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AN ANALYSIS OF EGG-SIZE REPEATABILITY IN BARN SWALLOWS *HIRUNDO RUSTICA*

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SUMMARY.—*An analysis of egg-size repeatability in Barn Swallows* Hirundo rustica. Variation in length, breadth and volume of eggs from complete clutches of Barn Swallows *Hirundo rustica* was studied in central Poland in 1978-1981 and 1994-1995. The main idea of this paper is that temporal variation in the environment may affect traits differently and that repeatability may be a good reverse indicator of environmental sensitivity. The egg traits (length, breadth and volume) were analysed using one-way and nested ANOVAs. Significant within-clutch repeatabilies of all traits were revealed, ranging from 0.60 to 0.85. Clutch mean values of dimensions of the eggs laid by particular females both in different clutches within a breeding season and in different seasons were similar, resulting in a high repeatability of ca. 0.7. In nested ANOVAs, among-female variance components as measured by intraclass correlation coefficients were 0.62-0.66 with respect to different clutches within breeding seasons, and 0.50-0.60 with respect to different breeding seasons. Interclutch differentiation of eggs within females was low, although significant. Interyear repeatability was also analysed for the sample of males that were mated to different females in subsequent years. Repeatabilities of clutch averages ranged from the insignificant value of 0.16 for egg breadth to 0.53 for egg length, the values being on average much lower than those for females. Female Swallows, showing much interindividual variation, are considerably consistent with respect to the characteristics of their eggs, which means that sensitivity to environmental impacts does not generate a large variation in egg size. The consistent interindividual variation in egg size may have some condition-dependent component.

Key words: Barn Swallow, egg size, *Hirundo rustica*, temporal variability, within-individual variability.

RESUMEN.—*Análisis de la repetibilidad del tamaño del huevo en la Golondrina Común* Hirundo rustica. Este trabajo analiza la variación en longitud, anchura y volumen de los huevos de Golondrinas Comunes reproductoras en Polonia en 1978-1981 y en 1994-1995. La hipótesis principal que trata de contrastarse es que la variación temporal del ambiente puede afectar de modo distinto a rasgos diferentes y que la repetibilidad del rasgo puede ser un buen indicador (inverso) de la sensibilidad a los cambios ambientales. Los rasgos de los huevos de Golondrina Común (longitud, anchura y volumen) se analizaron por medio de ANOVAs de clasificación simple y ANOVAs encajados, encontrándose una repetibilidad significativa de todos ellos (que varió entre 0,60 y 0,85) dentro de puestas. Los valores medios de estos rasgos para puestas completas de la misma hembra fueron similares tanto entre puestas del mismo año como entre puestas de distintos años, dando unos valores de repetibilidad en torno a 0,7. La componente de varianza (medida como correlación dentro de clases) entre hembras en ANOVAs encajados fue de 0,62-0,66 para puestas diferentes dentro de la misma época de cría y de 0,50-0,60 para diferentes épocas de cría. Las diferencias entre huevos de la misma puesta y hembra fueron escasas, aunque significativas. Se analizó también la repetibilidad entre años para una muestra de puestas correspondientes a machos que se aparearon con diferentes hembras en años subsiguientes. La repetibilidad de las medias por puesta variaron entre el valor no significativo de 0,16 para la anchura del huevo y el valor de 0,53 para su longitud, siendo estos valores mucho menores en promedio que los obtenidos para las hembras. Las hembras individuales de Golondrina Común ponen por tanto huevos de tamaño poco variable, de manera que este rasgo parece ser poco sensible a las variaciones ambientales. Sin embargo, existe una considerable variación interindividual, lo cual sugiere, junto con la consistencia para cada individuo, que la variación observada en el tamaño de los huevos de esta especie podría depender de la diferente condición corporal de cada invididuo.

Palabras clave: Golondrina Común, *Hirundo rustica*, repetibilidad, tamaño del huevo, variabilidad interindividual, variabilidad temporal.

