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Egg weight variation in Collared Flycatchers *Ficedula albicollis*

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Inter- and intra-clutch egg size variation in Collared Flycatchers (*Ficedula albicollis*) were studied during 1994–1995 on the Baltic Sea island of Gotland (Sweden). The main question was whether Collared Flycatchers increased egg size in laying order and employed a brood survival strategy, or decreased egg size and employed a brood reduction strategy. The relationship between egg weight and clutch size, and between egg weight and female and male characteristics was also investigated. In 1994 the study was performed in two distinct periods, but only in one period in 1995. Nest boxes were inspected daily during nest construction and during egg laying, and eggs were weighed the day of laying. Basic breeding data were collected and measurements of adults and young were taken. In general, egg weight increased versus laying order and in 1994 the increase was significant only among late breeders. Mean egg weight positively correlated with female body size (both years) and negatively with male body size (1994 only). Eggs in clutches of 6 were heavier than those from clutches of 7 in 1995 but not in 1994. This indicates a trade-off between egg size and egg number. It is concluded that the Collared Flycatcher possibly employs a brood survival strategy to prevent competition between nestlings.

1. Introduction

The question of how an organism allocates resources to diverse traits is becoming a central issue in life history analyses. Among those traits the most frequently investigated in birds has been clutch size (e.g. Stearns 1992). However, a female laying an optimal number of eggs may distribute the available resources unequally between eggs within the clutch. Within-clutch variation in egg size may be explained in adaptive or non-adaptive terms. There is evidence for the adaptive value of some patterns connected with the laying sequence in some species (e.g. Howe 1976) and that laying sequence might be affected by proximate constraints in the other species (Slagsvold & Lifjeld 1989).

Clark and Wilson (1981) argued that an increase in egg size versus the laying order may be an adaptation enhancing the competitive ability and survival probability of the last hatched nestlings. Slagsvold et al. (1984) discussed the possible importance of the variation in size of the final egg for the growth and survival of the last hatched nestling. They argued that birds laying a relatively small last egg were adopting a "brood reduction" strategy according to which the nestling hatched from the last egg might be sacrificed in case of strong competition between nestlings under poor feeding conditions, while those laying a relatively large last egg were using a "brood survival" strategy in which the last hatched nestling was able to compete with those hatched earlier. Thus, different patterns of allocation among eggs in the clutch can be observed in different species. Laying females are believed to be limited by the availability of energy for egg production, and some species seem to rely on current foraging to cover the demands for producing eggs (e.g. Perrins 1970, Ojanen 1983b). Since the daily costs of egg production in passerines is estimated to be at least 40% the basal metabolic rate, egg laying evidently places an energetic strain on the female (Ricklefs 1974, Walsberg 1983).

This paper presents the data on inter- and intraclutch egg size variation in the Collared Flycatcher (*Ficedula albicollis*). To find out whether the Collared Flycatcher employs a "brood reduction" strategy or "brood survival" strategy, changes in egg weight versus laying order were studied. The question of whether females laying larger clutches produce smaller eggs and whether egg size is related to female or male characteristics was also addressed.

2. Material and Methods

The study was conducted on Collared Flycatchers living on the island of Gotland, Sweden in 1994 and 1995 (for details about the study area see Gustafsson 1989). The Collared Flycacher is a small (13 g) migratory passerine bird species breeding mainly in eastern and central Europe and wintering in southern and central Africa. It nests in natural tree cavities, but prefers nest boxes when provided. On Gotland, breeding starts around May 20 and the latest females lay their eggs around June 15. Females usually lay 5–8 eggs which hatch after two weeks of incubation, and the young fledge two weeks later. The Collared Flycatcher feeds mainly on insects.

The study area was established in 1980 and since then flycatchers have been continuously studied there. In the present study, nest boxes were inspected every five days to look for new nests under construction. New nests were visited daily to record laying of the first egg. The following eggs in the clutch were marked and weighed the day of laying. Eggs were weighed with a 5-g spring balance to the nearest 0.01 g. Females were captured on the seventh day of incubation, and the males were caught while feeding the young. Tarsus length and wing length were measured, and weight was taken following a standard protocol (Gustafsson 1989).

