RESEARCH PAPER

Received 7 February 2024 | 15 November 2024, 28 January 2025 | Accepted 28 January 2025
Editor: Murielle Ålund

Long-term changes in eggshell thickness in the Peregrine Falcon *Falco peregrinus* in Sweden

Långsiktiga förändringar i äggskalstjocklek hos pilgrimsfalk Falco peregrinus *i Sverige*

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THE PEREGRINE FALCON *Falco peregrinus* populations across Europe and North America were almost exterminated in the 1970s; in Sweden, only 15 pairs were known by 1975. One of the main causes were reduced productivity due to eggshell thinning, attributed to the widespread use of organochlorine pesticides. This study analysed eggshell thickness in samples collected across Sweden between 1964 and 2023 and compared with eggs from 1864–1945. The results indicate very thin shells in the 1960s to 1980s, when eggshells were on average −16% relative normal thickness, with records of −29%. Since then, the average thickness has steadily increased. We observed small but insignificant differences in shell thickness between northern and southern Sweden. In the 2020s the average eggshell thickness is still 7% below normal, which is within safe levels. However, because new substances with the potential to affect eggshell thickness are increasing in the environment, it is worthwhile to continue to collect and measure eggshells as a simple and low-cost measure to monitor one of the effects of environmental contaminants. The Peregrine Falcon remains an important indicator for unintended side effects of chemical substances released into the environment.

Keywords: raptor | eggshell thinning | contaminants | DDT | environmental monitoring

Citation: Falk K, Lindberg P, Andersson L-Å, Järås T, Leksén L, Lindström B-O, Nilsson P & Olofsson F. 2025. Long-term changes in eggshell thickness in the Peregrine Falcon Falco peregrinus in Sweden. Ornis Svecica 35: 50–63. https://doi.org/10.34080/os.v35.26042.

Introduction

It is well established that the steep population declines of several raptor species across Europe and North America in the mid-20th century were due to reproductive failure and mortality caused by a mixture of organochlorine pesticides and other persistent organic pollutants released into the environment from the mid-1940s (Oli *et al.* 2023). In Scandinavia, the Peregrine Falcon *Falco peregrinus* (also called just Peregrine) was almost extirpated and in Sweden only 15 pairs were known by 1975. Most of them bred in northern Sweden, with only a few pairs left in central and southern Sweden, down from an estimated minimum of 900 pairs in the early 1900s (Lindberg *et al.* 1988, Lindberg 2009). Among the pesticides, Dichlorodiphenyltrichloroethane (DDT, and its degradation product DDE) interferes with calcium deposition when the eggshell is generated, and studies on eggshell thinning in Peregrines demonstrated a clear link between DDT/DDE exposure and thinner eggshells (Ratcliffe 1958, 1970, Risebrough 1986, Fyfe *et al.* 1988, Peakall 1993, Ratcliffe 1993, Peakall & Lincer 1996), resulting in reduced reproductive success (Newton 1979, Oli *et al.* 2023). The main effect of shell thinning is egg breakage, but also a change in gas exchange across the shell, leading to the death of embryos (Cooke 1979, Newton 1979, Ratcliffe 1993). After the discovery of these main effects, monitoring of changes in shell thickness became a simple proxy indicator for DDT/DDE exposure, and critical levels of eggshell thinning associated with reproductive failure in Peregrine populations were identified (Newton 1979, Fyfe *et al.* 1988, Peakall & Kiff 1988, Newton *et al.* 1989, Ratcliffe 1993). This type of research, conducted in many countries, played a pivotal role in shaping conservation policies and efforts to protect bird species from the harmful effects of pesticides, and turned the Peregrine and other top predators into indicators of environmental contaminants that may have wider impacts, including on human health.

Since the banning of the most directly harmful compounds from 1970 onwards (Turusov *et al.* 2002), along with active conservation efforts, Peregrine populations have largely recovered across Europe (Andreasen *et al.* 2018, Beran *et al.* 2018, Brunelli & Sarrocco 2018, Zuberogoitia *et al.* 2018, Oli *et al.* 2023) and globally (White *et al.* 2024). In parallel, eggshell thickness in Peregrines in Denmark and Germany, and in Swedish Ospreys *Pandion haliaetus*, have been shown to be back to near-normal about 20 years after DDT was phased out (Wegner *et al.* 2005, Odsjö & Sondell 2014, Andreasen *et al.* 2018). In Sweden, the Peregrine population is still increasing and currently estimated at around 650 occupied territories but not yet fully recovered in some parts of eastern Sweden (Järås 2023). Based on this background we expected that the shell thickness in the Swedish Peregrine population would have reached the pre-DTT normal level during the recent decades.

The Peregrine breeds in all parts of Sweden. Breeders in northernmost Sweden feed mainly on migrant waders and ducks, and themselves migrate as far as southern Europe or northern Africa (Lindberg 1983, Spina *et al.* 2022). In southern Sweden, the Peregrines have a more terrestrial prey choice during the breeding season (Lindberg 1983) and tend to migrate shorter distances or even remain near the territory year-round (Andersson & Sandberg 2015). Therefore, the overall exposure to contaminants during their annual cycle might differ between falcons breeding in the southern versus northern parts of Sweden. When the Peregrine population was at its lowest in Scandinavia in the 1970s, birds in the northern parts of Sweden and Finland fared relatively better than in the southern parts, and the population recovery also started earlier in the northern parts of Scandinavia (Lindberg *et al.* 1988, Lindberg 2009, Koskimies & Ollila 2022). Based on these differences in population response, we hypothesised that eggshell thinning in Peregrine clutches from northern Sweden could have been less pronounced during the critical period in the 1960s and 1970s.