INTRODUCTION

Many birds, including Passerines, use daily nutrient intake to produce eggs (Perrins, 1996); such birds are referred to as 'income users' (Drent & Daan, 1980) or 'daily surplus users' (Perrins & Birkhead, 1983). In these species, the abundance and availability of nutrients are

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likely to set a constraint on egg sizes by influencing the process of egg formation (Murphy & Haukioja, 1986; Martin, 1987). Temporal and spatial variation in the availability of nutrients, perhaps brought about by changing weather, could potentially generate interindividual and intraindividual variation in egg sizes laid by females. Besides its proximate meaning, variable natural selection may affect the level of plasticity in egg traits at different time scales (Hoffmann & Parsons, 1991). Many animal and plant species living in unpredictably changing habitats produce propagules of variable size rather than a unique optimum size (e.g. Caprinera, 1979; Kaplan & Cooper, 1984). In addition egg sizes in some bird species vary with the laying sequence within a clutch, which can be interpreted in terms of ultimate and/or proximate factors (Clark & Wilson, 1983; Slagsvold *et al.*, 1984; Järvinen & Ylimaunu, 1986; Jover *et al.*, 1993; Viñuela, 1997).

The daily-surplus-users might be expected to exhibit high plasticity, enabling them to track environmental conditions (*e.g.* Korpimäki, 1990). Traits that are sensitive to changes in the environment should be more variable in time, while resistant traits should have a stable level of variability. It is presumed that the longer the time scale analysed, the higher the variability of environmental conditions that is included, as the variability from day to day should be lower than the variability from month to month or from year to year. A female producing successive eggs within a clutch is therefore likely to experience a smaller variety of conditions than she experiences when producing subsequent clutches or when laying eggs in different years, which is just an example of a more general rule that long-term studies increase the chance of including very different conditions considerably (Martin, 1987).

The main idea of this paper is that repeatability can measure the susceptibility of a trait to environmental influences. In the previous literature, repeatability is considered as a first measure of heritability (e.g. Boag & van Noordwijk, 1987; Bańbura & Zieliński, 1990). While repeatability is certainly a worse measure of genetic variation of a trait than heritability, it seems to be as good or even better at measuring environmental components of variation. In contrast to heritability, repeatability distinguishes two components of environmental variation: *special environmental variance* and *general environmental variance* (Falconer, 1989). As pointed out by Falconer (1989), repeatability expresses the partitioning of the *total phenotypic variance* into two components, *special environmental variance* versus the sum of *genotypic variance* and *general environmental variance*, the former component being a within-individual component and the latter an among-individual one. The special environmental variance of a trait is directly proportional to the susceptibility of the trait to temporary and localised impacts of the environment.

In this paper we apply the above idea to the egg size of Barn Swallows *Hirundo rustica* by analysing repeatabilities in several different ways over different time scales. We have already investigated general aspects of egg size variation in Barn Swallows in a central Polish population and within-clutch patterns related to the laying sequence (Bańbura & Zieliński, 1995; Zielinski & Banbura, pers. obs.). There is no clear egg size variation within a Barn Swallow clutch sequence, except that the last eggs laid are slightly larger than the preceding ones in some years. The yearly mean length of eggs ranges from 19.4 to 19.7 mm, breadth from 13.5 to 13.8 mm, and volume from 1.8 to 1.9 cm^3. In this study population, Barn Swallows usually produce two regular broods per year, with mean clutch sizes 4.86 and 4.47, for first and second broods, respectively (Banbura & Zielinski, 1998).

In this paper we examine the susceptibility of egg length, width and volume to environmental influences (*cf.* Falconer, 1989) on female Swallows at different time scales. To do this, we analyse repeatabilities over various periods and compare repeatabilities for females with repeatabilities for males. This contributes some points to the discussion on mechanisms generating variability of egg sizes representing variation in one kind of reproductive traits. In particular, we discuss Smith *et al.*'s (1993) hypothesis that differences in egg size reflect the body condition of females.

MATERIAL AND METHODS

The study was carried out at small farms located in central Poland near the village of Ktery

(52°15'N; 19°25'E) during 1978-1981 and at Goslub (52°05'N; 19°28'E) in 1994-1995. Most clutches used to study egg dimensions in 1978-1981 were late clutches (repeat and second clutches). In 1994-1995 we studied both first and late clutches. We measured 2771 eggs from 24-211 full clutches per year.

