EGG-SIZE VARIATION IN ALGERIAN POPULATIONS OF THE BLUE TIT (*PARUS CAERULEUS ULTRAMARINUS*): EFFECTS OF ALTITUDE AND HABITAT

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RÉSUMÉ

La taille de l'œuf est un caractère que l'on s'attend à être lié à d'autres traits d'histoire de la vie de sorte qu'il devrait montrer des variations en fonction de l'habitat et de l'altitude. Fort peu de données probantes étant disponibles et pour un nombre limité d'espèces, nous avons conduit en 1991-93 une étude de la variation interhabitat et altitudinale des dimensions et du poids des œufs de la Mésange bleue *Parus caeruleus ultramarinus,* profitant de ce que cette espèce se montre dans toute une gamme d'habitats et d'altitudes en Afrique du Nord, notamment dans le nord-est de l'Algérie. Six stations d'étude ont été sélectionnées, représentant deux types d'habitat (les riches forêts caducifoliées dominées par *Alnus glutinosa* et *Quercus faginea* opposées aux forêts sempervirentes pauvres de *Quercus suber*) et trois altitudes (30 m, 500 m et 900-1 000 m). Nous avons analysé à la fois les variables à réponse multiple qui caractérisent les dimensions des œufs et les traits individuels de ces œufs. Les œufs sont apparus différer selon l'altitude (opposition entre le plus bas niveau et les suivants) mais pas selon l'habitat. Ils montrent aussi un relativement fort degré de répétabilité intraponte, de 0,6 en moyenne pour tous les caractères. Ceux-ci n'étaient pas significativement liés à la taille de la ponte dans un même site mais l'analyse d'une variable bivariée intégrant le volume de l'œuf et la taille de la ponte a suggéré que ces deux traits seraient négativement corrélés. De plus, cette variable bivariée différait à la fois d'un habitat et d'une altitude à l'autre.

SUMMARY

Egg-size, as a component of life history, is expected to be traded-off with other components and, consequently, to display a pattern of variation between different habitats and altitudes. Relevant data being very scarcely available for just a few bird species caused us to study interhabitat and interaltitude variation in egg dimensions and mass in the Blue Tit *Parus caeruleus ultramarinus,* taking the advantage of the occurrence of this species in a variety of habitats and at different altitudes in North Africa (north-eastern Algeria). In 1991-1993 we selected 6 study sites representing two types of habitat (rich deciduous forests dominated by *Alnus glutinosa* and *Quercus faginea vs* poor evergreen forests of *Quercus suber*) at three elevations (30 m asl, 500 m als and 900-1 000 m asl). We analysed both multiple response variables characterizing egg dimensions and individual egg traits. Eggs turned out to differ

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between altitudes (the lowest elevation against the two higher ones) but did not differ between habitats. They also display relatively high within-clutch repeatabilities, 0.6 on average for all traits. Egg traits were not significantly correlated with clutch-size within study stations, but the analysis of a bivariate response variable composed of egg volume and clutch-size suggested that these components of life history were negatively linked. Moreover, this bivariate response variable differed both between habitats and altitudes.

INTRODUCTION

In many different organisms, it has usually been assumed that offspring fitness is directly related to propagule size (Roff, 1992; Stearns, 1992). Larger avian eggs give larger nestlings with higher chances of surviving and recruiting into breeding populations (Ojanen, 1983). Theoretical expectations (Roff, 1992; Stearns, 1992) are that different aspects of life-histories are traded-off and, consequently, different traits should represent an interrelated set.

Some life-history traits of Blue Tits (*Parus caeruleus*) have been extensively studied in the Mediterranean region, resulting in novel and very important results concerning differentiation of life-history on small and large spatial scales (Blondel, 1985; Isenmann, 1987; Gil-Delgado *et al.*, 1992; Blondel *et al.*, 1993, 1999; Fargallo & Johnston, 1997; Lambrechts *et al.*, 1997; Catalan & Haeger, 1999). In spite of this, only scarce data on egg-size variation are available from this region (Catalan & Haeger, 1999), which results from the fact that life-history data on Blue Tits living south of 43° N are very scarce (Fargallo & Johnston, 1997). As life-history of Blue Tit populations living in Algeria, the South of the Mediterranean area, shows some variation linked with habitat and altitude (Chabi *et al.*, 1995; Chabi & Isenmann, 1996), the question arises if there is a corresponding variation in egg size and related egg traits.