Apart from the identification of shell thinning in 1972–1981 (Odsjö & Lindberg 1977, Lindberg 1983), long-term changes in eggshell thickness during the decline and recovery of the Swedish Peregrine population have not been investigated. In this paper we examine the changes in eggshell thickness of Swedish Peregrines over the past 160 years to 1) verify whether shell thickness is back to pre-DTT normal levels, 2) assess whether there are regional differences between the migratory Peregrines nesting in the northern parts of Sweden versus the semi-resident birds breeding in southern Sweden in shell thinning and recovery of shell thickness, and 3) assess the differences in sample materials (whole eggs versus eggshell fragments) and their feasibility in future monitoring of eggshell thickness at the population level.

Material and methods

THE PEREGRINE FALCON AND ITS EGGS

The Peregrine Falcon is distributed across the globe, with some variation in both plumage and size (White *et al.* 2013 refer to 23 subspecies while AviList Core Team 2025 recognize 18 subspecies) as well as clinal variation in clutch size, egg size and shell thickness (White *et al.* 2024). In Sweden, the population of *F. p. peregrinus* lays 2–4 eggs, average 3.55 eggs (standard deviation, SD = 0.61, n = 217 clutches; Pilgrimsfalk Sverige, unpublished data). The average egg size (length × breadth) is 52.06 (SD = 2.06) mm × 41.27 mm (SD = 1.43), n = 1,307 eggs), with eggs from northern Sweden on average 0.55 mm longer and 0.29 mm wider than eggs from southern Sweden (n = 173 and 1,134, respectively; Pilgrimsfalk Sverige, unpubl. data). The small average difference in *dimensions* leads to a 2.4% larger *volume* of eggs from northern Sweden, significantly different from southern Sweden ($z = 3.45$, $p = 0.0006$). The eggshell thickness differs among eggs: Burnham *et al.* (1984) found the largest variation in Peregrine eggs to occur among eggs (67.5%), not among clutches (26.2%), whereas Falk & Møller (1990) found the two sources of variation to be almost equal (49.2% and 42.3%, respectively) and concluded that "to obtain an unbiased estimate of shell thickness in a [Peregrine] population, it is worth the effort to collect eggs or fragments from as many nests and/or years as practically possible". Hence, in this study we include all available samples collected in all of Sweden to assess changes in eggshell thickness across the past six decades.

THE SAMPLES

Three different sample sets of eggshells (Figure 1) were measured: 1) 102 eggs in 36 clutches collected 1864–1965, curated at the Swedish Museum of Natural History, Stockholm; 2) 361 whole unhatched addled eggs representing 315 clutches from 1972–2023 curated at the Environmental Specimen Bank at the same museum; (3) eggshell fragments from hatched or broken eggs representing 115 nests (clutches) from 1974–2023, stored with the Environmental Specimen Bank, Pilgrimsfalk Sverige, or the County Administrative Board of Västernorrland. The distribution of sample types across periods and regions is summarized in Table 1. The addled eggs and fragments were collected during visits to Peregrine nests for assessing productivity and ringing young; nest visits were conducted by experienced climbers and ringers with relevant permits to the Swedish Peregrine monitoring scheme under The Swedish Society for Nature Conservation and BirdLife Sweden, or by the County Administrative Board of Västernorrland.

The egg samples came from all over Sweden, but for regional comparisons we grouped all samples from the

FIGURE 1. The three types of samples included in the analyses of Peregrine Falcon *Falco peregrinus* eggshell thickness: eggs in whole clutches from the collection at the Swedish Museum of Natural History, Stockholm, were measured at five points through the 3–5 mm blow whole at the equator of the egg (left); unhatched addled eggs curated at the Environmental Specimen Bank at the same museum were cut along the equator and measurements taken at five points along the cut edges (centre); for eggshell fragments from hatched or broken eggs, 20 pieces from each nest were measured (right). Photos: Knud Falk.

— *Tre typer av prover ingick i analyserna av skaltjockleken hos pilgrimsfalk* Falco peregrinus*: ägg i hela kullar i samlingen vid Naturhistoriska riksmuseet (NRM) i Stockholm mättes på fem punkter genom det 3–5 mm stora blåshålet vid äggets ekvator (vänster); okläckta rötägg i NRMs Miljöprovbank skars längs ekvatorn och mätningar utfördes på fem punkter längs de skurna kanterna (mitten); för äggskalsfragment från kläckta eller krossade ägg mättes 20 stycken från varje bo (höger).*

TABLE 1. Sample sizes of Peregrine Falcon *Falco peregrinus* clutches 1864–2023 from northern and southern Sweden examined for eggshell thickness; clutches from 1864–1945 represent the reference (three clutches from 1948 not included) for assessing changes during the later period. — *Provstorlekar av pilgrimsfalkens* Falco peregrinus *kullar 1864–2023 från norra och södra Sverige undersökta för äggskalstjocklek; kullar från 1864–1945 utgör referensen (tre kullar från 1948 ej inkluderade) för att bedöma förändringar under den senare perioden.*

Period	Region of Sweden	Clutches with > 20 fragments *Kullar med > 20 fragment*	Whole eggs / clutches *Hela ägg / kullar*	Total number of clutches *Totalt antal kullar*
1864–1948	Northern / *Norra*		36 / 12	12
	Southern / *Södra*		63 / 21	21
1964–2023	Northern / *Norra*	69	135 / 121	213
	Southern / *Södra*	46	232 / 199	246
Total	All of Sweden / *Hela Sverige*	115	466 / 353	468

region Norrland (roughly north of 61°N) as 'northern Sweden', and samples from the regions of Svealand and Götaland as 'southern Sweden'.

