VARIATION IN PEREGRINE FALCON EGGS

WILLIAM A. BURNHAM,[1] JAMES H. ENDERSON,[2] AND THOMAS J. BOARDMAN[3]

[1]*The Peregrine Fund, Cornell University, 1424 N. E. Frontage Road, Fort Collins, Colorado 80524 USA;*
[2]*Department of Biology, The Colorado College, Colorado Springs, Colorado 80903 USA; and*
[3]*Department of Statistics, Colorado State University, Fort Collins, Colorado 80523 USA*

ABSTRACT.—Eggs collected from captive and wild Peregrine Falcons (*Falco peregrinus*) were used to examine variation in eggshell thickness, length, breadth, and initial weight to resolve questions about eggshell data from wild falcons. For captive falcons, shell thickness of first clutches did not change over the years a falcon laid or with embryonic development. Eggshells in third clutches, but not second clutches, were significantly thinner than those from first clutches. Greatest variation in shell thickness existed between eggs within a clutch and did not differ significantly between wild and captive eggs. Entire clutches of wild falcons should be represented in future studies to maximize the chance of obtaining a representative sample in regard to shell thickness.

Egg size (L, B, and fresh weight) decreased over the years a captive falcon laid. A significant decrease in size (B and fresh weight) also occurred in second and third clutches laid the same year. Ratcliffe's Index generally appeared to be a reliable indicator of shell thickness in captive-laid eggs. *Received 30 September 1983, accepted 23 February 1984.*

EGGSHELL thickness has been reduced in a variety of predatory birds (Anderson and Hickey 1972), a phenomenon shown to be closely correlated to the presence of DDE (Cade et al. 1971, Lincer 1975, Peakall and Kiff 1979). Variation in shell thickness relating to embryonic development, the laying female's age, and production of multiple clutches has somewhat clouded an elucidation of the precise relationships between DDE and eggshell thinning.

Papers on nonraptorial birds have focused on variation in eggshell thickness, and some have defined sampling schemes to maximize the detection of thickness changes. Thickness decreases with embryonic development have been reported in Cedar Waxwings (*Bombycilla cedrorum*; Rothstein 1972), Japanese Quail (*Coturnix japonica*; Kreitzer 1972), and White-faced Ibises (*Plegadis chihi*; Capen 1977). In Cedar Waxwings, but not in the White-faced Ibis, eggs from smaller clutches also have thicker shells. In a study of museum eggshells of Clapper Rails (*Rallus longirostris*), Black-crowned Night Herons (*Nycticorax nycticorax*), White Ibises (*Eudocimus albus*), Northern Mockingbirds (*Mimus polygottos*), and Loggerhead Shrikes (*Lanius ludovicianus*), variation in shell thickness among eggs within clutches contributed as much to the sample variance as variation between clutches from different females (Klass et al. 1974).

The large captive population of breeding Peregrine Falcons (*Falco peregrinus*) developed by The Peregrine Fund (Fort Collins, Colorado and Ithaca, New York) to produce falcons for release provided a source of eggs from females of known age and origin. Additionally, the substitution of captive-reared young for wild Peregrine Falcon clutches in Colorado provided us with the opportunity to compare variation in egg parameters among wild-laid eggs with those produced in captivity (Burnham et al. 1978). The wild birds were subject to DDE-induced eggshell thinning and produced shells averaging 13% thinner than those of the captive birds (Enderson et al. 1982).

In this study we examined variations in shell thickness, egg breadth (*B*), and egg length (*L*) of wild-laid eggs within clutches, between clutches, among sites (females) by year, and between all sites over several years. We compared shell-thickness measurements for captive-laid eggs with embryonic development. Thickness, *L*, and *B* in captive-laid eggs were also related to female age and to second and third clutches laid within a year. Egg length and breadth were considered because they are used to calculate Ratcliffe's Index, a common measure for eval-

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uating shell thinning (Ratcliffe 1980). These analyses clarify historical data on Peregrine Falcon eggshell thickness and suggest sample techniques for collecting peregrine eggs that will provide the most accurate estimate of shell thinning resulting from DDE residues.