In this paper we present data on variation in several egg traits recorded in North-African Blue Tits (*Parus caeruleus ultramarinus*). We analyse within- and between-population variation in relation to habitat and altitude of population areas. The main aims of the analysis are:

1. To provide a description of egg-size variation in North-African Blue Tits.
2. To examine if variation in egg traits covary with habitat and altitude.
3. To extract within- and between- clutch sources of variation in egg features in order to show the degree of their repeatability.
4. To examine a hypothetical relationship in the allocation of resources between different reproductive traits, i.e. egg size and clutch size.

MATERIAL AND METHODS

Study sites were located in north-eastern Algeria (Fig. 1) at three altitudes: 30 m asl - Djebel Arrassa (36° 32' N; 8° 30' E), 500 m asl - Djebel Edough (36° 55' N; 7° 41' E) and 900-1 000 m asl - Djebel Ghorra (36° 32' N; 8° 20' E), these sites being located 40-70 km from each other. Two types of habitats 0.5-1.0 km from each other were studied at each altitude. Evergreen habitats with dominating Cork Oak *Quercus suber* were investigated in comparison with habitats dominated by deciduous tree species (summergreen Alder *Alnus glutinosa*

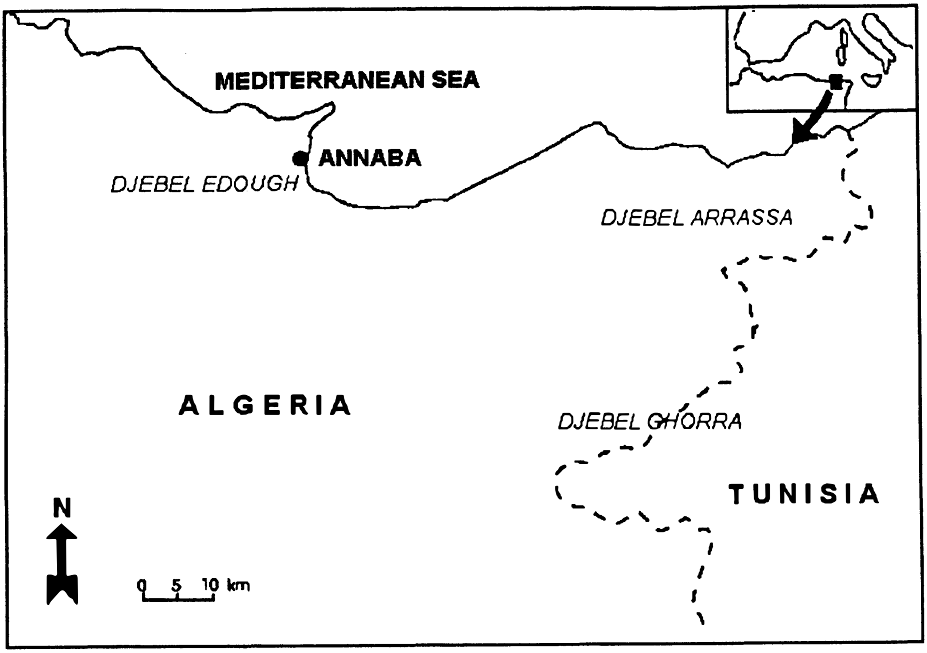

Figure 1. — Geographical location of the study area. Study sites were located at different altitudes: Djebel Arrassa — 30 m asl, Djebel Edough — 500 m asl and Djebel Ghorra — 900-1 000 m.

at 30 m asl and semi-evergreen Zeen Oak *Quercus faginea* at 500 and 900 m asl). Cork Oak trees were 7-8 m high on average *vs* 17-18 m for Zeen Oaks. The stage of leafing phenology at laying times was estimated following Du Merle & Mazet (1983). The climate in the study area is Mediterranean with dry and hot summers and wet and mild winters (annual rainfall exceeds 1 000 mm).

