BIOLOGY OF ELEONORA'S FALCON (*Falco eleonorae*): 7. VARIABILITY OF CLUTCH SIZE, EGG DIMENSIONS AND EGG COLORING

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Abstract — The variation of egg size, egg coloring and clutch size was studied in an Aegean colony of Eleonora's Falcon (*Falco eleonorae*). Egg-laying occurs between mid-July and early August with laying intervals of 2.6 and 2.9 d between first and second, and second and third egg, respectively. Mean clutch size was about 2.28. Three-egg clutches are started earlier than 2-egg or 1-egg clutches, which results in a negative correlation between laying date and clutch size. Within a laying sequence, third eggs are significantly smaller than first and second eggs. Egg breadth has a higher interclutch variation than intraclutch variation. A positive correlation can be established between female weight and egg breadth. Egg color corresponds to laying order; the second and third eggs show many dark spots, the first egg is pale brown. Clutch size was correlated with the weight of the male falcon but not with female weight. A correlation between the hunting success of a male falcon and its weight is assumed. Food availability is a limiting factor in the colony studied, and since the female falcon relies entirely upon the food supplied by the male, a correlation between male hunting success and clutch size is suggested.

Variability in clutch size and egg parameters has been studied in many birds, especially in species breeding colonially (gulls, terns, swallows), or species using nest boxes (tits, flycatchers, sparrows) (Lack 1966; Klomp 1970; Drent 1975). Birds of prey, except for the European Kestrel (*Falco tinnunculus*) (Cave 1969), the Red-footed Falcon (*Falco vespertinus*) (Horváth 1955), and the European Sparrowhawk (*Accipiter nisus*) (Newton 1979), have not been studied extensively, probably because of difficulties in acquiring sufficiently homogeneous data.

Since the Eleanora's Falcon (*Falco eleonorae*) breeds colonially and shows rather synchronized breeding, studies on reproductive biology and ecology are facilitated. On the other hand, field work is difficult to carry out because breeding colonies are usually situated on rocky, uninhabited islands of the Mediterranean Sea.

We studied a large breeding colony of Eleonora's Falcon in the Aegean Sea for 8 seasons and report here on the variability of clutch size, egg dimensions and egg coloring with respect to laying sequence and weight of the corresponding parent falcons.

Materials and Methods

The present study was carried out in July/August 1975 and in August/October 1977 near Crete in an Aegean colony of Eleonora's Falcon of about 250 breeding pairs. A few data were derived from a study in August/September 1979 (Ristow et al. 1980; Wink et al. 1980b). About 40 nests were monitored daily during the egg-laying period of 1975, and all eggs were marked individually with pencil so that the exact dates of laying and their sequence within a clutch were known.

Altogether, 240 eggs were measured. Egg weight was determined with a gauged spring balance to the nearest g. Egg length (L) and egg breadth (B) were measured with a micrometer to the nearest 0.1 mm. Egg volume was calculated as $V = (\pi \cdot L \cdot B^2)/6$, in analogy to the volume formula of a globe (Rheinwald, pers. comm.). The weight of captured adult falcons was measured with a spring balance to the nearest 5 g.

Results

Egg Dimensions. — The measurements of 240 eggs made in 1975 and 1977 are summarized in Table 1. The data of both yrs are pooled, since the parameters L, B and volume did not differ significantly ($P > 0.05$, *t*-Test) between years. Third eggs are significantly smaller ($P < 0.02$, *t*-Test) than first or second eggs (Table 1), whereas first and second eggs cannot be distinguished by size. The mean egg shape index (L/B) decreases from first egg (1.29) to second egg (1.25) to third egg (1.23); third eggs sometimes give the impression of being spherical.

Relationship With Female Weight. — The range of B for 31 three-egg clutches was 5.6 mm, whereas the range was only 1.7 mm within the respective clutches themselves. To quantify the degree of intraclutch and interclutch variation (Väisänen et al. 1972), 30 sequenced three-egg clutches were subjected to a one-way analysis of variance (ANOVA) (Table 2). The proportion of interclutch variation was 15% higher in L and 52% higher in B than intraclutch variation. The strong interclutch variation of B suggests that the anatomy and physiology of the female might be of importance. Unfortunately, these factors are difficult to measure, and the only factor that could be determined for the incubating female was weight.

