Korean J. Ecol., 25(4): 241~245, 2002

Some Aspects of Laying, Incubation and Hatching in the Great Reed-Warbler

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ABSTRACT : During the breeding season of 1998, breeding ecology of the Great Reed-Warbler (*Acrocephalus arundinaceus orientalis*) was studied at Yangsoo-ri and Yongdam-ri of the Yangpyung-gun, Kyunggi province, Korea. Egg-weight (CV: 6.25) was more variable than either length or breadth, and breadth was the least variable of the measures. Significant variations in overall egg-weight occurred between clutches, and that more of the total variation in egg-weight and shape are due to inter-clutch variation as to intra-clutch variation when the data were pooled. The last egg tends to be larger than the remaining eggs in the clutch of the Great Reed-Warbler, suggesting the Great Reed-Warbler may adopt the brood-survival strategy. When method 3 was used, the most common incubation period is 12 days. In the Great Reed-Warbler, the length of the incubation period was related to clutch-size when method 1 ($r=0.485$, $p<0.05$) and method 2 ($r=0.621$, $p<0.01$) were employed, but not related to egg weight. The averagee number of days of hatching asynchrony was 2.5, raging 0.5 ~ 2.5. Asynchronous hatching was related to the clutch size ($r=0.66$, $p<0.01$). Hatching sequence was closely related to the laying sequence ($r=0.93$, $p<0.001$), suggesting Great Reed-Warblers incubate their eggs before clutch completion. The effect of egg weight on hatching asynchrony was found in Great Reed-Warblers (t-test, $p<0.01$).

Key words: Breeding, Great Reed-Warbler, Hatching asynchrony, Incubation, Laying

INTRODUCTION

The ecological significance of laying, incubation and hatching pattern in relation to the breeding strategy have received attention from many ornithologists (Barth 1955, Drent 1970, Howe 1976, Baltz and Thompson 1988, Forbes and Ankney 1988, Magrath 1990, Yoo 1993).

Egg-size increases with laying sequence in many species of passerine bird (Howe 1978, Pinkowsk 1975). Ojanen et al. (1981) reported that the effect of the laying sequence was significant for egg breadth and volume in the largest clutches (6-8 egg) of Pied Flycatcher (*Ficedula hypoleuca*), but not in the smallest clutches (4-5 egg). The patterns of such egg-size variation may reflect physiological constraint on the laying female.

Altricial birds have relatively shorter incubation periods than precocial ones; birds whose young are completely independent of parental care after hatching lay relatively larger eggs, but the size factor adds time to the incubation period. Some birds start incubating gradually during egg laying, depending on the fianl clutch-size, and hatching occurs asynchronously over 1-2 days (Snow 1958). The onset of incubation seems to be related to clutch-size in some species.

Hatching asynchrony occurs in many altricial birds and many hypotheses have been proposed explain it (Lack 1954, Howe 1976, Skagen 1988, Slagsvold and Lifjeld 1989, Magrath 1990). Lack' s hypothesis(1954, 1968), proposing that asynchronous hatching in altricial birds is usually an adaptive response to potential unpredictable food shortage, has been tested and supported by many authors. Pijanowsk (1992) presented a model which predicts that generally, hatching asynchrony is favoured over synchronous hatching when good food years are not very frequent, when the survival rate of last-hatched nestlings during good food years is high, when the survival rate of nestlings raised in synchronously hatched broods high, when the survival rate of nestling raised in synchronously hatched broods during bad years is low, or when bad food years are nor severe.

The patterns of laying, incubation and hatching in the Great Reed-Warbler have not been studied yet in detail. In this study we investigate the ecological significance of laying, incubation and hatching patterns.

METHODS

The data for egg weight for Great Reed-Warblers were collected at Yangsoo-ri and Yongdam-ri of the Yangpyung-gun, Kyunggi province, Korea during the breeding season of 1998.

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Each egg was weighed with a 5 gram 'Pesola' spring-balance (accuracy 0.05 g) and measured with a 'Mitutoyo' digimatic calliper (accuracy 0.01 mm). In order to know the laying sequence in a clutch, each egg was marked with a water-proof felt tip pen on the day it was laid. Nests were visited daily to record the laying sequence and the onset of incubation and hatching asynchrony.

