gentina have been defined by patterns of variation in trill morphology, the terminal trill is absent at two of the three Costa Rican study sites. Handford and Lougheed (1991) report that some males recorded in Monte desert habitat in northwestern Argentina sang languid, whistled songs with no trill (or a very slow trill), yet these birds were exceptional. A more comprehensive survey of Rufous-collared Sparrows from Central America is now needed to determine whether the birds in this study were also exceptional.

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INTRACLUTCH VARIATION IN EGG VOLUME OF GREAT CRESTED GREBES[1]

KELD HENRIKSEN
Kervej 17, DK-8230 Åbyhoj, Denmark

Key words: Great Crested Grebes; Podiceps cristatus; *egg volume; hatching asynchrony.*

Grebes start incubating their eggs before the clutch is complete (Cramp and Simmons 1977). Grebe broods therefore hatch asynchronously and hatching asynchrony creates age and size hierarchies within broods. An often-cited hypothesis concerning the selection pressure to start incubation before the clutch is complete suggests that hatching asynchrony is adaptive because it facilitates a selective elimination of the younger offspring if food is short after hatching (Lack 1954). Slagsvold et al. (1984) suggested that variation in egg size within clutches is adaptive too, through its influence on hatching hierarchies (young hatching from larger eggs are heavier and survive better, at least in the short term), and used the relative size of the last-laid egg as a measure of intraclutch variation in egg size. Birds following a "brood-reduction" strategy are expected to have a relatively small final egg to accentuate the size hierarchy within the brood arising from asynchronous hatching.

Few have studied intraclutch variation in egg size of grebes. Fugle and Rothstein (1977) and Forbes and Ankney (1988) examined two and six clutches of the Pied-billed Grebe (*Podilymbus podiceps*), respectively,

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and Bäsecke (1953) measured the eggs in three clutches laid by the same female Great Crested Grebe (*Podiceps cristatus*). Measurements of eggs laid early and late in the laying sequence in clutches of Great Crested Grebes were obtained by Goc (1986).

The Great Crested Grebe usually lays clutches of three–five eggs which hatch over a period of several days (Cramp and Simmons 1977) and is inferred to possess a brood-reduction strategy (see Simmons 1970 for details). In this paper, I examine intraclutch variation in egg volume of this species in relation to clutch size and laying sequence.

MATERIALS AND METHODS

I collected data in 1993 and 1994 in eastern Jutland, Denmark, at Lake Brabrand, a shallow hypereutrophic lake with an area of 150 ha (see Henriksen 1992 for further description of the lake). Nests were searched for by boat daily from mid-April to late May and, when discovered, checked daily during the egg-laying period. Nests found with more than two eggs were excluded from analysis and laying sequence in nests with two eggs could be established by the degree of shell staining of each egg (pers. observ.; see also Goc 1986).

I obtained data from 61 clutches, of which 57 were three- or four-egg clutches. Twenty clutches were followed from the one-egg stage and nine from the two-egg stage in 1993 compared with 27 and five, respectively, in 1994. Each egg was numbered according to laying sequence with a felt-tip pen, measured with a Vernier caliper to determine length and maximum breath (L and B, ± 0.05 mm), and weighed (on the day of laying, but not on rainy or windy days, and in 1993 only) to ± 0.5 g with a 100-g Pesola spring balance. Egg volume (V; cm^3) was calculated using the equation: $V = 0.000496LB^2$ (Reynolds 1974).

In 1993, complete data on hatching asynchrony were obtained from three three-egg clutches and six four-egg clutches, each checked one to three times daily from the time of pipping of the first egg until all eggs had hatched.

Statistical tests follows procedures in Zar (1984) and results with *P*-values less than 0.05 are regarded as significant. Means are presented ± one SD.

RESULTS AND DISCUSSION

Fresh egg mass was highly correlated with calculated egg volume ($r^2 = 0.97$, $P < 0.0001$, $n = 84$). Egg volume averaged 37.1 ± 3.3 cm^3 (n = 229) and ranged from 30.2 to 45.1 cm^3. The average within-clutch difference between the largest and smallest eggs was 7%; the maximum difference was 18%. In three-egg clutches (n = 19), the final egg averaged 1.2% above the mean volume of all eggs in the clutch, in four-egg clutches (n = 38) 0.4% below, and in five-egg clutches (n = 4) 1.4% above.

Egg volume varied significantly with laying sequence for three-egg clutches in 1993, but not in 1994, and for four-egg clutches only in 1994 (Fig. 1; mixed model two-way ANOVA without replication; $F_{2,22} = 7.02$, $P = 0.004$; $F_{2,12} = 0.13$, ns; $F_{3,48} = 2.27$, ns; $F_{3,60} = 3.75$, $P = 0.02$, respectively). Tukey's test showed significant differences between first- and third-laid eggs within three-egg clutches in 1993 and between first- and second-laid eggs within four-egg clutches in 1994.