MEASUREMENTS

The historical museum collection consisted of whole eggs with blow holes at the equator and the shell thickness was measured to nearest 0.001 mm at five points around the blow hole with an analogue micrometre (Mitutoyo 147-301) modified to reach through the egg blow hole. Measurements were omitted at points appearing extremely thinner or thicker than neighbouring measuring points to avoid possible dried remains of egg contents or shell areas without membranes. The whole addled eggs collected during field work in recent decades were cut open along the equator (contents stored at the Environmental Specimen Bank (Odsjö 2006), Swedish Museum of Natural History, for chemical analyses) and dried at room temperature for at least nine months before measuring. These samples, as well as those consisting of eggshell fragments, were measured to nearest 0.001 mm with Mitutoyo digital micrometre devices with a stainless-steel ball fitted to one jaw in order to fit the inner concave surface of the eggshells (Falk & Møller 2023). The whole cut eggshells were measured at five points along the equator cut edges. For samples consisting of eggshell fragments, 20 pieces were measured to represent the average thickness of the clutch (Odsjö & Sondell 1982) and samples with less than 20 fragments were omitted.

There is a natural intra-egg variability in shell thickness in birds (Odsjö & Sondell 1982, Sun *et al.* 2012). In Osprey eggs in Sweden, Odsjö & Sondell (1982) confirmed that measurements at the equator were representative of the overall mean thickness of measurements across different parts of the egg, and that eggshell fragments could be used to assess the shell thickness of an egg/clutch provided no part of the egg is over- or underrepresented. Like Odsjö & Sondell (1982), we assume that the 20 eggshell fragments measured from each egg represented random parts of the eggs and the clutch and, therefore, provide an estimate of shell thickness of the clutch.

Two persons, KF and FO, measured the eggshells after calibrating measuring devices and procedures by comparing measurements taken by both persons on 105 reference eggshell fragments; the results were identical (mean difference 0.001 mm, SD = 0.003; $z = -0.56$, $p = 0.57$).

The measurements of whole eggs in the museum collections included the inner membrane usually attached to the inside of dried eggs. In most opened eggs or eggshell fragments, measurements included points or fragments with or without the egg membrane. To compare these measurements with historical reference eggs in museum collections it was therefore necessary to establish a "membrane constant" to correct the measurements of points or fragments without membrane. The membrane constant was derived in two ways: (1) pairwise measurements of adjacent shell areas with and without membranes (Odsjö & Sondell 1982, Falk & Møller 2023) on samples from 24 clutches gave a membrane thickness of 0.057 mm (SD = 0.015, range 0.034–0.087), and (2) comparing measurements of eggshell fragments from 23 clutches which included both types (with/without membrane; at least five fragments of each category) also gave 0.057 mm (SD = 0.013, range 0.034–0.085). Hence, we applied the membrane constant of 0.057 mm to convert measurements so that all correspond to shell thickness including the egg membrane.

In all analyses, mean shell thickness (per *clutch* or *annual means* as specified in each case; Vorkamp *et al.* 2017) is the response variable and year is the independent variable, while region (north, south) or sample type (whole eggs, fragments) are class variables. For statistical tests we used the functions 't-test' 'z-test', 'regression' and 'slope' available in the Microsoft Excel 2021 data Analysis ToolPak. All tests are two-tailed with significance level $\alpha = 0.05$.

It is not known exactly when DDT was introduced in Sweden but in the UK the first signs of shell thinning in Peregrines occurred in 1946, and thinning was evident by 1947 (Peakall 1993). Therefore, in this study we include clutches collected up to 1945 to represent the pre-DDT 'normal' shell thickness of the Swedish Peregrine population.

Results

In the museum reference collection, the shell thickness of 30 clutches from 1864 to 1945 ranged from 0.302 mm to 0.388 mm with an average thickness of 0.345 mm (SD = 0.020) – representing the pre-DDT reference shell thickness for assessing changes in shell thickness over time (Table 2, Figure 2a). There was a non-significant difference in shell thickness between clutches from southern Sweden and northern Sweden (Table 2, Figure 2a).

Three clutches from 1948 (yellow symbols in Figure 2a) showed normal shell thickness but, due to a large sample gap until 1964, there is no evidence of when eggshell thinning set in until it was evident by 1964–65 and onwards through the 1970s and 1980s (Figure 2c). In addition, too few samples until the mid-1970s—there were almost no breeding pairs to sample from—makes it hard to know how severe the shell thinning may have been. But the regression line in Figure 2c suggests that the average thinning was around 17% in the late 1960s; the overall average in the 10-year period 1974–1984 was 16% (Table 2). In 26 clutches the shell thinning in exceeded 20%; the thinnest clutches recorded were 29% thinner than the reference and came from Bohuslän in 1980 (0.244 mm) and Norrland in 1981 (0.243 mm, Figure 2b–c). We consider that a reduction beyond 14.5 to 17% in shell thickness is the critical thinning level, or risk threshold, for the Peregrine population in Sweden—indicated by the grey bars across all panels in Figure 2 (see Discussion). In the reference period 1864–1945 no clutches were thinner that the risk threshold, in contrast to the period 1964–1980 when 58% of all clutches showed a thinning beyond 14.5%. During the most recent decade, 2014–2023, 10% of clutches were still in the risk zone (Figure 2c).

From those low levels, the average shell thickness has increased significantly over the past 60 years (Figure 2c, linear regression $R^2 = 0.42$, slope significantly different from zero, $t_{47} = 5.73$, $p < 0.0001$) but the eggshell thickness is not yet fully restored to pre-DDT normal level. The mean shell thickness remained around 7% below the pre-DDT normal during the last decades (Table 2).