Thirty nest boxes per study site or 180 in total (30*3*2) were set up and observed in three subsequent years (1991-1993). They were placed in 35-40 m distance from each other and were checked once a week from mid-March to late June. The laying date of the first egg was recorded in every nestbox or estimated on the basis of the number of eggs. Length and breadth of successive eggs laid by particular females were measured to the nearest 0.01 mm with callipers. Complete clutches were weighed to the nearest 1 g and mean egg mass was calculated by dividing the total weight by clutch-size. The mean egg mass obtained in this way had unknown variance and because of this it was not shown in the descriptive part of this paper but was used as a variable in the multivariate analysis based on clutch mean values. Egg volumes (EV) were calculated from egg length (EL) and breadth (EB) expressed in cm using the formula worked out by Ojanen *et al.* (1978):

$$EV = 0.042 + 0.4673 * EL * EB^2$$

Only complete clutches, whose incubation started and no new eggs were laid, were included in the multivariate analysis of clutch-size - egg volume relationship.

Non-complete as well as complete clutches were included in the analysis of repeatability of egg traits. By non-complete clutches we understand clutches whose incubation did not start because of nest desertion or because of nest destruction by humans. Human destructive impact was considerable in all the study sites. As a consequence, the number of clutches and corresponding degrees of freedom differed between analyses.

The per clutch mean values of the egg traits were compared among altitudes and habitats using a two-way MANOVA with altitudes (1 = 30 m asl, 2 = 500 m asl, 3 = 900 m asl) and habitats (evergreen v. summergreen) as factors (Scheiner, 1993). Only Pillai's traces are reported as test statistics for MANOVAs because the alternative test statistics, i.e. Hotelling's trace and Wilk's lambda led to exactly the same conclusions in every case. Particular egg traits were further analysed by two-way ANOVAs with the same factors. Clutch mean egg trait values were used as unit observations in between-habitat and between-altitude comparisons. The Scheffe *a posteriori* test was applied to test differences in mean values.

Individual egg measurements were used in one-way ANOVAs in order to estimate within- and between-clutch variance components which were presented as repeatabilities (see Lessels & Boag, 1987; Bańbura & Zielinski, 1990, 1998). One-way ANOVAs with standard sums of squares and degrees of freedom were conducted on egg lengths, breadths and volumes in particular clutches (Sokal & Rohlf 1981). Intraclass correlations, being the statistical measure of repeatability (Sokal & Rohlf 1981, Lessels & Boag 1987), were calculated for these egg traits according to the formula:

$$R = (V_a - V_w)/[V_a + (n_0 - 1)V_w]$$

where V_a is the among-clutch mean square, V_w is the within-clutch mean square, n_0 is an adjusted mean clutch-size and is given by:

$$n_0 = \left[\sum_{i=1}^{a} n_i - \left(\sum_{i=1}^{a} n_i^2 / \sum_{i=1}^{a} n_i\right)\right] / (a - 1)$$

where n_i is the number of eggs in the i-th clutch and a is the number of clutches.

A two-way MANOVA was also used to investigate a relationship between egg volume and clutch-size. Clutch-size was transformed logarithmically (ln) in order to stabilize its variance. In this analysis egg volume and clutch-size were combined into a bivariate response variable following Scheiner (1993). This author showed that MANOVA can be used both to analyse effects of different factors or experimental treatments on a response variable and to explore the structure of the relationship between component variables of the response variable (clutch-size and egg volume in this case). The most important idea here is that such diagnostic tools of MANOVA as sphericity tests and canonical correlations can be applied to show trade-offs. Scheiner (1993) applied this method to show a trade-off between a plant's seed number and size. Univariate statistical procedures were applied following Sokal & Rohlf (1981). The software used for calculations was SPSS for Windows.