The residuals from a linear regression of body weight on tarsus length were used as an index of body condition. Residuals were preferred over body weight data as their use partly corrected for individual differences in structural size.

Laying gaps were detected in some nests and some nests were deserted before the female started incubating the eggs; both were excluded from the analysis. In 1994, data were recorded in two separate periods of the breeding season. Broods initiated between 10th May and 14th May 1994 (n = 19) were regarded as early broods, and those initiated between 25th May and 30th May (n = 18) as late broods. In 1995, data were collected from broods started from 22nd May to 30th May (n = 28). The spring of 1994 was early and the first clutches were initiated around 8th May, while in 1995 the first clutches were recorded around 20th May. Collared Flycatcher females laid 5 to 8 eggs in the clutch, but occasionally clutches of 4 and 9 were found. Most of the clutches consisted of 6–7 eggs and clutches of 5 eggs were represented only in 1994, so only clutches of 6–7 were considered in the analysis in 1995 and clutches of 5–7 in 1994.

3. Results

In most cases egg weight increased with laying order (Fig. 1, Table 1). This was true for both study seasons, but in 1994, when the data were collected in two distinct periods, a significant increase in egg weight was observed only among late breeders laying 6 or 7 eggs, but not among those laying 5 eggs. Clutches of 5 were represented only late in 1994. Two-way ANOVA accounting for the effect of clutch size did not reveal a significant

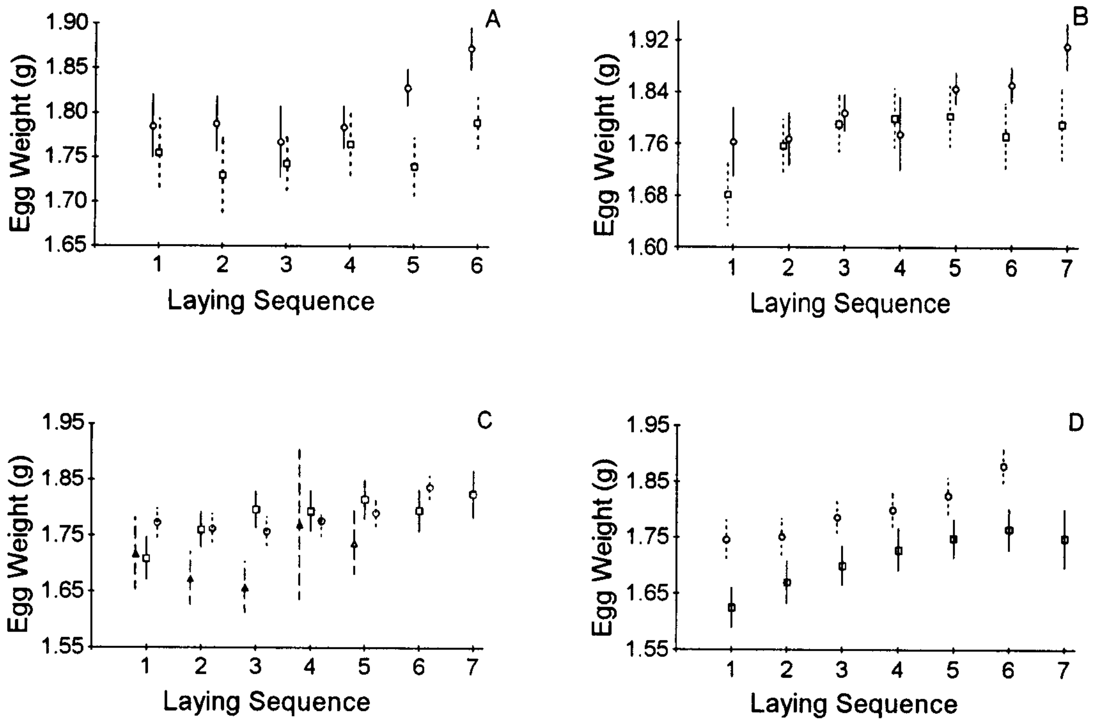

Fig. 1. Egg weight versus laying sequence, laying period and clutch size. Values represent the mean ± SE. A) Early (dotted line) and late (solid line) clutches of 6 in 1994, B) early and late clutches of 7 in 1994, C) all broods in 1994 (centered line clutches of 5, dotted line clutches of 6 and solid line clutches of 7) and D) all broods in 1995.