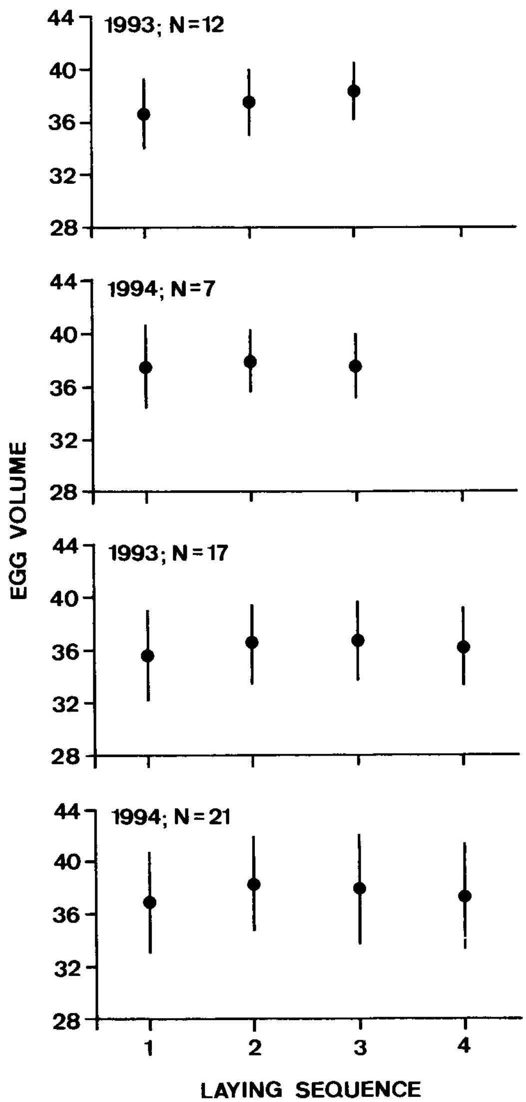

FIGURE 1. Egg volume (mean ± SD, cm^3) in clutches of Great Crested Grebes in relation to clutch size and laying sequence.

Thus, significant differences in egg volume within clutches always involved the first-laid egg that averaged smaller. Goc (1986) pooled measurements from different years and clutch sizes and also found significantly smaller first-laid than second-laid eggs and no significant difference between penultimate and ultimate eggs in clutches of Great Crested Grebes, Forbes and Ankney (1988) found that first-laid eggs averaged 8% lighter than subsequent eggs in clutches of Pied-billed Grebes.

Eggs hatched in the same order in which they were laid, with mean intervals of 1.2 ± 0.4 days between the first- and second-hatched chicks, 1.5 ± 0.3 days between the second- and third-hatched chicks, and 1.8

± 0.4 days between the third- and fourth-hatched chicks. If these limited data are representative (no other detailed information is available), all chicks are well separated in the pattern of size differences initially produced within broods by hatching asynchrony. First-laid eggs averaged 2.6% less than second-laid eggs in volume, but it seems safe to infer that this difference must be of little importance in reducing the initial body-mass difference between first- and second-hatched chicks.

In conclusion, egg volume seems to remain constant after the first-laid egg in clutches of Great Crested Grebes not adding to the size hierarchy of chicks arising from asynchronous hatching. In addition, many authors argue that the increase in size of the second-laid egg relative to the first-laid found in clutches of many bird species may be related to morphological or physiological constraints on the size of the first-laid egg (e.g., Parsons 1976, Leblanc 1987, Arnold 1991). Hence, no adaptive hypothesis seems necessary to explain intraclutch variation in egg volume of Great Crested Grebes.

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PIED FLYCATCHERS PREFER TO NEST IN CLEAN NEST BOXES IN AN AREA WITH DETRIMENTAL NEST ECTOPARASITES[1]

SANTIAGO MERINO AND JAIME POTTI
Departamento Biología Animal, Univ. Alcalá de Henares, E-28871 Madrid, Spain

Key words: Ectoparasitism; hole-nesting birds; nest box studies; nest site selection; Ficedula hypoleuca.

Møller (1989, 1992) pointed out a number of possible artifacts in nest box studies due to the common practice of removing old nests from nest boxes. There are apparently few bird species that remove old nest material before breeding (Møller 1989). Therefore, birds choosing previously used cavities for nesting could be exposed to higher levels of infestation by nest ectoparasites than birds choosing empty holes for breeding. Theory predicts that if reproductive costs due to nest ectoparasites are severe, birds should select empty cavities or remove old nest material before breeding (Møller 1989, 1992; but see Thompson and Neill 1991, Davis et al. 1994). Several studies have tested this prediction and failed to demonstrate discrimination of dirty/parasitized boxes in areas where the nest ectoparasites have few detrimental effects on birds' fitness (Thompson and Neill 1991, Orell et al. 1993, Davis et al. 1994, Mappes et al. 1994). Two studies were con-

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