The length (L) and breadth (B) of eggs was measured to the nearest 0.1 mm with callipers and the volume was calculated using the formula,

$$V = 0.507 \cdot L \cdot B^2$$

based on the American subspecies of the Barn Swallow (Manning, 1979).

Parental birds were captured with mist nets at their nesting sites (Bańbura, 1986) and ban-

TABLE I

Within-clutch repeatabilities (*R*) of egg length, breadth and volume in different years. In 1978-1981 all clutches analysed were late clutches (i.e. second and repeat). In 1994 and 1995 first and late clutches are shown separately. The numbers of clutches (Nc) and eggs (Ne) analysed are also given. n_o: the corrected mean clutch size.
*[Repetibilidad dentro de puesta (*R*) para la longitud (lenght), anchura (breadth) y volumen (volume) del huevo en años diferentes. Todas las puestas de los años 1978-1981 fueron puestas tardías (segundas puestas y puestas de reposición). Para 1994 y 1995 se muestran por separado los resultados para primeras puestas (first clutch) y para últimas puestas (late clutch). Se da el número de puestas (Nc) y el número de huevos (Ne) analizados. n_o: tamaño medio corregido de puesta.]*

Year *[año]*	Trait *[rasgo]*	n_o	*R*±SE	*F*	df	*P*	Nc	Ne
1978	Length	4.62	0.47±0.103	5.09	23,87	0.000	24	111
	Breadth		0.60±0.091	7.91		0.000		
	Volume		0.45±0.104	4.80		0.000		
1979	Length	4.29	0.70±0.037	10.95	100,332	0.000	101	433
	Breadth		0.69±0.038	10.70		0.000		
	Volume		0.65±0.041	8.96		0.000		
1980	Length	4.60	0.72±0.025	13.02	197,713	0.000	198	911
	Breadth		0.67±0.028	10.40		0.000		
	Volume		0.69±0.027	11.04		0.000		
1981	Length	4.43	0.70±0.027	11.40	186,643	0.000	187	830
	Breadth		0.67±0.029	10.14		0.000		
	Volume		0.65±0.030	9.07		0.000		
1994	Length	4.82	0.77±0.060	17.10	23,92	0.000	24	116
First	Breadth		0.82±0.052	22.10		0.000		
clutch	Volume		0.81±0.053	21.64		0.000		
1994	Length	4.31	0.60±0.086	7.51	27,93	0.000	28	121
Late	Breadth		0.85±0.040	26.24		0.000		
clu.	Volume		0.78±0.056	16.44		0.000		
1995	Length	4.73	0.77±0.063	17.31	22,86	0.000	23	109
First	Breadth		0.75±0.068	14.92		0.000		
clutch	Volume		0.73±0.073	13.53		0.000		
1995	Length	4.36	0.77±0.073	15.13	18,63	0.000	19	82
Late	Breadth		0.85±0.050	26.12		0.000		
clu.	Volume		0.83±0.056	22.61		0.000		

ded for individual identification. Analyses of the repeatability of egg measurements within a clutch were based on one randomly-chosen clutch per female, and a separate ANOVA was carried out for each year or period within season. Variance components and repeatabilities (intraclass correlation coefficients) were calculated for all egg traits (Sokal & Rohlf, 1981; Lessells & Boag, 1987), and standard errors estimated following Becker (1984).

Repeatabilities were also calculated on the mean egg measurement per clutch for particular females with more than one measured clutch per year (1980 and 1994-1995) or in different years (1978-1981 and 1994-1995). Variance components, intraclass correlation coefficients and their standard errors were calculated as above.

Individual egg measurements of females laying more than one clutch were also subjected to a nested ANOVA in which variance components were calculated among females, among years within females, among clutches within females, and within clutches. The within-female mean squares and degrees of freedom were approximated using Satterthwaite's method as described by Sokal & Rohlf (1981). These corrected mean squares were used as denominators while testing among-female mean squares. Standard errors of repeatabilities in this nested design were estimated by approximate methods following Becker (1984).

Similar procedures were applied for males. We only included males who were mated to different females, and this happened more often between years than within a single year. Because of a low divorce rate within a year, only variation between years was partitioned into components.