RESULTS

EGG-SIZE VARIATION IN RELATION TO HABITAT AND ALTITUDE

Table I displays descriptive data on clutch-size, egg length, breadth and volume for Blue Tits in our study sites (only complete clutches included). A multivariate analysis of variance conducted on the multiple response variable (centroid) composed of egg length, breadth, volume and weight showed that it differed between altitudes (Pillai's trace = 0.26; F = 5.50; df: 8, 300; P = 0.000) but not between habitats (Pillai's trace = 0.037; F = 1.43; df: 4, 149; P = 0.228) nor due to the effect of interaction between altitude and habitat (Pillai's trace = 0.09; F = 1.78; df: 8, 300; P = 0.081).

The differentiation of egg traits was further investigated by univariate ANOVAs which supported MANOVA results (Table II). Because the investigated traits did not vary between evergreen and deciduous habitats, we compared different altitudes by pooling habitats within altitudes. The Scheffe tests demonstrated that the significant altitude-related differentiation of the analysed egg traits resulted from differences between the lowest location and the other two (P for the difference in the Scheffe tests ranged from 0.015 to 0.000001) that did not differ from each other. This showed that the eggs at the altitude of 30 m asl are on average larger than those at the altitudes of 500 and 900 m asl (Table I).

TABLE I

Means and standard deviations of clutch-size and egg measurements (with per clutch mean egg trait as observation unit) of Blue Tits inhabiting two habitat types (evergreen — dominated by Quercus suber *and deciduous — dominated by* Alnus glutinosa *or* Quercus faginea*) at three altitudes (30 m, 500 m and 900-1 000 m).*

Altitude	Habitat	N clutches	Mean trait ± SD			
			Clutch-size	Egg length (mm)	Egg breadth (mm)	Egg volume (cm^3)
30 m	Evergreen	36	6.33 ± 0.96	15.78 ± 0.54	12.05 ± 0.28	1.07 ± 0.07
	Deciduous	12	6.54 ± 1.13	15.77 ± 0.86	11.96 ± 0.40	1.07 ± 0.10
500 m	Evergreen	14	6.00 ± 0.68	15.49 ± 0.68	11.82 ± 0.21	1.00 ± 0.06
	Deciduous	27	6.70 ± 0.95	15.22 ± 0.68	11.70 ± 0.27	0.98 ± 0.07
~ 900 m	Evergreen	27	6.52 ± 0.89	15.43 ± 0.68	11.52 ± 0.44	0.95 ± 0.10
	Deciduous	42	7.71 ± 1.46	15.45 ± 0.63	11.72 ± 0.36	0.99 ± 0.08
Pooled		158	6.77 ± 1.29	15.51 ± 0.65	11.78 ± 0.38	1.01 ± 0.09

Correlation between particular egg traits and clutch-size, laying date and the stage of leafing phenology was also analysed in all altitude-habitat combinations. Only 11 out of 72 correlations proved significant casewise (clutch size X egg traits: $-0.37 > r > -0.47$, df = 42; laying date X egg traits: r = 0.37-0.59, df = 12-36;

TABLE II

A summary of the results of two-way ANOVAs of egg weight (EW), length (EL), breadth (EB) and volume (EV) with the altitude and habitat type considered as factors. Mean squares (MS) for main factors (altitude and habitat) and their interaction are given with the respective F statistics (F) and degrees of freedom (DF).

Egg trait	$MS_{altitude}$(F)	$MS_{habitat}$(F)	$MS_{altitude*habitat}$(F)
EW	0.09 (7.19***)	0.002 (0.17)	0.02 (1.69)
EL	1.91 (4.83**)	0.26 (0.64)	0.27 (0.67)
EB	1.85 (16.07**)	0.001 (0.008)	0.41 (3.59*)
EV	0.13 (19.99***)	0.004 (0.61)	0.01 (2.16)
DF:	2; 152	1; 152	2; 152

* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$

leafing stage X egg traits: $r = -0.41$-0.65, df = 12-36) but none was significant taking into account a tablewise error rate established at the level of $P = 0.0042$ by the Bonferroni method (Rice, 1989).