In some Great Reed-Warblers, incubation was started before clutch completion, usually started on the day that the first egg was laid. Therefore, in this study we used three different methods to assess the duration of the incubation period: (1) from the laying of the first egg to the hatching of the first chick (2) from the laying of the last egg to the hatching of the last chick (3) from the laying the last egg to hatching of the first chick.

The hatching asynchrony data were collected, following the method used by Bryant(1978). Visits were made at 24 hour intervals to standardize the interval between two visits until all the eggs had hatched. The daily routine inspection of nests prevented the precise determination of the spread of hatching. For the purpose of analysis chicks which hatched entirely between visits(possible rang 0-24 hours) are called 'synchronous hatchlings'. If only some of the eggs had hatched on one visit and the others had hatched by the next visit, then the chicks are called 'asynchronous hatchling'. For example, clutches in which hatchling was spread over two visits or three visits, for which the limits are about one to almost 48h, just over 24h to almost 72h, respectively. For calculations, the hatching spread of each clutch was taken to be the probable intermediate value: respectively 0.5, 1.5, 2.5 and so on.

The statistical analyses for egg weight and characteristics were based on clutch means because individual eggs in a clutch are not independent. For the analyses of intra-clutch variation of egg weight, therefore, change in egg-weight was expressed as a residual (deviation) from clutch mean: for instance,

Residual egg-weight (g) = egg (weight) - clutch mean (weight).

RESULTS

Variability of egg size and shape

Average of egg characteristics and egg shape index, which were obtained from 19 clutches, are presented in Table 1. Egg-weight (CV: 6.25) was more variable than either length or breadth, and breadth was the least variable of the measures.

In Great Reed-Warblers, the weight of the egg is closely related to its length, but even more so to its breadth (Table 2). However, there is no relation between the shape of an egg and its weight. Therefore egg shape is independent of the egg-weight in the Great Reed-Warbler.

The present study from 19 clutches of Great Reed-Warblers shows that there is no relationship between clutch-size and egg-size: neither egg length (r= -0.015, n.s.) nor egg breadth (r=-0.071, n.s.).

Table 1. Egg-size and shape in 19 clutches of the Great Reed Warbler

	Mean	SD	Range	CV
Length (mm)	21.56	0.72	19.83~22.85	3.34
Breadth (mm)	15.63	0.40	14.59~16.20	2.53
Weight (g)	2.88	0.18	2.35~ 3.07	6.25
Shape (100xEB/EL)	72.56	2.18	68.83~76.02	3.01

Note: The calculations are based on clutch means.; SD(Standard Deviation); CV(Coefficient of Variance).

Table 2. Correlation between egg weight and dimensions

	Correlation (r)	*p* value
Length (mm)	0.77	<0.001
Breadth (mm)	0.93	<0.001
Weight (g)	- 0.07	n.s.

Variation in egg-weight within and between clutches

The primary concern of this section is to detect true differences in egg-weight variation between clutches. As a following question, however, we also examine what percentage of total variation in egg-size can be explained by variation within and between clutches.

The clutch-sizes used in this study were 15 clutches of 5 eggs (78.9%) and 4 clutches of 6 eggs (21.1%).

The coefficients of intraclass correlation (r_1) from One-way ANOVAs showed that significant variations in overall egg-weight occurred between clutches, and that more of the total variation in egg-weight and shape were due to inter-clutch variation as to intra-clutch variation when the data were pooled (Table 3). But this doesn't mean that there isn't variation within clutches. With a clutch-size of 6, relatively more variation in egg-weight occurred within clutches than between clutches, but this is likely to be due to the small sample size (only 4 nests).