RESULTS

All repeatabilities assessed for females in all clutch/year combinations were significant (Tables 1-4). The highest values were reached by within-clutch repeatabilities (Table 1), ranging from 0.60 up to 0.85, except in 1978 when relatively low values, 0.45-0.60, were found. Also clutch mean lengths, breadths and volumes of eggs of particular females were remarkably consistent both between clutches and between years, with repeatabilities of ca. 0.7 (Table 2). Thus, the special environmental variance constituted 15-40% of intraclutch variation in the length, breadth and volume of eggs and *ca.* 30% of variation in average values of these traits analysed within females over various intervals.

About 65% of variation in egg dimensions can be attributed to differences among females within years (Table 3). Differences among clutches within females account for much less variation, 11-13%. Although significant, these

TABLE 2

Repeatabilities (*R*) of average egg length, breadth and volume among clutches within females and years (1980 and 1994-1995 together) and among years within females (1978-1981 and 1994-1995). One-way ANOVAs were conducted on clutch means to estimate variance components. n_0: the corrected mean number of clutch means *per* female.
*[Repetibilidades (*R*) de la longitud (length), anchura (breadth) y volumen (volume) medios de los huevos en las puestas de las mismas hembras, entre puestas del mismo año (1980 y 1994-1995 agrupados) y entre años para la misma hembra (1978-1981 y 1994-1995). Se realizaron ANOVAs de clasificación simple sobre las medias para cada puesta para estimar los componentes de variación. n_0: número medio corregido de medias de puesta por hembra.]*

Level *[Nivel]*	Trait *[Rasgo]*	n_0	*R*±SE	*F*	df	*P*
Among clutches *[Entre puestas]*	Length	2.07	0.62±0.093	4.33	42,46	0.000
	Breadth		0.77±0.061	7.97		0.000
	Volume		0.71±0.074	6.13		0.000
Among years *[Entre años]*	Length	2.03	0.73±0.076	6.55	36,38	0.000
	Breadth		0.71±0.080	6.10		0.000
	Volume		0.62±0.101	4.26		0.000

TABLE 3

Repeatabilities of egg length, breadth and volume among broods within breeding seasons (1980 and 1994-1995). Nested ANOVA with different clutches within season nested in females was conducted to estimate among-female and among-clutches-within-female variance components. These components, expressed as proportions of the sum of all components, are repeatabilities (intraclass correlations) shown in this table, R_F and $R_{C\in F}$, respectively. Within-female-among-clutch mean square and degrees of freedom were approximated using Satterthwaite's method; corrected F-test values, F', and degrees of freedom, df', are given.
[Repetibilidades de la longitud (length), anchura (breadth) y volumen (volume) de los huevos entre puestas dentro de la misma época de cría (1980 y 1994-1995). Los componentes de varianza entre hembras y entre puestas de la misma hembra se calcularon mediante un ANOVA con las diferentes puestas de una misma época de cría encajadas en el factor hembras. Estos componentes de varianza, expresados como proporciones sobre la suma de todos los componentes, son las repetibilidades (correlaciones intraclase) que se muestran en la tabla (R_F: repetibilidad entre hembras; $R_{C\in F}$: repetibilidad entre puestas dentro de hembras). Las sumas de cuadrados medias y los grados de libertad para el componente entre puestas dentro de hembras se aproximaron mediante el método de Satterthwaite. Se dan los valores de F y de los grados de libertad corregidos (F' y df', respectivamente).]

Trait *[Rasgo]*	R_F±SE	F'	df'	P	$R_{C\in F}$±SE	F	df	P
Length	0.66±0.063	9.27	42,45	0.000	0.11±0.039	3.27	46,315	0.000
Breadth	0.65±0.063	8.19		0.000	0.14±0.041	3.70		0.000
Volume	0.62±0.062	7.29		0.000	0.15±0.043	3.81		0.000

components are small, which supports the idea of high within-season consistency of females with respect to their egg traits.

Females are also significantly consistent in their egg dimensions when the interyear aspect is considered, with interfemale variance component ranging from 50 to 61% (Table 4). The among-year-within-female variance component (17-25%) is higher than the corresponding values in the within-year analysis. This suggests that overall environmental conditions influencing females vary between years and this variation causes females to produce slightly different-sized eggs in different years (clutches).

