

Weights of yolk body and hatchling in relation to the egg weight in the Treecreeper *Certhia familiaris*

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Abstract

The weights of fresh eggs, yolk bodies, and hatchlings were measured during the period 1998–2000 in a Treecreeper *Certhia familiaris* population in a deciduous forest in south-western Sweden. The weight of the hard-boiled yolk body was positively and significantly correlated with the fresh egg weight among and within clutches. The same significant inter- and intra-clutch relations were also found between eggs and young nestlings (average age 12 hours) or fresh hatchlings, both with regression coefficients of a magnitude surpassing those of other investigated passerine species. The proportion of yolk weight tended to

decrease with increasing egg weight, whereas the proportional weight of the hatchlings increased, showing a significant linear regression upon egg weight. The pronounced weight increase of hatchlings from heavier eggs strongly suggests a possible adaptive significance of the likewise pronounced intra-clutch egg weight hierarchy in the Treecreeper population studied.

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Introduction

The size and weight of eggs vary considerably between and within clutches in the Treecreeper *Certhia familiaris*. The eggs increase in weight in the laying sequence. This weight hierarchy was considered adaptive presupposing that the larger eggs give rise to larger or heavier hatchlings (Enemar 1997). Such a relation in all probability applies to the Treecreeper, as a positive egg/hatchling correlation has been demonstrated, albeit with varying accuracy, in all of the fourteen other investigated passerine species (for references, see Discussion). Most results are based on comparisons among clutches, whereas information on the egg/hatchling relation within clutches is scarce or non-existent. Knowledge of the latter relation is crucial for the interpretation of the significance of the intra-clutch egg weight hierarchy and was therefore included in this study, together with estimations of the egg/hatchling relations among clutches.

Opinions differ regarding to what extent the weight variation reflects a corresponding variation in the quality and composition of the egg. It has been demonstrated in a few species that the weight in-

crease is mainly due to inclusion of more water (Bryant 1978, Ojanen 1983b, Clarkson 1984, Bancroft 1985) which may apply also to the hatchling (Clarkson 1984). As a matter of fact, there seems to be no consistent pattern in the relation between egg size and egg composition among passerines (Williams 1994). Thus, this study also focused on the relation between the weights of the egg and its yolk body, although the amount of yolk with its lipids provides only a coarse measure of the egg quality. However, a heavier hatchling may retain more yolk as a reserve (e.g. Bryant 1978, Rofstad & Sandvik 1985), which indicates at least one possible effect of the yolk mass variation to be considered when interpreting the meaning of the intra-clutch egg weight hierarchy

Methods

Hatchling weights of the Treecreeper were recorded during the springs of 1998–2000 in the Gunnebo recreational grounds outside the town of Mölndal in south-western Sweden. The investigated population

breeds in artificial nest pockets (cf. Enemar 1992). A small sample of fresh eggs was collected in spring 2000 for estimation of the yolk weights.

The occupied pockets were inspected daily, mostly before noon, during the laying period to mark the newly laid eggs according to their laying order and to weigh them with the aid of a portable electronic balance (Bonso model-337) to the nearest 0.01 g. The nest visits were resumed during the days of hatching to weigh the hatchlings. Some nests were inspected several times a day to increase the prospect of discovering a single new hatchling, whose origin could be traced among the eggs. In order to evaluate the significance of age differences between the eggs and between the hatchlings when weighed, the daily weight change of some eggs was recorded before the start of incubation. The weight increase of a few hatchlings was followed during the first one or two days after hatching.

In order to study the weight relation between yolk and egg within clutches, two of the last laid eggs were taken from six nests before the beginning of full incubation, i.e. when the swelling of the yolk bodies had not yet started (cf. Enemar 1995). To increase the number of egg pairs, a six-egg clutch was used which was deserted immediately after laying. The two heaviest and lightest eggs were selected as pairs to be included in the analysis. (The number of collected eggs had to be kept at a minimum to avoid too heavy a toll on the reproductive output of the sparse population under study.) The eggs were boiled hard to facilitate a precise separation and handling of the yolk bodies which were weighed on the above-mentioned balance (cf. Muma & Ankney 1987). In order to be able to use the obtained measurements for investigating the variation pattern of the yolk mass in relation to the egg mass, it was presumed that the hard-boiled yolk bodies had all lost in weight in proportion to their fresh weights.