REPEATABILITY OF EGG TRAITS

Egg length, breadth and volume showed a lot of variation between different clutches and little variation within clutches, resulting in significant values of repeatabilities in all study sites (Table III). The within-clutch repeatabilities of any trait do not seem to represent any particular pattern linked with habitat or altitude. Except a very low value of 0.25 in the case of egg volume in deciduous habitat at the lowest altitude, repeatabilities are moderate to high in range (Table III).

RELATIONSHIP OF EGG SIZE AND NUMBER

To explore further a potential relationship between egg-size and clutch-size we used a two-way MANOVA with a bivariate response variable composed of egg volume and ln clutch-size. In this case the bivariate means were significantly different between both habitat types (Pillai's trace = 0.085; F = 7.05; df: 2, 151; P = 0.001) and altitudes (Pillai's trace = 0.26; F = 11.41; df: 4, 304; P = 0.000) but the interaction of these main factors was non-significant (Pillai's trace = 0.059; f = 2.34; df: 4, 304; P > 0.05). Bartlett's test of sphericity suggested that clutch-size and egg volume were correlated across habitats and altitudes ($\chi^2 = 73.43$; df = 2; $P < 0.0001$). Moreover, for altitude, clutch-size and egg volume showed opposite signs of the canonical coefficients of the canonical variates, indicating that clutch-size and egg-size were negatively correlated across altitudes.

TABLE III

Within-clutch repeatabilities (R) of egg length (EL), breadth (EB) and volume (EV) of Blue Tits living in two types of habitat (evergreen v. summergreen) at three altitudes (30 m, 500 m and 900-1 000 m. F — statistics for corresponding ANOVAs are given with degrees of freedom (DF), adjusted clutch size (n_0), and level of significance (P).

Trait	Altitude	Habitat	R	n_0	DF	F	P
EL	30 m	Evergreen	0.65	6.18	47; 248	12.46	0.0000
		Deciduous	0.57	6.27	17; 95	9.39	0.0000
	500 m	Evergreen	0.69	5.18	19; 91	12.47	0.0000
		Deciduous	0.78	6.29	18; 102	23.70	0.0000
	900 m	Evergreen	0.83	5.47	21; 113	27.18	0.0000
		Deciduous	0.63	7.52	33; 222	6.92	0.0000
EB	30 m	Evergreen	0.42	6.18	47; 248	7.23	0.0000
		Deciduous	0.77	6.27	17; 95	21.46	0.0000
	500 m	Evergreen	0.56	5.18	19; 91	7.48	0.0000
		Deciduous	0.62	6.29	18; 102	11.44	0.0000
	900 m	Evergreen	0.74	5.47	21; 113	16.40	0.0000
		Deciduous	0.72	7.52	33; 222	20.41	0.0000
EV	30 m	Evergreen	0.59	6.18	47; 248	9.77	0.0000
		Deciduous	0.25	6.27	17; 95	3.09	0.0003
	500 m	Evergreen	0.67	5.18	19; 91	11.69	0.0000
		Deciduous	0.65	6.29	18; 102	12.54	0.0000
	900 m	Evergreen	0.50	5.47	21; 113	6.45	0.0000
		Deciduous	0.44	7.52	33; 222	6.98	0.0000

DISCUSSION

There are no comparative data on other populations of *P. c. ultramarinus* available in the literature. Mean values of all the egg traits analysed (Table I) are within the range reported for European Blue Tits. Egg-size variation does not seem to display any consistent geographic pattern in Western Palearctic (Cramp & Perrins, 1993). Mean egg volume is similar to that recently reported for a relatively close Spanish population (Catalan & Haeger, 1999).