TABLE 4

Repeatabilities of egg length, breadth and volume among years (1978-1981 and 1994-1995). Nested ANOVA with clutches in different breeding seasons nested in females was conducted to estimate among-female and among-year-within-female variance components. These components, expressed as proportions of the sum of all components, are repeatabilities (intraclass correlations) shown in this table, R_F and $R_{Y\in F}$, respectively. Within-female-among-year mean square and degrees of freedom were approximated using Satterthwaite's method; corrected F-test values, F', and degrees of freedom, df', are given.
[Repetibilidades de la longitud (length), anchura (breadth) y volumen (volume) entre años (1978-1981 y 1994-1995). Los componentes de varianza entre hembras y entre años dentro de hembras se calcularon mediante un ANOVA con las puestas de años diferentes encajadas en el factor hembras. Estos componentes de varianza, expresados como proporciones sobre la suma de todos los componentes, son las repetibilidades (correlaciones intraclase) que se muestran en la tabla (R_F: repetibilidad entre hembras; $R_{Y\in F}$: repetibilidad entre años dentro de hembras). Las sumas de cuadrados medias y los grados de libertad para el componente entre años dentro de hembras se aproximaron mediante el método de Satterthwaite. Se dan los valores de F y de los grados de libertad corregidos (F' y df', respectivamente).]

Trait *[Rasgo]*	R_F±SE	F'	df'	P	$R_{Y\in F}$±SE	F	df	P
Length	0.61±0.067	6.22	36,38	0.000	0.19±0.051	5.19	38,278	0.000
Breadth	0.59±0.066	6.32		0.000	0.17±0.049	4.22		0.000
Volume	0.50±0.066	4.26		0.000	0.25±0.315	5.73		0.000

TABLE 5

Within male repeatabilities (*R*) of average egg length, breadth and volume among years. Only males paired with different females (1978-1981 and 1994-1995) were included. A one-way ANOVA was conducted on clutch means to estimate variance components. n_0: corrected mean number of clutch means *per* male.
[Repetibilidades (R) *de la longitud (length), anchura (breadth) y volumen (volume) entre años para puestas de hembras apareadas con el mismo macho. Sólo se incluyen puestas en las que participaron machos que se aparearon con hembras diferentes en los periodos 1978-1981 y 1994-1995. Se realizó un ANOVA de clasificación simple sobre las medias para cada puesta para estimar los componentes de variación.* n_0*: número medio corregido de medias de puesta por macho.]*

Trait *[Rasgo]*	n_0	*R*±SE	*F*	df	*P*
Length	2.07	0.53±0.192	3.31	13,28	0.015
Breadth		0.16±0.255	1.40		0.265
Volume		0.49±0.200	2.98		0.023

The analysis of repeatability of egg sizes among clutches fathered by particular males paired to different females on different breeding occasions shows a different pattern (Table 5). When the clutch average values are considered, the repeatability of egg breadth turned out to be non-significant and the repeatability of length and volume were relatively low, *ca.* 0.5. Hierarchical partitioning of variance into components showed that variation among males explained from 15% (insignificant value) to 39% of variation in egg dimensions (Table 6). The among-year-within-male components proved high when compared with the corresponding values for females and they brought about from 25% of variance in egg lengths to 69% in egg breadths (Table 6). So the relation between the two variance components is completely opposite to that in females (Table 4). In general, this means a low consistency of males with regard to the traits of eggs they fathered.