Table 1. Dimensions ($\bar{X} \pm$ S.D.) of the first, second and third egg of Eleonora's Falcon. The third egg differs significantly in breadth ($P < 0.02$, *t*-Test), length, weight and volume ($P < 0.001$, *t*-Test) from the first and second egg.

PARAMETER	N	DIMENSIONS
Egg Length		
Total	240	42.14 ± 1.61
First Egg	23	42.63 ± 1.03
Second Egg	21	42.16 ± 1.40
Third Egg	23	40.41 ± 1.37
Egg Breadth		
Total	240	33.54 ± 1.01
First Egg	23	33.61 ± 0.98
Second Egg	21	33.80 ± 0.74
Third Egg	23	32.90 ± 0.72
Egg Weight		
Total	163	26.37 ± 2.32
First Egg	23	27.13 ± 1.89
Second Egg	21	26.57 ± 1.85
Third Egg	23	23.54 ± 1.74
Egg Volume		
Total	240	24.78 ± 2.56
First Egg	23	25.24 ± 1.62
Second Egg	21	25.26 ± 1.63
Third Egg	23	22.88 ± 1.40

The relationship between female weight and egg dimensions is illustrated in Figure 1. Breadth, volume, but not L, are the most influenced parameters, and in consequence, egg weight also. The heavier the female, the heavier the resulting eggs and probably the hatching young also.

Evaporative Water Loss. — Egg weight is subjected to a steady reduction during incubation due to H_2O evaporation and CO_2 production (Bezzel 1977). Sixty-four eggs weighed 22.8 ± 2.09 g ($\bar{X} \pm$ S.D.) at the end of incubation in 1977. Taking 30 d as incubation period and 26.4 g as initial egg weight, a daily loss of 116 mg occurred. On this basis, a 13.3% total loss occurred which may be influenced by climatic conditions at the breeding site (Table 3) with its relatively high temp and low humidity during daytime.

Relationship With Laying Period. — Egg-laying was rather synchronized and occurred between mid-July to early August with an interval of 2 or 3 d between each egg being laid (Table 4). The sizes of 54 eggs ordered by their date of laying show a negative correlation for L and weight, but not for B (Table 5). This effect can be easily explained by the fact that third eggs were smaller than preceding ones and laid about 5 to 6 d later than the first egg. Consequently, only slight negative correlations were established for first and third eggs analyzed separately.

Egg Coloring. — First eggs are pale brown with numerous small dots, whereas second or third eggs are dark brown with many dots, usually larger, which are concentrated at the blunt poles of the eggs (Table 6). Therefore, egg sequence of any clutch can be determined according to egg color

Table 2. Results of one-way analysis of variance (ANOVA) of inter- and intraclutch differences in egg breadth of 30 sequenced three-egg clutches of Eleonora's Falcon. The figures indicate percentage estimates of variance components. Significance of F-test is shown with stars (actual F-values not given).

	PERCENT OF VARIANCE	
VARIABLES	INTRACLUTCH	INTERCLUTCH
Egg Length	25.3***	39.8*
Egg Breadth	16.2***	68.5***

* - $P < 0.05$; *** - $P < 0.001$.

Table 3. Temperature and relative humidity ($\bar{X} \pm$ S.D.) measured with a thermohygrograph at 15 Eleonora's Falcon nests in August/September 1977.

TIME	TEMP (°C)	REL. HUMID. (%)
Night	20.92 ± 2.5	85.00 ± 6.7
Midday[a]	32.00 ± 4.5	49.50 ± 9.2

[a] 6 - 8 h after sunrise.

