On the eggshell thickness and reproduction of the Peregrine Falcon Falco peregrinus in Finland

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There are two different Peregrine breeding areas in Finland, which are rather clearly separated from each other. The size of the northern part of the population is increasing and its production of young is fairly good, while the southern population is static and has poor reproductive parameters. The eggshell thickness was measured for six northern and four southern Peregrine clutches by an X-ray back-scatter method indicating the amount of calcium per unit area (Ca index) in the eggshell. The northern clutches had about 10 % thicker eggshells than the southern ones. There was a slight negative correlation (r = -0.35) between the evaporation rate of the egg and the Ca index. The production of young showed statistically significant dependence on the Ca index, which may be attributed to breakage of thin-shelled eggs, and possibly to disturbances in embryo development caused by abnormal evaporation. The growth rate of the chicks was also closely dependent on the Ca index. The exceptional habit of Finnish Peregrines of nesting almost entirely on bogs and the greater success of bog-nesters as compared to cliff-nesters are discussed.

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Introduction

In the 1960s the Peregrine Falco peregrinus population in Finland was rapidly declining, and the fate of the species seemed very uncertain (Linkola & Suominen 1969). The decline in Finland was very similar to those observed in Sweden (Lindberg 1975) and Norway (Nygård 1983) and in other countries in the northern hemisphere (e.g. Ratcliffe 1980). Since the mid-1970s the Finnish Peregrine population has increased slightly, especially in the north (Wikman 1983).

There are marked differences in breeding success between the northern $(+66^{\circ}N)$ and southern $(-66^{\circ}N)$ parts of the Peregrine population in Finland; the southern part of the population has had 45 % lower production of young than the northern one (Fig. 1). In consequence, the size of the southern population does not show any increasing trend (Wikman 1983, 1984). The majority of nest losses in the south seem attributable to egg breakage, due to eggshell thinning. This phenomenon has been shown to be connected with high DDE contents of the eggs (e.g. Ratcliffe 1970, Cade et al. 1971, Miller et al. 1976).

The main goals of this paper are to report on the geographical variation in the eggshell thickness within Finland and on its relation to the evaporation rate of the egg during incubation, and to the breeding success and postnatal growth of the chick.

Material and methods

The use of addled eggs only, in studies of this kind, may lead to samples biased in favour of the more heavily contaminated eggs, as a negative correlation has been shown between the organochlorine content and hatching success in raptors (Newton & Bogan 1978). An unbiased sample of eggshells can, however, be obtained by using a special apparatus: A weak non-destructive X-ray source is used to irradiate the eggs, and the back-scattered rays are picked up by a detector coupled to a unit with a pulse height analyser, counter and timer (see Odsjö & Forberg 1977 and Forberg & Odsjö 1983 for details of the method).

The back-scatter efficiency of the egg will vary exponentially with the calcium content per unit area of the eggshell. This is expressed as a Ca index, where the back-scatter from the eggshell is compared with that of a reference egg of polyester.

Ca index = 1000 log r/e, where: r = net count rate of the reference egg e = net count rate of the egg.

The Ca index can be roughly converted to an eggshell index (Ratcliffe 1970) with our empirical equation: shell index = $4.13 \times 10^{-4} \times Ca$ index — 0.90 (r=0.99). This equation is based on measurements of 14 hens' eggs and one Merlin *Falco columbarius* egg. The shell indices are highly correlated with the actual shell thickness (For-

berg & Odsjö 1983). Four measurements were taken on each egg, and the Ca index is given as a mean value. A correction was made for the background radiation.

Ca indices were calculated for 10 Peregrine clutches on 18-27 May 1983. Most clutches were complete and fresh when measured. In two cases one additional egg was laid afterwards. Four clutches were located in the southern region (south of 66°N) and six in the northern region (north of 66°N). These two regions are clearly separated from each other by an "empty" zone of about 100 km. The clutch size was four in nine cases and two in one case. The total number of eggs measured was 35. The female with the two-egg clutch was in juvenile plumage (2nd year). Three other females were colour ringed; two were in their 7-8th year and one in its 5-6th year.