TABLE 6

Repeatabilities of egg length, breadth and volume within males among years (1978-1981 and 1994-1995). A nested ANOVA with clutches laid by different females paired with a given male in different breeding seasons nested in males was conducted to estimate among-male and among-year-within-male variance components. These components, expressed as proportions of the sum of all components, are repeatabilities (intraclass correlations) shown in this table, R_M and $R_{Y\subset M}$, respectively. Among-year-within-male mean squares and degrees of freedom were approximated using Satterthwaite's method; corrected F-test values, F', and degrees of freedom, df', are given.
[Repetibilidades de la longitud (length), anchura (breadth) y volumen (volume) entre años (1978-1981 y 1994-1995) para puestas de hembras apareadas con el mismo macho. Los componentes de varianza entre machos y entre años dentro de machos se calcularon mediante un ANOVA con las puestas de hembras diferentes emparejadas con un macho concreto en años diferentes encajadas en el factor machos. Estos componentes de varianza, expresados como proporciones sobre la suma de todos los componentes, son las repetibilidades (correlaciones intraclase) que se muestran en la tabla (R_M*: repetibilidad entre machos;* $R_{Y\subset M}$*: repetibilidad entre años dentro de machos). Las sumas de cuadrados medias y los grados de libertad para el componente entre años dentro de hembras se aproximaron mediante el método de Satterthwaite. Se dan los valores de F y de los grados de libertad corregidos (F' y df', respectivamente).]*

Trait *[Rasgo]*	R_M±SE	F'	df'	*P*	$R_{Y\subset M}$±SE	*F*	df	*P*
Length	0.32±0.096	2.85	13,15	0.030	0.25±0.097	3.51	15,100	0.000
Breadth	0.15±0.108	1.48		0.245	0.69±0.138	19.00		0.000
Volume	0.39±0.106	2.96		0.025	0.37±0.106	7.58		0.000

Discussion

The major findings of this study were:

1. Female Swallows were highly consistent in the length, breadth and volume of eggs produced over shorter and longer time intervals. The corresponding consistency of males with respect to traits of eggs they fathered was clearly lower.
2. The special environmental variance of the egg traits constituted 15 to 40%.
3. There was a striking difference between females and males with respect to the relation between the among-individual and among-breeding-event-within-individual components of variance (but see below).

The special environmental variance is the component of total phenotypic variance that constitutes a synthetic measure of variable environmental factors which modify phenotypic traits on different spatio-temporal scales (Falconer, 1989). Modifying effects of the environment in the case of insectivorous birds are presumably usually mediated by the abundance and quality of food which is often related to the weather (Nilsson & Svensson, 1993a, 1993b; Nager & Zandt, 1994; Perrins, 1996). Nilsson & Svensson (1993a, 1993b) reduced the within-clutch variance without influencing the average egg size per clutch in Blue Tits (*Parus caeruleus*) by providing their territories with additional food, which means a reduction in the special environmental variance.

When a relatively low special environmental variance concurs with a high between-individual variance component, high repeatability arises. This is the case in the Barn Swallow traits analysed in this paper. It is interesting that the factors producing special environmental variance affect the variability of eggs within the clutches more intensely than the variability of the averages for different clutches of particular females. This explains why repeatabilities of clutch averages both within and between years are especially high. The low values of within-clutch repeatability observed in 1978 probably result from the fact that we started measuring eggs very late that year, so that we were only able to do it for very late second clutches. We included the 1978 data in order to use them for interyear comparison of the eggs of particular females.

There is apparently an element of strategic decision-making in consistently producing eggs of similar, even if not identical dimensions. Indirect evidence for this results from our observation that during some periods of adverse weather conditions with low temperature and intense rainfall, females who had already started laying eggs skipped from one up to four days rather than laying smaller eggs daily (Bańbura, Bartos & Zieliński, pers. obs.). This fact contrasts with Martin's (1987) deduction that food constraints should affect egg production through a reduction in egg size rather than clutch size. We found no significant influence of the ambient temperature prevailing during the period before laying on the traits of eggs (Bańbura & Zieliński, 1995). If females were only constrained in producing eggs of particular dimensions by some characters of their oviducts (Bernardo, 1996), the constraints should mostly prevent them from laying too big eggs and not smaller than the average that would be expected during periods of bad weather.