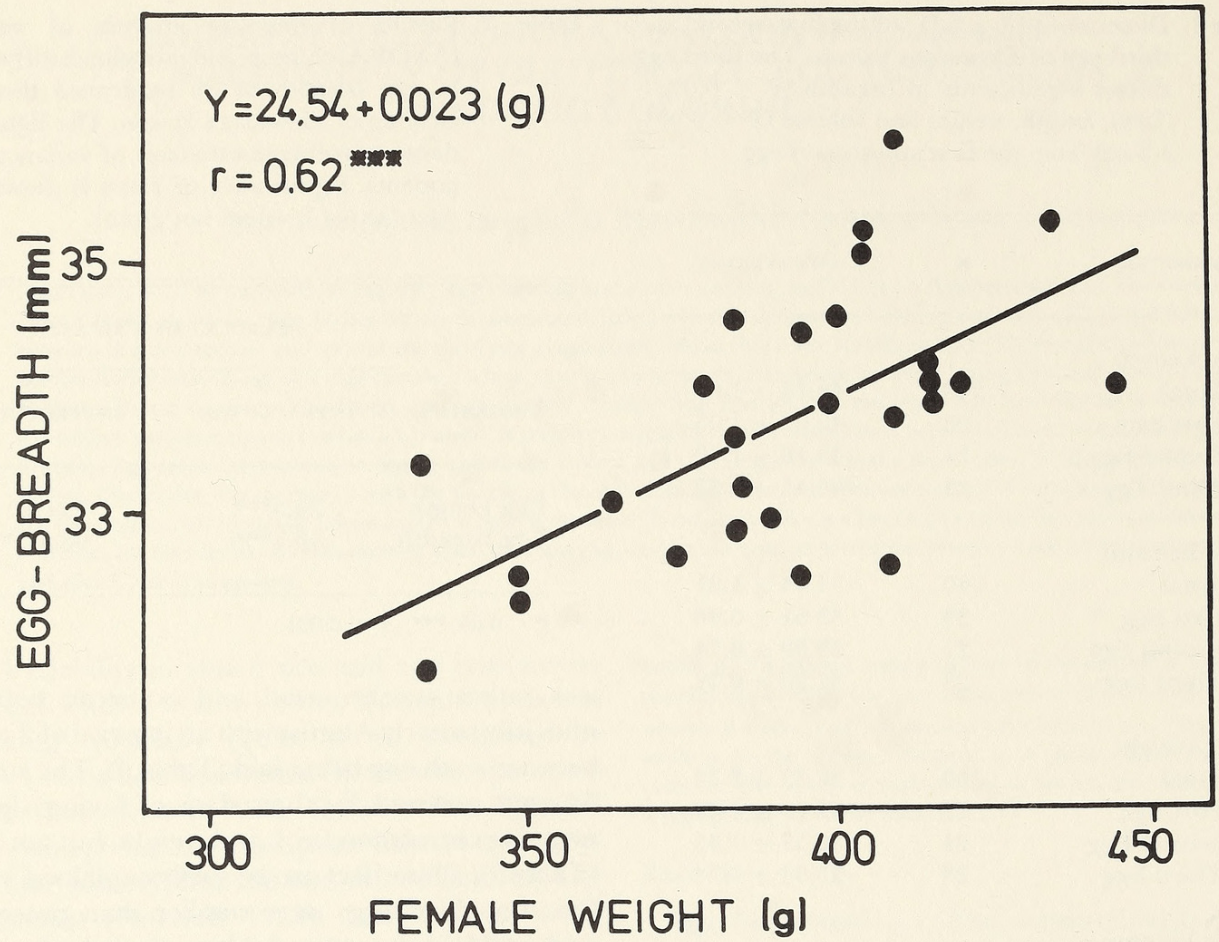

Figure 1. Linear regression analysis between weight of parent female Eleonora's Falcons and egg breadth (*** - $P < 0.001$).

and egg size, as is also the case in eggs of the Red-footed Falcon (Horváth 1955).

Clutch Size. — Clutch size data are summarized in Table 7. Only data obtained at the beginning of the incubation period (i.e., as soon as clutches are completed) were considered in order to avoid artifacts due to loss of eggs or clutches during incubation. A negative correlation ($P < 0.001$) existed

Table 4. Date of egg laying ($\bar{x}$ ± S.D.; Range) and interval ($\bar{x}$ ± S.D.) in days between laying of first and second egg and laying of second and third egg in an Aegean colony of Eleonora's Falcon.

Egg Sequence	Laying Date	n	Interval (d)
First Egg	24.5 July ± 3.3 d 18 July - 27 July	21	
Second Egg	27.1 July ± 3.3 d 21 July - 2 August	22	2.61 ± 0.92 (Between 1st & 2nd egg)
Third Egg	29.1 July ± 3.3 d 24 July - 7 August	17	2.91 ± 2.12 (Between 2nd & 3rd egg)

Table 5. Correlation values resulting from a linear regression analysis between sequence of laying and egg size in Eleonora's Falcon.