effect of laying order on egg weight in 1994 ($F_{6,197} = 1.49$, $P > 0.05$), but a significant effect was seen for 1995 ($F_{6,155} = 2.18$, $P < 0.05$). The Tukey post hoc test indicated the effect of differences between the first and sixth egg, and between the second and sixth egg in the laying sequence in 1995 (see Fig. 1D).

Mean egg weight was positively correlated with female weight during incubation (both years) and with residuals of body weight on tarsus length (only in 1994; Table 2). In males, tarsus length and residuals of body weight on tarsus length were negatively correlated with mean egg weight, but only in 1994. Female age did not affect mean egg weight in either study year (one-way ANOVA; 1994: $F_{2,15} = 1.19$, $P > 0.05$, 1995: $F_{2,14} = 0.68$, $P > 0.05$).

There was no significant correlation between mean egg weight and laying date besides a negative one among early broods in 1994 (Spearman

Table 1. Laying order versus egg weight for different clutch sizes (Spearman rank correlations, ns = P > 0.05).

Clutch size	1994 Early			1994 Late			1994 Total			1995 All		
	r	N	P	r	N	P	r	N	P	r	N	P
5	–	–	–	0.11	25	ns	0.11	25	ns	–	–	–
6	0.16	36	ns	0.33	48	< 0.020	0.23	84	< 0.030	0.26	126	< 0.003
7	0.11	91	ns	0.58	35	< 0.001	0.19	126	< 0.030	0.47	42	< 0.002
Combined	0.10	127	ns	0.39	108	< 0.001	0.21	235	< 0.001	0.23	168	< 0.002

rank correlation; $r_s = -0.61$, N = 19, P = 0.005). Eggs in the clutches of 6 were lighter early in the season in 1994 when the study covered two periods (two-way ANOVA; $F_{1,72} = 7.36$, P > 0.008), but not for clutches of 7 (two-way ANOVA; $F_{1,112} = 2.37$, P > 0.05).

Clutches of 6 and 7 eggs did not differ significantly in egg weight in 1994 (two-way ANOVA; $F_{1,197} = 0.01$, P > 0.05), while the eggs in clutches of 6 were heavier in 1995 (two-way ANOVA; $F_{1,155} = 12.99$, P < 0.001), when laying order was also taken into account.

4. Discussion

Egg size within clutches has been found to vary greatly. Different patterns of egg size variation versus laying sequence have been observed, with egg size increasing (e.g. Howe 1976, Ojanen et al. 1981, Slagsvold et al. 1984), decreasing (e.g. Lack 1968, Rofstad & Sandvik 1985) or unrelated (e.g. Bryant 1975, Ojanen et al. 1981). In this study, egg size increased versus laying sequence in the Collared Flycatcher. In 1994, when the study was done in two separate periods, the relationship was significant only for late clutches, but was also significant when both periods were pooled. This may have been an effect of generally poorer weather early in the season. Clutches of 6 were lighter early in the season. Egg size increased versus laying sequence except for clutches of 5 observed late in 1994 (Fig. 1, Table 1). A similar increase in egg size versus laying order was reported for the closely related Pied Flycatcher (*Ficedula hypoleuca*, Ojanen et al. 1981, Hillström 1992).