We observed small, non-significant differences in shell thinning between pairs breeding in northern and southern Sweden (Table 2). The separate regression lines (black and blue dashed lines in Figure 2c) suggest different recovery rates in annual mean shell thickness in northern and southern Sweden, respectively, but the difference in slopes between the two samples was not significant ($t_{82} = 0.44$, $p = 0.66$).

The results above are based on pooled data for whole eggs and eggshell fragments. Although the fragment samples tended to give slightly higher shell thickness readings on average (see regression lines in Figure 2b), there was no difference in the average shell thickness measured on whole eggs and fragments sampled in the same years (paired *t*-test, $t_{26} = 1.08$, $P = 0.29$, $n = 27$ years) and no difference in the regression line slopes (Figure 2b) between the sample types ($t_{71} = 0.16$, $p = 0.87$).

Discussion

EGGSHELL THICKNESS, TRENDS AND RISK LEVELS

The mean shell thickness of eggs in the museum collections from the pre-DDT era 1864–1945 (0.345 mm) was close to the 0.347 mm identified by Odsjö & Lindberg (1977), confirming the normal thickness of Swedish Peregrine eggs that have not been affected by environmental contaminants. The normal level measured in the Norwegian population was 0.359 mm (Nygård 1983) and for Danish Peregrines it was 0.335 mm (Falk & Møller 1990, Andreasen *et al.* 2018); at least in the latter case, a slightly different measurement protocol may partly explain the difference.

TABLE 2. Eggshell thickness (clutch means, SD, n) and levels of shell thinning (%) in eggs of the Peregrine Falcon *Falco peregrinus* in different periods; first row (1864–1945, grey shading) is the historical museum collection with eggs from the pre-DDT era serving as reference (mean for all Sweden) for estimates of eggshell thinning in subsequent periods. The column with *t*-test compares shell thickness in southern and northern areas; thinning values 1964–1973 within parentheses are based on too small sample sizes.
— Äggskallstjocklek (kullgenomsnitt) och skalförtunning (%) i ägg från pilgrimsfalk Falco peregrinus *i Sverige under olika perioder; första raden (1864–1945, grå skuggning) är från historiska samlingar med ägg från före DDT togs i användning och ger referensvärdet (hela Sverige) för att bedöma skalförtunning i senare perioder. Kolumnen med t-test jämför skaltjocklek i södra och norra Sverige; värden för skalförtunning 1964–1973 i parentes har för liten provstorlek.*

	Southern Sweden *Södra Sverige*		Northern Sweden *Norra Sverige*			All of Sweden *Hela Sverige*	
Period	Thickness *Tjocklek* mm (SD), n	Thinning *Förtunning* %	Thickness *Tjocklek* mm (SD), n	Thinning *Förtunning* %	*t*-test p (df)	Thickness *Tjocklek* mm (SD), n	Thinning *Förtunning* %
1864–1945	0.340 (0.022), 19	–	0.353 (0.014), 11	–	0.081 (28)	0.345 (0.020), 30	–
1964–1973	0.278 (0.037), 2	(19)	0.302 (0.003), 2	(12)	–	0.290 (0.026), 4	(16)
1974–1983	0.285 (0.018), 21	17	0.291 (0.025), 21	16	0.354 (40)	0.288 (0.022), 42	16
1984–1993	0.304 (0.027), 21	12	0.318 (0.026), 23	8	0.090 (42)	0.311 (0.027), 44	10
1994–2003	0.317 (0.027), 46	8	0.319 (0.022), 25	8	0.867 (69)	0.318 (0.025), 71	8
2004–2013	0.328 (0.027), 77	5	0.322 (0.027), 32	7	0.298 (107)	0.327 (0.027), 109	5
2014–2023	0.318 (0.021), 78	8	0.322 (0.015), 84	7	0.189 (160)	0.320 (0.018), 162	7