We examined the size of the final eggs in relation to the mean egg-size of the clutch in order to look at whether the Great Reed-Warbler adopts brood-reduction strategy or brood-survival strategy. The last egg tends to be larger than the remaining eggs in the clutch of the Great Reed-Warbler, suggesting the Great

Table 3. Variation in egg-weight (g) within and between clutches in the Great Reed-Warbler

Clutch size	Nests (N)	Egg Mean	Weight SD	r_I	F	*p*
5	15	2.88	0.23	0.84	11.08	<0.001
6	4	2.87	0.16	0.64	4.57	<0.05
Pooled	19	2.88	0.21	0.81	9.33	<0.001

Note: r_I: the coefficient of intraclass correlation.

Table 4. Comparison of the weight and dimensions of the last egg with the remaining eggs in a clutch of the Great Reed-Warbler (19 clutches)

	The last egg		The remaining eggs(k-1)		t-test
	Mean	SD	Mean	SD	(two-tailed)
Weight(g)	0.12	0.09	-0.03	0.02	$p<0.001$
Length (mm)	0.46	0.48	-0.11	0.11	$p<0.001$
Breadth(mm)	0.17	0.19	-0.04	0.05	$p<0.001$

Note: Data were expressed as residuals (deviations) from clutch mean; t-test was carried out with weights of the last eggs and average values except last eggs from individuals clutches; k=clutch-size.

Reed-Warbler may adopt the brood-survival strategy (Table 4).

Incubation and hatching asynchrony

Between clutches, there is variation in the interval between the start of incubation and the time at which the eggs hatch, suggesting that the rhythm or intensity of incubation between females was very variable. When we look at the distribution of the duration of incubation using method 1 (which excludes prolonged days caused by asynchronous hatching), the most common incubation period was 16 days (Table 5). When method 3 (which is used generally in the field to estimate the incubation period) was used, the most common incubation period is 12 days.

The influence of egg weight, clutch-size on incubation period was examined. In the Great Reed-Warbler, the length of the incubation period was related to clutch-size when method 1 ($r=0.485$, $p<0.05$) and method 2 ($r=0.621$, $p<0.01$) were employed, but not related to egg weight (Table 6). However, when method 3, which does not consider the effect of the timing of onset of incubation, was used, the incubation period was not related to clutch size.

We examined the degree of hatching asynchrony in detail. The average number of days of hatching asynchrony is 2.5, raging 0.5~2.5 for the Great Ree-Warbler (Table 7). The most common hatching asynchrony 2.5 days (47.1%) and the next was 3.5 days (29.4%) (Fig. 1). We examined whether hatching asynchrony may be a breeding strategy in order for the tits to have their young when the caterpillars for them are most abundant, especially in ones which lay clutch later. This study shows that there is no relationship between hatching asynchrony and laying date (Table 8). Asynchronous hatching is related to the clutch

Table 5. Distribution of the duration of incubation in the Great Reed-Warbler measured by three different methods in relation to the laying and hatching

	Duration of incubation in days							Mean
	11	12	13	14	15	16	17	
Method 1	-	-	-	-	4	10	3	15.9
Method 2	-	1	6	8	2	-	-	13.6
Method 3	6	11	-	-	-	-	-	11.6

Method 1 - from the laying of the first egg to the hatching of the first chick.
Method 2 - from the laying of the last egg to the hatching of the last chick.
Method 3 - from the laying of the last egg to hatching of the first chick.

Table 6. Incubation period in relation to egg-weight and clutch-size

	Egg weight[1]	Clutch size
Method 1	-0.189	0.485*
Method 2	-0.044	0.621**
Method 3	-0.271	-0.171

Note: [1]. The calculation are based on clutch means (17 clutches).
*, $p<0.05$; **, $p<0.001$.
Method 1 - from the laying of the first egg to the hatching of the first chick.
Method 2 - from the laying of the last egg to the hatching of the last chick.
Method 3 - from the laying of the last egg to hatching of the first chick.

Table 7. Hatching asynchrony in the Great Reed Warbler (17 nests)

	Mean	SD	Range
Hatching asynchrony (days)	2.5	0.87	0.5~3.5

Note: Hatching asynchrony day 0.5 means that all chicks/eggs in a nest hatched within one day (possible range is 0-24 hours).