A number of studies have shown that egg size has a positive effect on hatching success, subsequent nestling survival, and the growth and weight of fledglings (e.g. Parson 1970, Jones 1973, Murton et al. 1974, Howe 1976, Järvinen & Ylimaunu 1984). Potti and Merino (1994) suggested that the existence of a maternal effect can be mediated via egg size in Pied Flycatchers: chicks were larger when hatched from large eggs. The effect was found to persist into adulthood and to confound the heritability estimations. However, there is a possibility that the relationship between egg size and offspring size is mediated by the quality of the parents that lay larger eggs. Parents in better condition might care better for their nestlings. Nevertheless, intra-clutch egg weight variation can be regarded as adaptive. Because females can start incubation before clutch completion, asynchronous hatchings could produce a size hierarchy of nestlings and lead to strong competition between them. Thus, females might increase the size of successive eggs to prevent the competition (Wiggins 1990). According to the adaptive view of intra-clutch egg size variation, the Collared Flycatcher should be associated with the so-called brood survival strategy (Slagsvold et al. 1984), in which a female laying larger eggs at the end of laying increases the survival probability of the nestlings hatched from the last-laid eggs. The fact that in 1994 a significant increase in egg weight with the laying order was observed only among late broods may confirm this hypothesis, since females initiating broods late are more likely to start incubation before clutch completion (Cichoń, unpublished data), which might generate asynchronous hatchings and a nestling size hierarchy. On the other hand, some proximate factors such as energetic or nutritional constraints at the stage of egg formation may account for the observed pattern. Such an explanation was proposed by Slagsvold and Lifjeld (1989) for the Pied Flycatcher's increasing egg size versus the laying sequence. Ojanen (1983a) argued that the Pied Flycatcher

Table 2. Mean egg weight versus female and male characteristics (Spearman rank correlations, ns = P > 0.05).

	1994						1995					
	Female			Male			Female			Male		
	r	N	P	r	N	P	r	N	P	r	N	P
Weight	0.50	28	< 0.006	0.07	23	ns	0.57	22	< 0.006	0.20	27	ns
Tarsus	0.01	29	ns	– 0.44	23	< 0.04	0.27	28	ns	0.13	27	ns
Wing	– 0.11	29	ns	– 0.31	23	ns	0.05	28	ns	– 0.05	27	ns
Resid.	0.54	28	< 0.003	– 0.48	23	< 0.02	0.20	22	ns	– 0.04	27	ns

can be classified as an "income breeder", which means that it relies mainly on foraging to cover the protein demands for its eggs, and because it has several eggs simultaneously developing, the highest maximum investment rate occurs only during the first two days of the laying period. Moreover, he found that the increase in egg size was due to inclusion of water, not nutrients (Ojanen 1983b).

Egg size is usually highly repeatable among clutches of the same female and it might be an effect of female body size (Boarg & Van Nordwijk 1987). A positive correlation between mean egg size and female weight has been reported by several authors (e.g. Jones 1973, Ojanen et al. 1979, Järvinen & Väisänen 1983, Nager & Zandt 1994, the present study). This study shows that egg weight may also be related to male body size. The negative correlation between egg size and tarsus length suggests that larger males tended to mate with females laying small eggs. However, this was true for only one study year (1994). Since clutch size and time of breeding in the Collared Flycatcher is known to be influenced by female age (Gustafsson & Pärt 1991), a similar effect of the female age on egg size should be expected. However, it was not the case in the present study or in the previous studies on egg size variation (e.g., Ojanen et al. 1979, Järvinen & Pryl 1989, Wiggins 1990, Nager & Zandt 1994). High repeatability of egg size among clutches of the same females (Boarg & Van Noordwijk 1987) also suggests a lack of age effect on egg size.

In a recent paper, Dufva (1996) showed that Great Tit females infected with the blood parasite *Trypanosoma* laid smaller eggs and raised fewer nestlings in a generally worse body condition. Moreover, females with low body weight and short tarsi laid smaller eggs, independent of parasite status. Most of the females considered in the present study were tested for blood parasites as well as for leukocyte contents of the blood and hematocrit (D. Nordling, unpublished data). In contrast to the Great Tit (Dufva 1996), Collared Flycatcher females infected with *Trypanosoma* tended to lay bigger eggs, though the difference was non-significant. *Hemoproteus sp.*, another blood parasite found in the blood of the studied females, did not significantly affect egg size either. Moreover, there was no evidence that females of better condition measured by blood parameters laid heavier eggs: there was no relationship between the leukocyte content of the female's blood and mean egg weight nor between hematocrits and mean egg weight.