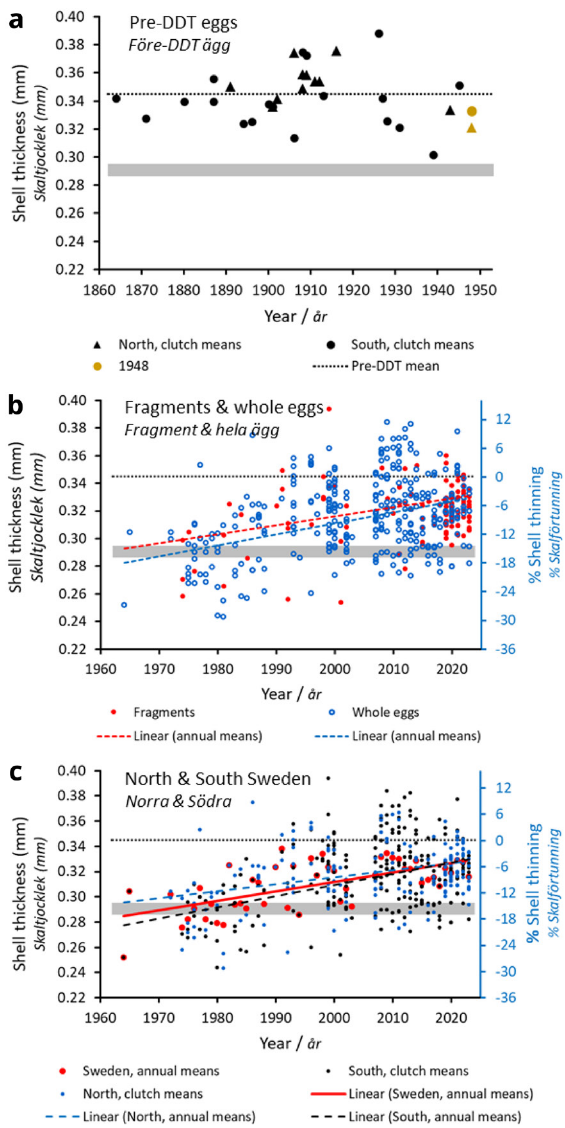

FIGURE 2. Eggshell thickness (left axis) and percent change relative the pre-DDT reference thickness (right axis) in eggs from Peregrine Falcons *Falco peregrinus* in Sweden 1864–2023. (**a**) Clutch means for 1864–1948 and the average thickness (0.345 mm, black dashed line across all panels) serving as Pre-DDT period reference for assessing eggshell thinning of more recent samples; clutches from 1948 (yellow markers) excluded from the reference average. (**b**) Comparison of clutch means across 1964–2023 from samples of whole eggs (blue) and eggshell fragments (red). (**c**) Clutch means (sample types pooled) and trend lines across 1964–2023 in northern (blue) and southern (black) Sweden, and annual means for all of Sweden (red). The broad grey bars across all panels indicate the approximate critical threshold (14.5–17%) of eggshell thinning at the population level that is associated with reduced productivity and population decline.

— Äggskalstjocklek och procentuell förändring i tjocklek, relativt referensvärdet uppmätt före introduktionen av DDT, för ägg från pilgrimsfalk Falco peregrinus *i Sverige under perioden 1864–2023. (**a**) Medelvärden för varje kull under 1864–1945 (triangel = norra Sverige, cirkel = södra Sverige), där medelvärdet för hela perioden (0,345 mm) fungerar som referens för bedömning av äggskalets förtunning i nyare prover (streckad svart linje genom alla figurer); kullar från 1948 (gula symboler) ingår ej i referensvärdet. (**b**) En jämförelse av kullmedelvärden under 1964–2023 för hela ägg (öppna blå cirklar) och äggskalsfragment (fyllda röda cirklar). (**c**) Kullmedelvärden 1964–2023 för kullar från norra (små blå cirklar; blå streckad trendlinje) och södra (små svarta cirklar; svart streckad trendlinje) Sverige, medan stora röda cirklar indikerar årliga medelvärden för hela Sverige, med heldragen röd trendlinje. Det grå fältet som presenteras i alla grafer visar den ungefärliga kritiska gränsen (14,5–17%) för äggskalets förtunning på populationsnivå som är associerad med minskad häckningsframgång och populationsminskning.*

Due to the lack of samples from the period when the Peregrine population was almost extirpated in Scandinavia, we do not know how severe the eggshell thinning was at its lowest levels, but two clutches from 1980–1981 held the record of 29%. Since then, shell thickness has recovered to near-normal levels and was on average about 7% thinner during the most recent 10-year period (Table 2, Figure 2c). This is very similar to findings from central Norway, where Nygård *et al.* (2019) noted that "eggshells were relatively thin throughout the 1970s, 1980s, and 1990s, but have increased to almost normal levels during the last 2 decades" and that "shell thinning after the turn of the millennium seems to be somewhere between −5 and −10%, a level that is believed not to harm reproduction."

The effects of pesticides on eggshell thickness were first identified by changes in an *eggshell index* (EI) calculated as the weight of the whole empty eggshell in relation to the egg size (Ratcliffe 1967), a method most suitable for museum collections of whole eggs (Ratcliffe 1993). To analyse samples from broken eggs and fragments from hatched eggs, as in this study, measurements of the actual *shell thickness* (ST) are required. However, when assessing the degree of *eggshell thinning*—how much thinner compared to the normal pre-DDT thickness—the two methods provide different results. Since the EI is based on the mass of the eggshell, it captures changes in both *thickness* and *density* of the shell, i.e., that the shell may also become more porous with increasing contaminant loads (Cooke 1979).

Fyfe *et al.* (1988) found that the two methods only differ by 1%, but for Swedish Peregrines, Odsjö & Lindberg (1977) reported a reduction of 17.7% when comparing the EI of eggs from 1861–1943 vs. 1948–1976, and only by 12.1% in the ST. Similarly, in Norwegian Peregrines Nygård (1983) found a reduction of 22.7% in EI and 18.7% in ST. These variations in how the level of shell thinning in a population is reported influence the identification of a critical threshold for when shell thinning affects falcon reproduction and population stability.

By comparing the shell thinning and population trends in various Peregrine populations, Peakall & Kiff (1988) identified eggshell thickness change of −17% as the critical threshold for population *decline*. Their compilation included mostly ST, but at least for Swedish and Finnish Peregrines the data included (Figure 3 in Peakall & Kiff 1988) were EI, so the real limit should be closer to −15%. Fyfe *et al.* (1988) studied eggshell thinning effects on *productivity* of Peregrine pairs and found that a mean thinning of 14.5% in the ST was the threshold for observing any impact on number of young produced. Hence, we considered a reduction of 14.5% to 17% in shell *thickness* to be the risk threshold as indicated by grey bars in Figure 2. As seen in Figure 2c, a large proportion of the clutches were below that threshold until around 1990, i.e. around the time when the recovery of the Peregrine population in Sweden gained momentum; the Swedish Peregrine population increased by 5–10% annually in the 1990s (Lindberg 2009).

Because the population in northernmost Sweden and neighbouring Finland had fared slightly better during and after the population crash in the 1960s and 1970s (Lindberg *et al.* 1988, Koskimies & Ollila 2022), we hypothesised that shell thinning could have been less pronounced than in southern Sweden. However, we could not detect a significant difference in shell thickness between northern and southern clutches (Table 2), nor any significant rate of change in the recovery of shell thickness (Figure 2c). Nevertheless, compatible with the results in Table 2, it is not impossible that the population impact of eggshell thinning might have been slightly weaker in northern areas, potentially masked by the large natural variation in the material. The notion is supported by a study from Finland where Lindén *et al.* (1984), based on a sample of 10 clutches only, found that eggshells were significantly thinner in southern Finland compared to clutches from northern Finland.