Egg weights were taken with a Pesola spring balance, with an accuracy of 0.1 g, on two occasions with an interval of at least two weeks. Data on the weight loss, indicating the evaporation rate (g day⁻¹), were obtained for 19 eggs in six clutches. Three of the southern elutable bed failed after the fortune weight loss. clutches had failed after the first weighing, and thus no figures on weight loss are available for these. The fourth clutch in the southern region had one broken egg when the eggs were reweighed. Hence the figures on weight loss for the southern region are limited to three eggs.



Variation in eggshell thickness and evaporation rate. The between-clutch variation in eggshell thickness was significantly higher than the withinclutch variation (ANOVA, P<0.001). We have therefore let the clutch means of the Ca indices represent the female's typical eggshell thickness in all cases.

The Ca indices for the northern clutches (612.5 ± 16.5 (SE), N=6) were significantly higher (t = 2.74, df = 8, P < 0.05) than for the southern ones (555.9 ± 12.3 N=4). Converted to eggshell indices, these figures gave means of 1.63 and 1.40 respectively.

The evaporation rate of the eggs (weight loss, g day⁻¹) during incubation was inversely proportional to the eggshell thickness (r = -0.345, df = 17, $0.20 < \overline{P} < 0.10$). Though not statistically significant, this result may be of importance, because the opposite result could have been predicted (see Discussion). The average daily weight loss \pm SE was 0.194 \pm 0.018 g (N = 19). The within-clutch variation was greatest in the clutch with the lowest Ca index (range 0.14 to 0.47 g day⁻¹). The lowest value $(0.08 \text{ g day}^{-1})$ was found for an egg in a clutch where the three other eggs had normal evaporation.

According to the linear regression, the average evaporation rate of an egg with a Ca index of 550 is 0.23 g day⁻¹, and the rate for a Ca index of 650 is 0.18 g day⁻¹. These rates give total evaporative weight losses during incubation of 18 and 15 % respectively - assuming 0.3 g preincu-

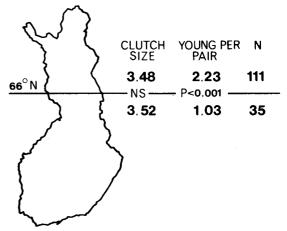


Fig. 1. Brandt-Snedecor X²-test.

Comparison of two reproductive parameters (clutch size and young per territorial pair) between northern $(+66^{\circ}N)$ and southern $(-66^{\circ}N)$ Peregrine populations in Finland. Differences tested with the

bational and 1.03 g pip-to-hatch weight loss, and 33 days for incubation (see Burnham 1983).

Eggshell thickness and breeding success. The relative production of young (chicks/eggs in clutch) was found to be significantly dependent on the Ca index (Fig. 2). The southern pairs did not hatch one single chick from 16 thin-shelled eggs, while the northern ones raised 14 young from 22 thicker-shelled eggs (64 %).

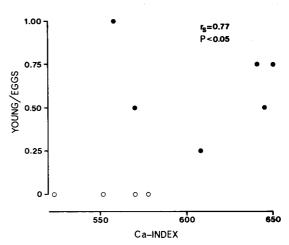


Fig. 2. Mean Ca index of the clutch in relation to relative reproductive success (young/eggs in clutch) in the Peregrine (Spearman rank correlation test). O = southern, and \bullet = northern clutches.

The relation between wing length and chick weight was relatively poor for 7 male chicks (r = 0.73, P<0.10, Fig. 3A), indicating marked individual variation in growth rates. The residual variation (R) around the obtained regression can be calculated as the deviation (in grams) from the predicted value given by the regression in Fig. 3A. This residual variation can further be explained (P<0.05) by the eggshell thickness, i.e. the chicks with more rapid growth originate from eggs with thick shells (Fig. 3B).