METHODS

All eggs were treated similarly. Egg length and breadth were measured to the nearest 0.1 mm with vernier calipers. We calculated fresh egg weights for captive-laid eggs by using $K_w(LB^2)$, where $K_w(0.0005474)$ is the observed coefficient for peregrine eggs, as described by Burnham (1983). Infertile eggs and those with dead embryos were stored in a refrigerator for up to several days before they were opened and emptied. When the contents were removed, or when fertile eggs hatched, the shells were rinsed with tap water and allowed to dry at low ambient humidity. Eggshell thickness was measured optically to ± 0.004 mm from fresh chips taken from three places at the shell equator. The ocular scale employed was calibrated with a Bausch and Lomb 0.001-mm stage micrometer (Enderson et al. 1982).

The 153 wild-laid eggs measured for shell thickness and the 146 measured for breadth and length were from first and second clutches laid at 14 territories in Colorado and northern New Mexico over as many as 5 yr in the period 1977–1981. In most instances, we could not verify that the same female laid at a particular territory in successive years. Usually, 3 or 4 eggs were available for measurement from each clutch. A nested analysis of variance was used to determine sources of variation (Sokal and Rohlf 1969).

For captive peregrines, we determined shell thickness for eggs fertilized as a result of both copulation and artificial insemination and performed an analysis of variance to determine whether or not a difference in thickness occurred. We measured 15 eggs that were infertile or developed for less than 1 week and 14 hatched eggs from the same clutches laid by 11 females. The means of shell thickness for each group were compared by a paired t-test. Shell-thickness means, usually for 3 or 4 eggs, were calculated for first, second, and third clutches and compared by t-tests. In all, 13 sets of three clutches produced by 4 females were used.

Measurements of 299 eggs laid in first clutches throughout a period as long as 11 yr by 14 captive peregrines were used to assess the potential effect of female age on shell thickness. We performed an analysis of variance on the yearly means to determine differences.

Eighty-eight first clutches from 16 captive females over as many as 11 yr provided data on egg breadth, length, and initial weight. From 1 to 4 eggs were available per clutch; sometimes eggs were broken by falcons and lost in the lofts. An analysis of variance was performed to determine possible linear and quadractic changes over years of laying on length, breadth, and calculated initial weight. Additionally, clutch averages were calculated for length, breadth, and initial weight of first, second, and third clutches of eggs laid within a year by 4 captive peregrines, and the averages were compared by t-tests.

RESULTS

Variation among eggs within clutches accounted for two-thirds (67.1%) of the variation in shell thickness of eggs laid by wild peregrines (Table 1). Differences between clutches accounted for 26.2% of the variation. Little variation in shell thickness existed among eggs at a nest-site location over years (2.4%) or between all nest-site locations over years (4.3%).

Within-clutch variation in shell thickness (with membranes) was great among both wild and captive eggs. The mean coefficient of variation ($CV = SD/\bar{x}$) of shell thickness of captive eggs (0.046, $n = 71$) was not significantly different ($P > 0.10$, t-test) from that of wild eggs (0.054, $n = 29$) when only 3- and 4-egg clutches were considered.

Thickness of captive-laid eggshells produced by females that were copulating with their mates and those that were artificially inseminated had similar average thicknesses ($F = 2.07$, $P > 0.15$). These means are 0.34 mm ($n = 143$) and 0.35 mm ($n = 111$), respectively.

Embryonic development had no apparent effect on thickness of captive-laid eggshells. The mean thicknesses of clutches of hatched eggs (0.281 mm) were not significantly different ($P > 0.50$, df = 27, t-test) from those of clutches of infertile eggs or eggs dying within 7 days (0.282 mm). Membranes from eggs with full-term embryos (0.077 mm, $n = 65$) were not significantly different in thickness ($P > 0.05$, t-test) from membranes from eggs with no development (0.079 mm, $n = 27$).