Götaland in southern Sweden is the core breeding area for Peregrines and also the country's most intensive agricultural production area (Jordbruksverket 2022), so it is reasonable to assume that the falcons in that region would have been exposed to relatively higher doses of contaminants during the peak DDT-use. In the UK, Newton *et al.* (1989) showed that the spatial patterns of DDT/DDE in Peregrine eggs closely corresponded with the extent of farmland. In a subsequent long-term study in southern Scotland, Oli *et al.* (2023) found that, in a farmland study region, nearly all Peregrine productivity parameters had reached lower levels in the peak pesticide period, and improved later after the main pesticides were phased out, compared to Peregrines in a neighbouring more forested area. However, contaminant exposure patterns are highly complex, and the migrant Peregrines breeding in northern Scandinavia could have been exposed to heightened contaminant loads in their wintering grounds (Lindberg *et al.* 1985), so the net exposure and loads even out, which could lead to similar levels of shell thinning.

DATA CHALLENGES AND SAMPLING RECOMMENDATIONS

Studying eggshell thinning involves detecting rather small differences in a heterogenous sample material with considerable natural variation ("noise"). As shown by the scatter of dots (clutch means) in Figure 2, there is a huge variation in the data across all 16 decades. To manage that challenge, we have made all efforts to minimize the potential errors from the process of measuring the shell thickness. Some of the material had been measured in the 1980s and 1990s by different persons and measuring devices so we opted for re-measuring available samples, calibrated devices and procedures, cleaned egg surfaces as needed, selected measuring points at the equator of whole eggs, measured many fragments from each nest, and established an average membrane correction value confirmed by different methods. Hence, we are confident that the data represent the inherent variation in the eggshell thickness.

However, the material included samples with and without shell membranes, and the thickness of membranes is also variable, both naturally during the development of a viable egg (Castilla *et al.* 2010a) and between samples (in our material it ranged between 0.034 and 0.087 mm). The cluster of red dots for the period 2017–2023 in Figure 2b shows measurements (from Västernorrland) mainly based on eggshell fragments *without* membranes, where the standard membrane constant (0.057 mm) was applied. This contrasts to the data from earlier years based on a mixture of samples, many of them *with* membranes, giving a larger variation in the clutch means plotted in Figure 2b.

The uneven distribution of sample sizes and types (with/without membranes) across years could introduce a bias affecting the overall estimated recovery rate (regression slope) of shell thickness but the potential effect was minimized by analysing the long-term trend on annual means, not clutch means.

The average membrane thickness (0.057 mm) that we added to measurements without membranes for comparisons with museum collection reference eggs was lower than reported from other studies of Peregrines, e.g., Nygård (1983): 0.070 mm; Wegner *et al.* (2005): 0.06–0.08 mm; Falk *et al.* (2006): 0.071 mm; and Castilla *et al.* (2010a): 0.066 mm. Our measurement technique exerted a minimal pressure, so a compression of the relatively soft membrane structure cannot explain the lower value. However, we noticed that some samples (e.g. addled eggs opened during this study and dried for nine months) had higher average membrane thickness than others (e.g. old fragments), adding to the variability in thickness measurements. Hence, measuring shells *without* membranes provide the most consistent data and this approach should be encouraged in monitoring future trends in shell thinning, so a membrane constant is only applied to compare the results with reference collections which usually do include membranes.

Earlier studies of Peregrine eggshell variation recommended to include as many samples as possible for detecting shell thinning and trends (Burnham *et al.* 1984, Falk & Møller 1990). We made use of whole eggs as well as eggshell fragments from broken and/or hatched eggs in order to increase overall sample size and found no differences in shell thickness between the two sample types. Following Odsjö and Sondell (1982) we assumed that the 20 eggshell fragments measured from each nest would provide an estimate of mean shell thickness of each clutch, although results from some clutches may have been biased due to over- and underrepresentation of certain eggs in the clutch, or of thinner or thicker parts of an egg. However, such potential bias must be randomly distributed across clutches and years and cannot influence the overall findings of neither the levels of shell thinning nor the long-term trends. For continued monitoring of shell thickness, fragments have a few advantages over whole eggs: they are relatively easy to collect from a large number of nests while whole eggs are encountered more rarely; they are less cumbersome to manage in relation to permits, transport and storage; and they do not require lengthy laboratory procedures before they are ready to be measured. We conclude that eggshell fragments are a valuable sample type that should be routinely collected in the future as a supplement to whole addled eggs.

SHELL THINNING EFFECTS AND PROSPECTS

It was slightly surprising that shell thickness in Sweden (and Norway; Nygård *et al.* 2019) was still not fully back to pre-DDT levels by the 2020s. In Germany, Peregrine "shell thickness had normalised to large extent by 2002" (Wegner *et al.* 2005) and in Denmark at least by 2016, albeit based on a small sample size (Andreasen *et al.* 2018). However, Schwarz *et al.* (2016) found 4% shell thinning in southern Germany and suggested that it could be due to the persistent presence of residues of DDE and other harmful chemicals. Indeed, DDT/DDE is still detected in low concentrations in typical Peregrine prey species in Europe, e.g. in Blackbirds *Turdus merula* in Spain (Díez-Fernández *et al.* 2023), so migrant prey as well as the Peregrines themselves could still carry contaminants to the breeding grounds in Sweden. The Swedish and Norwegian studies represent the northernmost Peregrine populations in Europe where the long-term changes in shell thickness have been examined. A parallel example is the highly migratory Peregrines in Greenland, where shell thickness is not yet back to normal, possibly due to some limited DDT exposure in their wintering grounds in Latin America (Falk *et al.* 2006, 2018).