PARAMETER	N	R	Y = A - B(X)*
All Eggs			
Length	54	-0.43**	Y = 46.15 - 0.16(d)
Breadth	54	-0.11	
Weight	54	-0.36**	Y = 31.54 - 0.21(d)
First Eggs			
Length	21	-0.19	
Weight	21	-0.36	
Third Eggs			
Length	16	-0.06	
Weight	16	-0.17	

* - Sadis 1972; ** - P < 0.01.

between the date of laying and clutch size (i.e., 3-egg clutches were started earlier than 2-egg or 1-egg clutches).

Looking for an explanation, we studied the weight of the corresponding parent falcons. Clutch size was independent of female weight ($r = 0.53$, $P < 0.01$). The implication of this phenomenon was dealt with in detail in another paper (Wink et al. 1980a). We conclude that male weight and hunting efficiency are correlated; probably the mates of large males (which usually have 3-egg clutches) start laying at an earlier date than the mates of younger and smaller males.

DISCUSSION

In Eleonora's Falcon and all larids hitherto studied (Lundberg and Väisänen 1979) egg size decreases with laying sequence. The opposite has been found in several passerines (Svensson 1978) [e.g., the Song Thrush (*Turdus philomelos*) (Pitelka 1971), the Eastern Bluebird (*Sialis sialis*) (Pinkowski 1975], as well as waders (Väisänen et al. 1972; Miller 1979), and the Red-footed Falcon (Horváth 1955) whose egg size increases with laying order. Passerines start incubation with the last egg and an adaptive value can be assumed for the observed egg size variation. Since the probability of predation is higher for the first than for the last egg, it is of advantage if the last eggs are bigger. The loss of a small first egg would be less costly than the loss of a large last egg (Miller 1979). This assumption demands that in the opposite case (i.e., Eleonora's Falcon) the female should start incubation with the first egg in order to minimize the probability of a loss of the first and largest egg, and this is exactly what happens.

Is there any adaptive value of the third egg being the smallest and darkest? In order to answer this question it should be recalled that the interval be tween laying of the first and the third egg is about 5 to 6 d, but that incubation starts with the first egg. Hatching takes place within a 2 to 3 d (seldom 4 d)

Table 6. Observed numbers of eggs and color in relation to egg color and laying sequence in Eleonora's Falcon. A = all eggs individually known; B = includes data from eggs which were categorized by their size.

EGG COLOR	FIRST EGG	SECOND EGG	THIRD EGG
A. Pale Brown	21	1	1
Dark Brown	1	17	18
B. Pale Brown	90	2	
Dark Brown	4	91	36