An important result of this paper is the finding of an altitude-related pattern of variation in the set of egg traits as a whole (egg length, breadth, volume and mass as a multiple response variable) and particular traits, as shown by a MANOVA and ANOVAs, respectively. This results from a difference between the two lowest study sites and mean values of these egg traits did not vary between studied habitats, evergreen Cork Oak *Quercus suber* forests *versus* the forests dominated by deciduous tree species, i.e. the Alder *Alnus glutinosa* and the Zeen Oak *Quercus faginea*. Both altitude and habitat (or habitat quality) are usually expected to influence life-history (e.g. Blondel *et al.*, 1993, 1999; Riddington & Gosler, 1995; Badyaev, 1997; Fargallo & Johnston, 1997; Fargallo & Johnston, 1997; Lambrechts *et al.*, 1997, Beldal *et al.*, 1998; Catalan & Haeger, 1999), although there are only few studies detailed enough to distinguish between altitude and habitat effects in the case of egg size (Ojanen, 1983).

Interhabitat effects are expected on the basis of habitat-specific variation in food abundance and quality. Our aim in this study has been to contrast two types of habitats: evergreen and semi-evergreen-deciduous. While evergreen oaks renew only c. 30 % of their foliage a year, both deciduous and semi-evergreen trees renew leaves in 100 % (Blondel & Dias, 1994). Because only new leaves are edible for caterpillars, these two types of habitat greatly differ in quality from the tit viewpoint (e.g. Blondel & Dias, 1994; Bańbura *et al.*, 1994). Blondel *et al.* (1999) showed that marked habitat-related differences in life history can be established by selection even between very close populations. In accordance with this, the less suitable habitats are characterized by a reduced average clutch-size in comparison with the rich habitats (Chabi *et al.*, 1995; Chabi & Isenmann, 1996). However, we did not observe any generally significant correlation between egg-size and clutch-size within our study sites, so that we suppose that in poorer evergreen habitats the tits were still capable of producing eggs of relatively stable size even if they had to reduce clutch-size. This is only a suggestion needing experimental studies to test it.

This remains in agreement with the opinion that egg traits seem generally insensitive to external conditions (e.g. Ojanen, 1983; Bańbura & Zielinski, 1995, 1998). In an experimental study by Nilsson & Svensson (1993) Blue Tits which were supplied with extra food before egg laying did not lay bigger but more similar eggs within a clutch. No interhabitat difference in egg-size was observed in the Great Tit *Parus major* by Nager & Zandt (1994) and Horak *et al.* (1995). Baldi & Csorgo (1993) suggested, in contrast, that Hungarian Great Tit populations show clear differences in egg-size between habitats of different quality but it seems to result from their flawed analysis (multiple use of t-test).

In a study of Great Tit egg-size variation (Hamann *et al.*, 1989) the effects of habitat and altitude were to some extent confounded because different habitat stations were located at different altitudes. However, the authors showed a relatively clear positive relationship between egg-size and altitude. Our data do not show such a clear trend as we only observed that eggs at the lowest altitude were bigger than at higher altitudes. Thus the interaltitude difference in egg dimensions we report is in the opposite direction to the trend reported by Hamann *et al.* (1989).

The result from the experimental study by Nilsson & Svensson (1993) that within clutches in better conditions eggs tend to become more similar in size suggests that we could expect some pattern appearing from an analysis of repeatability across habitats and altitudes. However, the repeatabilities were significant and relatively high in almost every case and no clear trend was detected in our study populations.

An increase in clutch-size with altitude was previously recorded in our study populations (Chabi *et al.*, 1995; Chabi & Isenmann, 1996). Because there was no significant correlation between clutch-size and egg-size within study sites, we carried out a multivariate analysis of variance for a bivariate response variable composed of clutch-size and egg volume with altitudes and habitats as factors. Scheiner (1993) showed that this type of analysis could be a useful tool in an analogous case of resource allocation in seed-size and number in plants. This analysis indeed provided interesting results, showing that when considered together, clutch-size and egg-size varied both between altitudes and habitats. There also appeared results suggesting that these reproductive traits were negatively related across altitudes, which could be expected from the fact that both egg-size and clutch-size did differ between altitudes (this paper; see also Chabi *et al.*, 1995; Chabi & Isenmann, 1996).

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