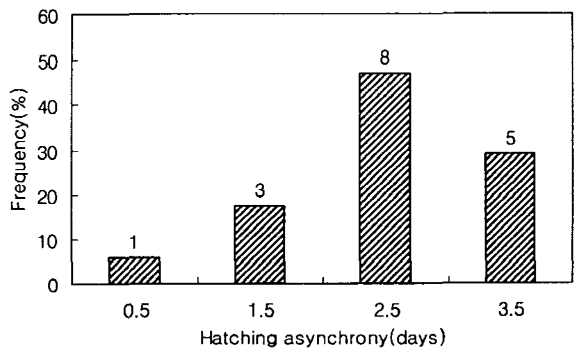

Fig. 1. The distribution of hatching asynchrony in the Great Reed Warbler (17 nests). Hatching asynchrony day 0.5 means that all chicks/eggs in a nest hatched within one day (possible range is 0-24 hours). Sample size (no. of nests) are given above each bar.

Table 8. Correlations between laying date and clutch size to hatching asynchrony in the Great Reed-Warbler (17 nests)

	Laying date	Clutch size
Hatching asynchrony (days)	0.05	0.66**

Note: **, $p<0.01$.

Table 8. Correlation between laying sequence and hatching sequence in the Great Reed-Warbler (17 nests).

	Laying sequence
Hatching asynchrony (days)	0.93***

Note: Spearman lank correlation (r_s); ***, p<0.001.

Table 10. The difference of the fresh egg weight (g) and dimensions between the eggs hatched on the first hatching day and the eggs hatched after the first hatching day in the clutches (17 clutches).

	Eggs hatched on the first hatched day		Eggs hatched after the first hatching day		t-test
	Mean	SD	Mean	SD	(two-tailed)
Weight (g)	2.80	0.12	3.02	0.17	p<0.01
Length (mm)	21.15	0.72	21.72	0.67	p=0.07
Breadth (mm)	15.57	0.39	15.93	0.37	p<0.001

Note: The calculations are based on clutch means of eggs hatched after the first hatching day in a clutch.

size (r=0.66, p<0.01).

Hatching sequence was closely related to the laying sequence (r=0.93, p<0.001), suggesting Great Reed-Warblers incubate their eggs before clutch completion (Table 9). We examined the difference in fresh weight between eggs hatched on the first day and eggs hatched on subsequent days. The effect of egg weight on hatching asynchrony was found in Great Reed-Warblers (t-test, p<0.01) (Table 10).

DISCUSSION

Slagsvold et al. (1984) suggested that birds adopting the "brood-reduction strategy" have a small final egg so that it food becomes scarce, the youngest offspring within the brood can be rapidly eliminated without too much loss of already invested parental effort, particularly those birds with large clutches, whereas birds adopting the "brood-survival strategy" have a relatively large final eggs so that the nestling hatched from such an egg will fledge successfully, particularly those birds with large clutches. In the Great Reed-Warbler, the weight of the first egg in a clutch tends to be lighter than that of subsequent eggs (p<0.001), and the last egg tends to be larger than the remaining eggs in the clutch of the Great Reed-Warbler (p<0.001). These results indicate that the Great Reed-Warbler may adopt the brood-survival strategy.

When we look at the distribution of the duration of incubation using method 2 (which excludes the effect of onset of incubation and hatching asynchrony on incubation period), there is considerable variation in the incubation period in the Great Reed-Warbler, ranging 12~15 days: the most common incubation period was 14 days.

Table 8 showed that clutch size affected hatching asynchrony in the Great Reed-Warbler. This means that females incubate eggs before clutch completion, especially in larger clutches. To clarify this, further studies are needed. In the Common Grackle, females laying small clutches start incubation after the last egg is laid and the young hatch synchronously, whereas females laying large clutches start incubation before the clutch is complete so that the young hatch asynchronously. In order to maximize their breeding success, the warblers laying large clutches may advance the hatching of their chicks by starting to incubate earlier in relation to clutch completion. Lack (1947, 1954, 1968) suggested that asynchronous hatching in altricial birds is usually an adaptation to cope with potentially unpredictable food shortage during the raising of the brood.

ACKNOWLEDGEMENTS

This study was supported by Kyung Hee University.

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(*Received May 20, 2002, Accepted July 15, 2002*)