The average of mean thicknesses (with membranes) of captive-laid eggs was 0.357 in first clutches, 0.350 in second clutches, and 0.342 mm in third clutches, with 95% confidence intervals of ± 0.014, 0.016, and 0.014, respectively. The differences in clutch means of shell thickness (with membranes) between first and second clutches, second and third clutches, and first and third clutches were compared by paired t-tests. The latter was significant ($P <$

TABLE 1. Analysis of variance of measurements of eggs from wild peregrines in Colorado and northern New Mexico, 1977-1981.

Source of variation	df	Mean squares	Variance component	Percentage variability
Shell thickness[a]				
Among sites	13	0.001015	0.000022	4.30
Among years	19	0.000815	0.000012	2.41
Among clutches	13	0.000732	0.000131	26.16
Among eggs	99	0.000336	0.000336	67.51
Egg length				
Among sites	13	19.7885	1.3167	31.72
Among years	19	6.4774	0.5818	14.01
Among clutches	12	3.7716	0.7080	17.05
Among eggs	102	1.5450	1.5450	37.22
Egg breadth				
Among sites	13	8.1097	0.3724	20.92
Among years	19	4.3833	0.8374	48.17
Among clutches	12	0.5631	0.0060	0.34
Among eggs	102	0.5441	0.5441	30.57

[a] 144 eggs in 46 clutches with mean thickness of 0.305 mm with shell membrane.

0.025, $n = 13$), and there was an apparent trend to thinner eggshells after the first clutch. The number of years a captive falcon laid eggs had no significant effect upon or apparent trend in shell thickness (Fig. 1 and Table 2).

The amount of variation in length and breadth of wild eggs was much more evenly dispersed over the sources of variation than was variation in shell thickness (Table 1). Approximately one-third of the variation existed among eggs within a clutch. Most of the remaining variation occurred among years and sites.

We analyzed measured averages of clutches of captive-laid eggs and found trends toward narrower eggs of lighter weight when first,

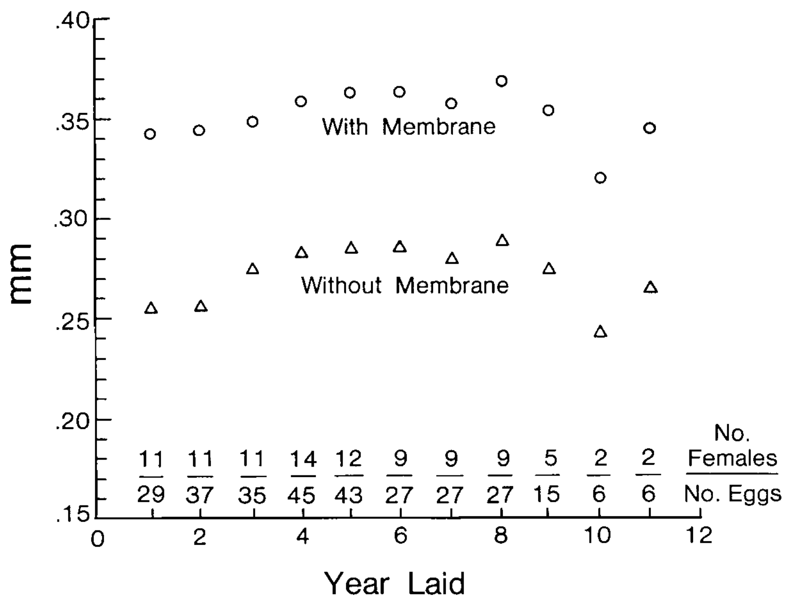

Fig. 1. Peregrine Falcon eggshell thickness over years of laying. The mean shell thickness was 0.354 mm with membranes and 0.275 mm without membranes.