The reproductive success was extremely poor in the southern region in 1983. In the eight territories occupied by pairs, only one pair raised young. Six pairs failed due to egg breakage or nest desertion and one pair did not lay at all. The northern territories, on the other hand, produced 2.4 young per territorial pair. The low figures obtained in 1983 are perhaps somewhat

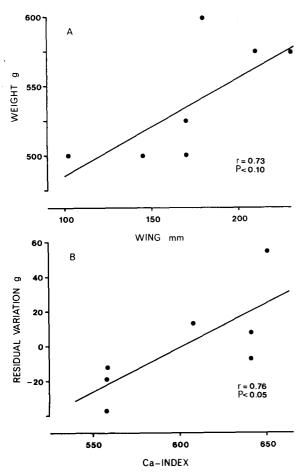


Fig. 3A. Chick weight in relation to wing length in seven male Peregrines. 3B. The residual variation (in grams) from the regression (in Fig. 3A) correlated with the Ca index.

exaggerated and may not prevail over time, as slight improvements in reproductive success for the southern territories have been recorded since the late 1970s (Wikman 1983).

Discussion

Our finding that the southern part of the Peregrine population lays eggs with thinner shells than those of the northern birds is consistent with the pattern of reproduction and population decline observed in different parts of Finland (Salminen & Wikman 1977, Wikman 1983). The low Ca indices and subsequent egg breakage suggest that DDE is one of the main agents depressing the reproductive output (see Peakall et al. 1975, Newton & Bogan 1978). High residual levels of DDE have been found in Finnish Peregrine eggs, ranging from 85 to 1580 ppm (lipid weight), and quite high levels of PCBs have also been recorded (Lindberg et al. 1983a: Table 6). The large variation (CV 107 %) in DDE levels indicates that the contamination of the population is not uniform. One further important fact to bear in mind is the finding of Lindberg et al. (1983b) that the levels of residues in some important prey species on the breeding grounds are not high enough to account for the levels found in the Peregrines. which implies that most residues are accumulated outside the breeding grounds, probably in the wintering areas, as shown for migrating North American Peregrines (Henny et al. 1982). It is reasonable to assume that there are clear inter-individual differences in the wintering areas, and also that individual birds winter in the same locality from year to year. Such behaviour would explain the large variations observed in residue levels and the difference in reproductive success between the northern and southern territories. The southern Peregrines may winter in more contaminated areas than the northern ones. However, there are not enough recent ring recoveries to test this hypothesis.

Although our present conversions of Ca indices to more generally applicable shell indices may be only approximative, these figures are alarming. If 1.87 is taken as a normal mean pre-DDT shell index for Fennoscandian Peregrine eggs (Odsjö & Lindberg 1977), our 1983 means of 1.40 and 1.63 give a degree of shell thinning of 25 and 13 %, respectively. Eggshell thinning of 25 % will severely depress reproductive output (e.g. Newton 1979), and thus further desertions of southern territories can be expected, without compensatory immigration. It is therefore obvious that any conservation or manipulatory measures considered, should clearly focus on these few remaining southern territories.

Our present figures on nestling growth are admittedly scanty, but their interpretation is serious, if they reflect a general trend. Retarded nestling growth is commonly taken as a sign of weakness and may lead to lower fledging weight and higher postfledging mortality (see Schifferli 1973). This would further depress the already low reproductive output of the southern part of the population. We do not know of any studies dealing specifically with nestling growth in pesticidecontaminated raptors, and this is thus a matter calling for further attention.

The daily weight loss of the eggs during incubation was mostly within the normal range, as judged from the values for Peregrine eggs incubated artificially (Burnham 1983). No figures were obtained for three of the southern clutches, whose Ca indices were below 600, as they failed before reweighing. Thus we lack sufficient data for the more interesting thin-shelled eggs. Artificially incubated Peregrine eggs from Finland showed a high rate of evaporation (Wikman 1981, unpubl.) and required exceptionally high humidity (80 % RH) to keep the weight loss with a normal range. In eggs of captive American Kestrels Falco sparverius given food containing DDT, the rates of evaporation were lower than normal (Peakall et al. 1973). Electron microscopy revealed larger but fewer pores in the shells. Cooke (1979) found reduced water loss in recent eggs compared with old ones, though the recent eggs had a greater mean number of pores and mean pore area per unit area of egg surface. Our results do not agree with these earlier studies and the relationship between shell thinning and evaporation rate still seems obscure.