Our hierarchical analyses with successive clutches or years nested in females corroborate the above conclusions. The within-female-among-clutch/year component of variance in length, breadth and volume of eggs is low compared to the value among years, as expected. The inference from all these facts is that the egg traits have a relatively low but not negligible level of sensitivity to environmental impacts. This is also implied by other results on birds, as differences among females are apparently a major source of variation in egg size (Kendeigh *et al.*, 1956; Kendeigh, 1975; Väisanen *et al.*, 1972; Ojanen *et al.*, 1979; van Noordwijk *et al.*, 1981; Järvinen & Väisanen, 1983; Pietiäinen *et al.*, 1986; Forbes & Ankney, 1988; Lessells *et al.*, 1989; Potti, 1993; Nol *et al.*, 1997). This fact is usually supposed to reflect genetic differences among females, as in some studies high concordance of repeatabilities and heritabilities has been found (Ojanen *et al.*, 1979; van Noordwijk *et al.*, 1981; Lessells *et al.*, 1989; but see Potti, 1993). It is only recently that repeatability of life-history traits has started to be considered as a useful index of individual quality (Sydeman & Eddy, 1995).

Natural selection operating in populations in changing environments should favour genotypes that sustain the expression of high fitness under a wide range of environmental conditions (Hoffman & Parsons, 1991). For many groups of animals and plants it has been suggested that maternal effects generating within-female variation in propagule size might represent a bet-hedging strategy in response to unpredictable environments (e.g. Capinera, 1979; Crump, 1981; McGinley *et al.*, 1987; Rossiter, 1991; Bernardo, 1996). In contrast to those organisms characterised by making an entire clutch simultaneously, birds usually produce only one egg per day. In the case of the Passerines, this is done on the basis of the daily surplus of energy and nutrients (Perrins, 1996). This means that in changing environments every egg is produced under somewhat different conditions that are characterised by a level of temporal autocorrelation. Thus in birds we can distinguish between those displaying a strategic pattern of variation within a clutch and those in which there is no such particular pattern (Clark & Wilson, 1981; Slagsvold *et al.*, 1984; Järvinen & Ylimaunu, 1986; Jover *et al.*, 1993; Viñuela, 1997). In the latter group the intra-clutch variation may be just a more or less exact response to the conditions under which different eggs are formed, the level of response being limited in the Swallow by moderate sensitivity of its egg traits. Slight nonadaptive within-clutch variations in egg size in response to environmental influences were inferred from the study on American Kestrels *Falco sparverius* by Wiebe & Bortolotti (1996).

It is unclear why different females produce eggs of different size. In addition to interfemale differences in their genetic makeup as well as genetic and non-genetic maternal components of egg size, an explanation might be that inter-female variation in egg size is caused by differences in female condition in such a way that females in good condition lay larger eggs than females in poor condition (Smith *et al.*, 1993). This implies that female condition should be consistent within and among breeding seasons and, consequently, should generate egg size consistency. It has been recently demonstrated that body condition may indeed have a significant heritable component in birds (Merilä, 1996; Potti, 1999). However, some indirect arguments against Smith *et al.*'s hypothesis can be inferred from van Noordwijk *et al.* (1981) and Potti (1993) who did not find significant repeatabilities of egg characteristics for male Great Tits and Pied Flycatchers, respectively. It is evident that egg size is determined by maternal genotype and environment rather than the zygotic genotype of offspring, although this latter, resulting from both the maternal and paternal genotypes, may influence the growth rate of embryos and, consequently, the initial size of hatchlings in oviparous animals (Weigensberg *et al.*, 1998). Thus there is no direct contribution of paternal genotype to egg size and, as a result, any egg size repeatability for males should simply reflect the respective consistency of their mates. Accordingly, to test the hypothesis that egg-size differences among females are condition-dependent, one can use repeatability estimates for the males mated to new partners rather than the males mated to the same partners in several breeding episodes. If the process of pair formation is non-random with respect to body condition and its indicators on both the female and male side (Price *et al.*, 1988; Andersson, 1994), assuming that body condition is consistent and egg size reflects female condition (Smith *et al.*, 1993), a significant level of repeatability in egg size for males should arise.

Our results on Swallows show some significant but rather low repeatability of lengths and volumes of the eggs fathered by a sample of males, which to some extent supports Smith *et al.*'s (1993) hypothesis. However, hierarchical analyses show that in contrast to the case of females, the inter-year component of variance in eggs fathered by particular males is as high as or even higher than the inter-male component. This results from the fact that the inter-year component includes both the variation among years itself and the very large variation among females. All this suggests that the relationships in question may be more complex and needs further exploration by properly designed experiments.

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