TABLE 2. Analysis of variance of measurements of eggs from captive Peregrine Falcon taken over the years of laying.

	Sum of squares	df	Mean square	*F*	Significance of *F*
Shell thickness with membrane					
Linear	1.427	1	1.427	0.4272	0.514
Quadratic	1.499	1	1.499	0.4489	0.504
Shell thickness without membrane					
Linear	3.684	1	3.684	1.247	0.266
Quadratic	3.803	1	3.803	1.287	0.258
Length					
Linear	16.144	1	16.144	19.447	<0.005
Quadratic	5.527	1	5.527	6.658	0.012
Breadth					
Linear	18.852	1	18.852	38.784	<0.001
Quadratic	5.585	1	5.85	11.490	0.001
Initial weight					
Linear	188.244	1	188.244	53.068	<0.001
Quadratic	6.904	1	6.904	1.946	0.168

second, and third clutches laid in the same year were compared (Table 3). We also found a significant decrease in length, breadth, and initial weight over years of laying (Fig. 2 and Table 2).

DISCUSSION

The large variation (within clutches) that we have found among wild-laid eggs suggests that samples based on one egg in a clutch or a few fragments may insufficiently represent the average shell thickness produced by a falcon. If eggs or shell fragments were from second or third clutches, a further increase in variation would be possible because of the trend toward thinner eggshells after the first clutch. Because little variation exists in mean shell thickness among clutches of different females within a year or of the same female (nest site) in different years, accuracy may not be enhanced by collecting eggs annually from many females within a population. The great within-clutch variation in shell thickness seen in wild-laid eggs may not be due to DDE contamination, because the much thicker captive-laid shells vary similarly.

The average shell thickness of first clutches laid throughout the entire reproductive life of captive falcons does not change significantly

TABLE 3. Variation in egg size between clutches from captive peregrines.

	Initial weight (g)					Length (mm)					Breadth (mm)				
	df	Variance	Mean	*t*	*P*	df	Variance	Mean	*t*	*P*	df	Variance	Mean	*t*	*P*
Clutches															
C_1	9	3.11	47.64			11	2.55	51.56			10	0.91	40.91		
C_2	9	2.70	44.99			11	1.95	51.17			10	0.93	40.00		
C_3	9	7.00	42.46			11	3.74	50.71			10	1.24	38.92		
Contrasts															
C_1 vs. C_2	18			3.49	0.01	22			0.61	0.5	20			2.20	0.05
C_2 vs. C_3	18			2.58	0.02	22			0.64	0.5	20			2.26	0.02
C_1 vs. C_3	18			5.15	0.001	22			1.12	0.2	20			6.51	0.001