This leads to the mystery of the present distribution and nesting habits of the Finnish Peregrine population. Why did cliff-nesters perish, while bog-nesters persist? Bog nesting in Peregrines is a habit found only around the Baltic (Hickey 1969). The southern birds were evidently more contaminated and this part of the population was wiped out, but the last territories occupied south of 64°N in the early 1970s were all bog sites. We have records of only two cliff sites still occupied, and these are the two northernmost (north of 68°N) territories known in Finland. Could the high humidity of the microclimate on bogs counteract excessive water loss, and enhance successful hatching of moderately contaminated eggs? We cannot, however, totally discard the possibility that the disappearance of cliff nesting is the result of chance, because bogs vastly outnumber crags in the areas where Peregrines still persist.

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Selostus: Tämän päivän muuttohaukkojen munankuoren paksuudesta Suomessa

Suomen muuttohaukat pesivät nykyisellään kahdella, toisistaan selvästi erillään olevalla alueella, joiden parhaana erottelijana on 66. leveyspiiri. Pohjoisemmat haukat ovat viime aikoina runsastuneet ja niiden poikastuotto on selvästi parempi kuin eteläisten haukkojen (kuva 1). Eteläinen muuttohaukkakanta on pysytellyt pienenä, mikä lähinnä johtuu munien rikkoutumisesta haudonnan aikana. Klooratut hiilivedyt ovat tähän pääsyyllisiä.

Yhteensä 10 pesyeen 35 munan kuoren paksuudet mi-tattiin toukokuun loppupuoliskolla 1983 radiometrisesti. Mittaus paljastaa itse asiassa kuoren kalkin määrän. Kalkin määrä on suoraan verrannollinen kuoren paksuuteen. Pohjoisia pesyeitä mitattiin kuusi ja eteläisiä neljä. Kaikki munat pyrittiin punnitsemaan kahteen otteeseen haudonnan aikana haihduttamisnopeuden määrittämiseksi. Poikastuoton toteamisen yhteydessä määritettiin myös poikasten kasvunopeus painon ja siivenmitan suhteesta (vrt. kuva 3). Pohjoisten pesyeiden munien Ca-indeksi (paksuus) oli merkitsevästi suurempi Ca-indeksi (paksuus) oli merkitsevästi suurempi (612.5±16.5; SE) kuin eteläisten (555.9±12.3). Näyttää siltä, että ohutkuoriset munat haihduttavat enemmän kuin paksukuoriset; paksuuden ja haihdunnan välinen korrelaatio (r = -0.35) ei tosin ole merkitsevä. Oikea haihdunta on kehittyvälle alkiolle oleellisen tärkeä.

Poikastuotto (poikasia/munia) oli merkitsevästi riippuvainen munankuoren paksuudesta (kuva 2). Eteläiset, ohutkuoriset munat eivät tuottaneet poikasia lainkaan. Myös poikasten kasvunopeus oli riippuvainen Ca-indeksistä (kuva 3). Poikasen paino korreloi tietenkin positiivisesti siiven pituuden kanssa (kuva 3A), mutta yllättä-vän heikosti; siiven pituus selitti vain 53 % painon vaihtelusta. Kuoren paksuus selitti vielä merkitsevästi todettua jäännösvaihtelua (kuva 3B). Paksukuorisista munista kuoriutuneet poikaset kehittyvät nopeammin kuin ohutkuoristen munien poikaset.

Aikaisemmin on todettu, että muuttohaukkojen täytyy saada suurimman osan ympäristömyrkkykuormitukses-taan talvehtimisalueilta. Mikäli meikäläiset eteläiset ja pohjoiset muuttohaukat talvehtisivat erillään toisistaan, se saattaisi selittää erot kuoren paksuudessakin. Onko ohutkuorisuudella, liiallisella haihdunnalla ja pesinnällä kosteissa suoympäristöissä yhteyttä keskenään? Meikäläiset haukathan ovat lähestulkoon ainoita suopesijöitä maailmassa.

Suomen muuttohaukkakanta on lievästi kohentunut viime vuosina, mutta se on kuitenkin vielä niin pieni, että jokin katastrofi saattaisi ajaa kannan sukupuuton partaalle. Tällaisessa tilanteessa tarvittaisiin runsaasti lisätietoja munien ominaisuuksista ja mahdollisuuksista manipuloida munia tuloksekasta keinohaudontaa varten.

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