecies group, see VAURIE 1959). If we consider a clutch-size of about 9.5 eggs for the Blue Tit in Holm-Oak habitats in Southern France, the decrease is then of 2.0 eggs as far as Southern Spain and of 2.7 eggs as far as Morocco. A geographical reduction in the clutch-size towards the South is obvious. Another sharp decrease is that between Morocco and the Canary Islands (6.8 to 3.5 eggs). As for Corsica, factors probably associated with isolation are again suspected to be responsible for this drop.

How do all these comparisons fit with the two major hypotheses on geographical clutch-size variations? The first by LACK (1966) predicts that the clutch-size is adjusted to the maximum number of young a pair can raise; the latitudinal decrease toward the south may be related to the shorter spring day in the south allowing the parents less time to feed their young. In that respect, there is a difference of 1.5 to 2.0 hours of daylight in May – June between Southern Sweden and Southern France, and of 1.0 to 1.5 hours between Southern France and Morocco. In deciduous oak woods in Southern France, Blue Tits do not lay 1.1 less eggs than they do in Southern Sweden and this difference disappear completely between Northern Germany and Southern France though in the latter they have nearly 1.5 hours less time per day to feed their young. Thus, there is not evidence that under optimal conditions the duration of daylight plays a major role in clutch-size determination. It may play a minor role as do the the few other factors mentioned above. The role of daylight duration is again problematic in the drop in clutch-size between Southern France and Morocco (and Southern Spain): this drop is higher than that between Southern France and Southern Sweden although the daylight difference is smaller.

The second hypothesis by ASHMOLE (RICKLEFS 1980) says that clutch-size varies in direct proportion to the degree of seasonal fluctuation in the level of resources utilized by a population. Hence, the greater the seasonal fluctuations in resources, the larger the average clutch-size. If we take into consideration only deciduous oak forests, we notice that clutch-sizes do not vary or vary only weakly. They are in fact adjusted to high surpluses of feeding resources during the breeding season and, thus, remain high. As soon as we consider the data collected in the evergreen oak belt a reduction in clutch-size which increases progressively towards the south becomes obvious. Clutch-size reaches its lowest value at the extreme south of the breeding area. This might be considered as an adjustement to progressively declining surpluses which increase the cost of brood rearing. So, it becomes plausible that the clutch-size reduction agrees with ASHMOLE's hypothesis.

Finally, clutch-size in a population may reflect the adjustement the birds have to make to match the different environmental constraints. Further, the drastic clutch-size reduction in the south recalls what JÄRVINEN (1986) has pointed out when he discussed the influence of the harsh northern european environment on the clutch-size of some passerines. At the northern fringe of their breeding ranges their clutch-sizes drop. The same is true as the southern fringe at least for the Blue Tit. This may be a general rule in peripheral populations which are confronted with worse environmental conditions during the breeding season than central ones

(SLAGSVOLD 1981). Unfortunately, we do not possess data for the Blue Tit at its northern range limits (64–66° N). Nevertheless, in Southern Finland at 60° (HILDEN 1982) and in Norway at 63° N (HAFTORN & REINERTSEN 1985) the clutch-size still remains high with average values of 11.3 respectively 11.0 eggs!

Summary

This paper contains data on the geographical variations in clutch-size of Blue Tits from the Western Mediteranean area (Table 1). There is a striking variation in the mean value of the clutch-sizes recorded at the eleven study sites. The highest value (10.9 eggs) is about three times higher than the lowest one (3.5 eggs). In the deciduous oak habitats of Southern France the clutch-size remains as high as in similar habitats in Central and Northern Europe. In the evergreen Holm-Oak habitats, the clutch-size diminishes progressively toward the south. It is argued that clutch size is predominantly linked to habitat quality.

Zusammenfassung

Ein Vergleich der durchschnittlichen Gelegestärke von elf verschiedenen Blaumeisen-Populationen aus dem westmediterranen Raum (Tab. 1) ergab folgendes: In den Eichenlaubwäldern Süd-Frankreichs war die Eizahl so hoch wie in ähnlichen Habitaten in Mittel- bzw. Nord-Europa (Tab. 2); in den immergrünen Eichenwäldern Süd-Frankreichs wurde dagegen eine niedrigere Gelegestärke festgestellt: am niedrigsten war sie in Marokko und auf den Kanaren (auf letzteren im Mittel nur noch 3,5 Eier!). Als Ursache dieser starken geographischen Variation im südwestlichen Teil des Brutareals der Blaumeise wird eine starke Bindung der jeweiligen Gelegestärke einer Population an die entsprechende Habitatsqualität erörtert.

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