A potential challenge in interpreting shell thinning based on different sample types is that the developing embryo extracts calcium from the eggshell, so fully developed and hatched eggs could have slightly thinner eggshells than undeveloped and addled eggs (see overview by Orłowski & Hałupka 2015). Burnham *et al.* (1984) and Bunck *et al.* (1984) found no such effect, but Castilla *et al.* (2010b) found 1.6% and 4.9% reduction in shell thickness in fully developed eggs from two Peregrine subspecies, respectively. In our study, ¾ of all samples came from whole addled eggs, i.e., eggs mostly without embryo development, and we found no difference between whole egg and fragment samples from the same years. Our results based on fragments, of which most would derive from successfully hatched eggs, tended to be slightly thicker, not thinner (but far from significantly so—see Figure 2b), so we consider that any potential effect of embryo-induced thinning on the results must be negligible.

Could there be other factors slowing down the recovery of shell thickness? While it was well established that, among the classical contaminants, only DDT and its breakdown products directly affect calcium deposition during eggshell formation leading to shell thinning (Newton 1979, Fyfe *et al.* 1988, Peakall 1993), limited shell thinning effects of other substances have been reported in falcons. For example, some flame retardants (PBDEs and HBCDD) caused up to 6% thinner eggshells in captive American Kestrels *Falco sparverius* (Fernie *et al.* 2009); high concentrations of PBDEs have been found in Swedish Peregrines and linked to decreasing brood size (Johansson *et al.* 2009). In fact, many chemical compounds and pharmaceuticals have been shown to induce changes in eggshell thickness in birds of prey (see comprehensive list in Table 2 of de Solla *et al.* 2023). One group of pharmaceuticals, the NSAIDs (non-steroidal anti-inflammatory drugs; ingredients in pain killers such as Naproxen and Voltaren) can influence calcium pathways during the eggshell formation in similar ways as DDT/DDE, and the substances have been found in many bird species, in particular in scavengers such as vultures but also in gulls and terns (de Solla *et al.* 2023), which are typical peregrine prey species. The use of NSAIDs, and leakage into the environment, has drastically increased over the past decades, and de Solla *et al.* (2023) conclude that "the available evidence indicates that NSAIDs are a hazard to birds in terms of inducing eggshell thinning". The Peregrine may not be among the species most likely to be highly exposed, but this is an emerging risk to keep an eye on.

Conclusions

Eggshell thinning in Swedish Peregrines exceeded critical levels at least in the 1960s–1980s, and while eggshell thickness has since recovered to safe levels, it is still 7% thinner than before organochlorine pesticides were introduced. No significant differences in thickness or rate of recovery could be detected between Peregrines breeding in northern and southern Sweden, respectively. Since the shell thickness is not fully restored to normal, and because new substances may be of emerging concern, it is worthwhile to continue the relatively simple and low-cost way to monitor one of the effects of environmental contaminants. Based on our experiences from measuring and comparing the different types of samples, we recommend collecting eggshell material from as many clutches as possible, measuring eggshells without membranes whenever possible to obtain the most consistent data for trends analyses, and only involving a membrane constant when comparing to normal level in historical reference collections. Birds of prey, including the Peregrine, remain important indicators for unintended side effects of chemical substances released into the environment.

ACKNOWLEDGEMENTS

Firstly, our heartfelt thanks to the many volunteers who made this study possible by helping monitor the Peregrine population in Sweden and collect the samples over many decades under the auspices of, and support from, the Swedish Society for Nature Conservation and BirdLife Sweden. We thank Sara Danielsson and Ulf Johansson at the Swedish Museum of Natural History for support in the laboratory and access to the archived material in the Environmental Specimen Bank and the historical collections. A grant from Alvin's Fond to PL (NV-02830-21) covered materials and logistics for conducting this study, while sampling and measuring the material from Västernorrland 2015–2023 by PN and FO was part of the environmental monitoring of the County Administrative Board of Västernorrland.

DATA AVAILABILITY

Raw measurement data are available as Supplementary Information deposited at the Arctic Raptors Monitoring community at Zenodo: https://doi.org/10.5281/zenodo.14692789.

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Svensk sammanfattning

INLEDNING

Under mitten av 1900-talet stod populationsstorlekarna för pilgrimsfalken *Falco peregrinus* i Europa och Nordamerika inför betydande nedgångar. I Sverige var endast 15 par kända år 1975, vilket var en kraftig minskning från det uppskattade minimum på 900 par i början av 1900-talet. Den huvudsakliga orsaken var minskad reproduktion och ökat dödlighet orsakad av pesticider, främst DDT, som stör kalciumdepositionen under bildandet av äggskal. Detta ledde till tunnare äggskal och i slutändan färre flygga ungar. Mätningar av äggskalens tjocklek blev en indikator för DDT-exponering och upptäckten av sådana oväntade sidoeffekter av besprutningsmedel påverkade hela den globala miljöpolitiken. Sedan förbudet mot de mest skadliga ämnen på 1970-talet, tillsammans med bevarandeinsatser, har pilgrimsfalkspopulationerna i stort sett återhämtat sig. Den svenska populationen uppskattas nu till cirka 650 besatta revir.

Denna artikel undersöker förändringarna i äggskaltjocklek under en 160-årsperiod och ställer frågan om eventuella regionala skillnader finns mellan de flyttande pilgrimsfalkar i norra Sverige och falkarna i söder, som i högre grad stannar i eller nära sina häckningsplatser året om. Resultaten bidrar till de pågående övervakningsinsatserna och betonar vikten av rovfåglar som indikatorer för miljöföroreningar.