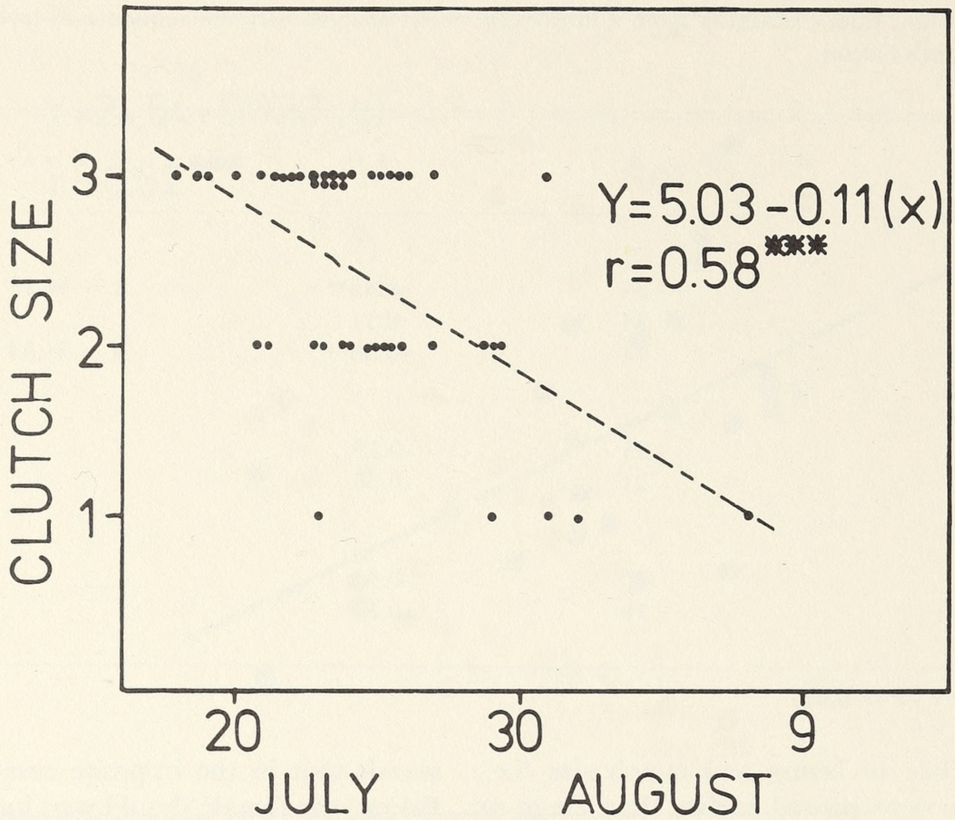

Figure 2. Linear regression analysis between laying dates of first egg and clutch size of Eleonora's Falcon (*** - P < 0.001).

interval, however. To explain the gain of 2 to 3 d in laying time several factors have to be considered. The female may incubate the first egg less intensively during the first 3 days. "Clicking" calls of the young birds prior to hatching, which occurs in *Falco eleonorae*, can speed up hatching of an embryo to some extent (Drent 1975). Incubation time is positively correlated with egg weight and incubation temp. According to basic physics, a dark body collects more radiation energy than a light one, thus we assume that a small and darker egg (i.e., the third egg in *Falco eleonorae*) would need a shorter incubation period. This would be of advantage, since the first young to hatch is the largest and the last young the smallest, which reduces the latter's chances of survival.

Table 7. Mean clutch size in an Aegean colony of Eleonora's Falcon. Initial clutch size data were derived from the beginning of the incubation period (July/August) in 1975.

		Clutch Size (n)			
Parameter	Mean	1 Egg	2 Eggs	3 Eggs	4 Eggs
Initial Size	2.28	5	45	26	-
Post-Incubation Size[b]	1.97	21	76	18	(1) [a]

[a]In 1982 a 4-egg clutch was found, but according to egg size measurements it was derived from 2 females.

[b]Most data were collected in 1977. If clutch size is determined at the end of the incubation period, clutch size is biased by egg loss due to predation.

Comparing the clutch size in different colonies of Eleonora's Falcon, the highest values are reached in the western Mediterranean: 2.55 eggs/clutch in the Balearic Islands (Mayol 1977), 2.85 - 3.05 eggs/ clutch in Morocco (Conant and de Naurois 1958; Vaughan 1961; Walter 1968; Clark 1981) compared with 2.28 eggs/clutch in the Aegean region for our study period. Clutches of 4 eggs are more common in the Moroccan colonies (the mode being 3-egg clutches, Clark 1981) than in the eastern Mediterranean where 4-egg clutches are uncommon. It remains to be studied whether this gradient in clutch size from eastern to western Mediterranean regions is primarily due to a better food supply, or due to other factors such as climate, aridity, or genetic differences (Ojanen et al. 1979).

The clutch size within a colony seems to depend on the hunting success of the male, who supplies the female and the young with food during the breeding period. A larger falcon generally has a better hunting efficiency than a small one (Bezzel 1977; Newton 1979). Since food availability is a limiting factor for Eleonora's Falcon, it is not surprising that the clutch size is positively correlated with the weight of the male (Wink et al. 1980a). The physical condition of the female does not influence clutch size, but seems to be important for egg size and, in consequence, for the weight of the hatching young. The heavier a hatchling, the better its chances of survival (LeCroy and LeCroy 1974; Coulson and Thomas 1978; Lundberg and Väisänen 1979; Parsons 1970). Consequently, the offspring of a larger female may have an advanage over the young of a smaller female.

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