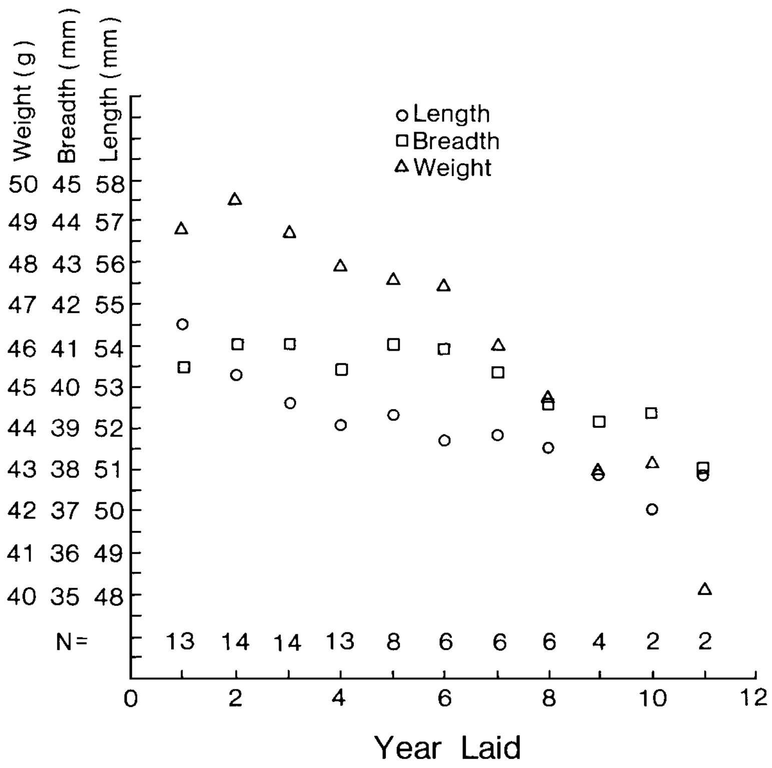

Fig. 2. Peregrine Falcon egg measurements over years of laying. Each datum represents the average of 2–4 eggs laid in the first clutch·year^{-1}·female^{-1}.

TABLE 4. The effect on Ratcliffe's Index values of the number of years a female has laid.

Year laid	Breadth[a]	Length[a]	Initial weight[a]	Number of clutches[b]	Shell weight[c]	Ratcliffe's Index[d]	Change in index from Year 1 (%)	Change in index from Year 2 (%)
1	40.41	54.56	48.76	13	3.90	1.77		−2.2
2	41.08	53.28	49.52	14	3.96	1.81	+2.3	
3	41.02	52.61	48.73	14	3.90	1.82	+2.8	+0.6
4	40.90	52.16	47.88	13	3.83	1.80	+1.7	−0.6
5	41.06	52.28	47.62	8	3.81	1.77	0.0	−2.2
6	40.89	51.74	47.36	6	3.79	1.79	+1.1	−1.1
7	40.30	51.78	46.08	6	3.69	1.77	0.0	−2.2
8	39.64	51.59	44.61	6	3.57	1.75	−1.1	−3.3
9	39.28	50.79	42.95	4	3.44	1.72	−2.8	−5.0
10	39.43	50.14	43.23	2	3.46	1.75	−1.1	−3.3
11	38.05	50.85	40.28	2	3.22	1.66	−6.2	−8.3

[a] Mean values of clutch averages (graphed on Fig. 2).
[b] Number of clutches and females; all clutches represented are the first laid each year.
[c] Eight percent of initial weight.
[d] Ratcliffe (1980).

(Fig. 2). Therefore, this statistic from wild populations, which may have skewed age distributions, may not be biased toward thinner or thicker shells. Shell-thickness data from hatched, addled, or infertile eggs are equally representative.

The second common analysis of shell thinning is Ratcliffe's Index, which is the dry weight of the shell (mg) divided by the product of its length (mm) and breadth (mm) (Ratcliffe 1980). A decrease in length or breadth over the years of laying could bias the Index downwards. To test this, we held shell weight to be 8% of initial egg weight and determined the Index values over the years of laying (Table 4). The change in the Index did not exceed ±2.8% from the first to seventh years of laying, whether the average Index from the first or second year of laying was used as the base. After the seventh year of laying, smaller Index values result, even though shell thickness (Fig. 1) may remain constant. A population with an age distribution skewed toward very old birds could produce eggs with Indecies biased downwards.

If many egg samples from a population were from second or even third clutches, a further bias could be introduced, because a significant reduction in egg breadth and initial weight occurred between clutches laid in a single year by a falcon (Table 3). A reduction of length was also evident, but not significant.

Conclusions

Our results from wild-laid eggs suggested little need to collect eggs from a large number of females each year within an ecologically similar population. To maximize the chance of obtaining a representative sample of shell-thickness changes, all eggs in either first or second clutches should be represented, or the number of collection sites or collection years should be increased. Eggshells from hatched, infertile, or addled eggs were equally representative. Ratcliffe's Index appears to be a reliable indicator of shell thickness unless measurements are from second or third clutches or from eggs laid by very old females.

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