METODER

Tre provtyper av äggskal (figur 1) från olika tidsperioder mättes: (a) 102 ägg från 36 kullar från tidsperioden 1864–1965 som förvaras på Naturhistoriska Riksmuseet (NRM) i Stockholm, (b) 361 okläckta döda ägg, s.k. ”rötägg” från 315 kullar som samlats in under tidsperioden 1972–2023 och förvaras vid Miljöprovbanken, också på NRM, och (c) äggskalsfragment från 115 bon från åren mellan 1972 och 2023. Se fördelning av proven i tidsperioder och områden i tabell 1. Proverna har samlats in över hela Sverige under aktuell tidsperiod och vi har kategoriserat dem som ”norra” (över 61°N) respektive ”södra” (Svealand och Götaland) i datasetet. Mätningarna utfördes med en analog mikrometer för hela ägg i museets samling och digitala mikrometrar för nyligen tagna prover och äggskalsfragment. Kalibrering och konsistens säkerställdes genom att jämföra mätningar tagna av två personer (KF och FO) på 105 referensäggskalsfragment. För att jämföra prover utan äggskalmembran med museets samlingar identifierades en ”membrankonstant” på 0,057 mm som lades till mätningarna utan membran. Äggkullar från 1864 till 1945 representerar den normala skaltjockleken före DDT började spridas i miljön.

RESULTAT

Äggen i museets referenssamling (1864–1945) hade en genomsnittlig skaltjocklek på 0,345 mm, vilket får räknas som det normala (referensvärdet) utan inverkan av miljögifter (tabell 2). Tre kullar från 1948 (gula markörer i figur 2a) visade normal skaltjocklek, men på grund av ett stort prov gap fram till 1964 finns det ingen information om när äggskalsförtunningen började förrän det var uppenbart 1964–1965 (figur 2c). Den röda regressionslinjen i figur 2c antyder att genomsnittet var runt 17% tunnare än referensvärdet i slutet av 1960-talet; det totala genomsnittet under 10-årsperioden 1974–1984 var 16% tunnare (tabell 2). De tunnaste registrerade kullarna var 29% under referensvärdet och kom från Bohuslän 1980 och Norrland 1981 (figur 2b–c). Under de senaste 60 åren har det skett en signifikant återhämtning, med genomsnittlig skaltjocklek som nu är 7% under nivån före DDT (tabell 2, figur 2c). Regionala skillnader i äggskaltjocklek och återhämtningstakt observerades mellan norra och södra Sverige, men var inte statistiskt signifikanta (figur 2c). Studien identifierade en genomsnittlig förtunning om 14,5–17% på populationsnivå som riskzon för den svenska pilgrimsfalkspopulationen. Under perioden 1964–1980 var 58% av kullarna i riskzonen, medan endast 10% var i riskzonen under det senaste decenniet.

DISKUSSION

Att studera äggskalförtunning innebär att upptäcka relativt små skillnader i ett heterogent material med betydande naturlig variation. För att minimera fel kalibrerade vi mätinstrument och metoder, rengjorde äggens ytor och etablerade ett membrankorrigeringsvärde. Vi är övertygade om att data representerar den verkliga variationen i äggskalstjocklek.

I Tyskland och Danmark är skaltjockleken hos pilgrimsfalk numera i stort på normal nivå, men i Sverige observeras fortfarande en förtunning kring 7%. Utvecklingen liknar resultat från Norge, där äggskal hos pilgrimsfalk var relativt tunna under 1970- till 1990-talen, för att sedan ha ökat till nästan normala nivåer under de senaste två decennierna. Men de norska äggen ligger fortfarande cirka 5 och 10% under det normala, en nivå som dock inte skadar populationens reproduktion. En förtunning om 14,5–17% identifieras som en kritisk nivå, eftersom uttunning över denna nivå kopplas till minskad häckningsframgång och populationsnedgång. Inga signifikanta regionala skillnader observerades i tjocklek eller återhämtningshastighet mellan norra och södra Sverige.

Även om DDT/DDE har visats vara det kemiska ämne som har mest direkt inverkan på äggskalens tjocklek finns en rad andra ämnen som kan bidra, inklusive vissa flamskyddsmedel. En grupp ämnen som nyligen uppmärksammats ha liknande effekt som DDT/DDE är så kallade NSAID – anti-inflammatoriska och smärtstillande medel – som ökar i miljön och har hittats i en rad fågelarter.

SLUTSATSER

Äggskalsförtunning hos svenska pilgrimsfalkar översteg kritiska nivåer från 1960-talet till 1980-talet, men skaltjockleken har sedan återhämtat sig till en säker nivå och är nu 7% tunnare än innan besprutningsmedel började spridas i miljön. Vi rekommenderar detta enkla och billiga sätt att övervaka en av effekterna av miljögifter fortsätter. Rovfåglar, som pilgrimsfalken, fungerar som miljöindikatorer för oavsiktliga kemiska effekter i allas vår gemensamma livsmiljö.

BirdLife Sverige

Ornis Svecica (ISSN 2003-2633) is an open access, peer-reviewed scientific journal published in English and Swedish by BirdLife Sweden. It covers all aspects of ornithology, and welcomes contributions from scientists as well as non-professional ornithologists. Accepted articles are published at no charge to the authors. Read papers or make a submission at os.birdlife.se.

Ornis Svecica (ISSN 2003-2633) är en fritt tillgänglig granskad vetenskaplig tidskrift som ges ut på svenska och engelska av BirdLife Sverige. Den täcker ornitologins alla områden och välkomnar bidrag från såväl forskare som icke-professionella ornitologer. Accepterade uppsatser publiceras utan kostnad för författarna. Läs uppsatser eller skicka in ditt bidrag på os.birdlife.se.