This study indicates that the female may partition the available resources between many small eggs or a few larger eggs. However, ANOVA revealed significant differences between clutches of 6 and 7 only in 1995. The trade-off between egg size and egg number probably depended on environmental conditions. If resources or the time needed to gather them are not restricted, we might observe no relationship or even a positive one (Van Nordwijk & De Jong 1986). For example, in Finnish studies of Pied Flycatchers, egg size correlated negatively with clutch size in the south and was positive in the north (Järvinen & Väisänen 1983). Wiggins (1990) found a non-linear relationship in which the intermediate clutch size was associated with the largest eggs.

The effect of laying date on egg weight variation is not clear. The relationship was negative and significant only among early broods in 1994. Moreover, among the clutches of 6 in 1994, heavier eggs were laid later in the season. Hillström (1992) and Nager and Zandt (1994) did not find any correlation between egg size and laying date.

In conclusion, the present study suggests that the Collared Flycatcher possibly employs a strategy of increasing egg size in laying order, which may reduce size hierarchy between nestling and may prevent competition between them. It seems also that the female restricted by the amount of available resources is able to decide whether to lay many small eggs or a few larger eggs.

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Selostus: **Munien painon vaihtelu sepelsiepolla**

Kirjoittaja tutki sepelsieppopesyeiden sisäistä ja välistä munan painon vaihtelua Gotlannissa pöntöissä pesivässä populaatiossa. Tutkimuksen lähtökohtana oli selvittää, painoivatko myöhemmmin munitut munat enemmän vai vähemmän kuin aikaisemmin munitut. Jos munan paino nousee munimisjärjestyksen myötä, munan painon vaihtelu olisi selitettävissä pesyeen selvitymisstrategian (brood survival strategy) kautta: myöhemmin munituista munista (mahd. myöhemmin) kuoriutuvilla poikasilla olisi vähintään yhtä suuri todennäköisyys selviytyä lentokykyiseksi kuin aikaisemmin munituilla. Jos taas munan paino laskee munimisjärjestyksen myötä, myöhemmin munituista munista kuoriutuneet poikaset kuolevat todennäköisemmin pesyeen sisäisen kilpailun takia, ja munan painon vaihtelu olisi tässä tapauksessa selitettävissä pesyeen pienentämisstrategian (brood reduction strategy) avulla. Kirjoittaja tutki myös, miten sepelsiepponaaraan ja -koiraan ominaisuudet olivat yhteydessä munien painoon. Vuonna 1994 aineistossa verrattiin aikaisin aloitettuja (muninta aloitettu 10.–14. toukokuuta) ja myöhään aloitettuja (muninta aloitettu 22.–30. toukokuuta) pesyeitä, mutta myöhäisenä keväänä 1995 kaikki tutkimuksessa mukana olleet pesyeet oli aloitettu 20. toukokuuta jälkeen.

Sepelsieppopesyeissä munan paino tavallisimmin nousi munintajärjestyksen myötä (Kuva 1, Taulukko 1). Keväällä 1994 nousu havaittiin vain myöhäisissä pesyeissä. Kirjoittaja päättelee, että munan painon nousu munimisjärjestyksen myötä kielii mahdollisuudesta, että sepelsieppo panostaa viimeisiin muniin voimakkaammin turvatakseen koko pesyeen selviytymisen lentokykyiseksi. Pesyeen keskimääräinen munan paino korreloi positiivisesti naaraan painon kanssa molempina vuosina ja negatiivisesti koiraan painon kanssa keväällä 1994 (Taulukko 2). Keskimääräinen munan paino oli korkeampi 6 munan pesyeissä kuin 7 munan pesyeissä keväällä 1995 ilmentäen munan painon ja pesyekoon välistä käänteistä suhdetta sepelsiepolla.

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