The statistical tests used are two-tailed: the parametric two-sample t-tests and regression (Bonnier & Tedin 1940), and the t-test for matched pairs (Fowler & Cohen, printing year lacking).

Results

The weight loss of eggs during the laying period

The weight loss of the first three eggs from clutches of five and six eggs was slightly more than one half per cent during the first day after laying (mean 0.64

$\pm 0.54\%$ (S.D.), $n = 40$). This corresponds to only 0.008 g of the mean weight of a fresh egg (1.26 ± 0.10 g, $n=133$ (Enemar 1997)), which may on average reduce the last figure of the weight measurements by about one unit only. Therefore the weights of the one day old eggs have been included in the analyses without adjustments, in the few instances ($n = 7$) when the laying start was not discovered until two eggs were present in the nest, i.e. on the second day of laying.

The initial increase of hatchling weight

The weight change of chicks that had hatched during the same day or the preceding night was followed during their first day as hatchlings. Fourteen young were checked over a total of 23 periods lasting from four to nine hours. The weight increase per hour was calculated, resulting in an overall mean of 0.023 ± 0.009 g (S.D.) ($n=23$). This figure was used when deriving the chick weight at the moment of hatching in cases when the weighing occurred several hours later.

Hatchling weight in relation to egg weight

All hatchlings of 39 clutches were weighed within 24 hours after hatching (average age 12 hours). A positive correlation was found between the clutch means of the hatchling weight and the egg weight (unhatched eggs excluded) ($y = -0.54 + 1.28x$; $r = 0.731$; $n = 39$; $p < 0.001$).

Seventeen eggs from 14 of these clutches hatched during daytime and within inspection intervals of 12 hours or less. In these cases it could be established to which egg the hatchling belonged. The age of the hatchling was considered to be, on average, half of the interval between the inspections when hatching occurred. The weight was reduced accordingly to correspond to that at the hatching moment. The highly significant and positive correlation between the weights of these hatchlings and their eggs is presented in the diagram in Figure 1.

One chick from each of four clutches had just hatched with part of the egg-shell still attached to the body or left quite close when the nest was inspected. The weights (g) of these eggs and fresh hatchlings were as follows (hatchling first): 0.80/1.15, 0.86/1.21, 0.87/1.24 and 1.02/1.30. Also in this very restricted data set, was the relation between egg and hatchling significant and positive ($r = 0.95$; $n = 4$; $p = 0.05$).

The conclusion drawn from these analyses is that

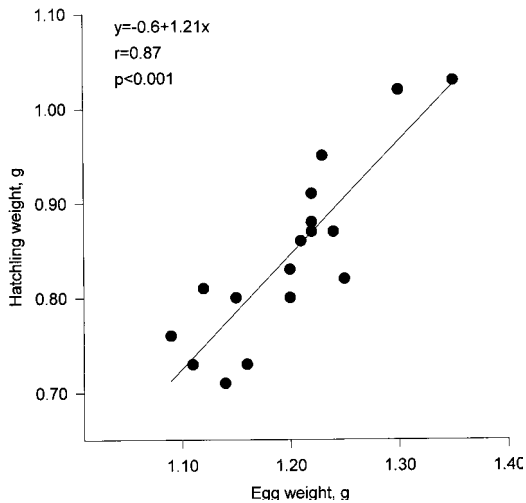


Figure 1. The relation between the weights of hatchling and egg. The hatchlings were weighed within 12 hours from hatching and the weights were adjusted to correspond to that of the moment of hatching using the mean weight increase per hour (see text).

Diagram som visar sambandet mellan vikterna för nykläckt unge (lodräta axeln) och dess ägg (vågräta axeln). De tyngre äggen kläcker fram tyngre ungar. Alla ungar har vägts inom 12 timmar efter kläckningen. Med hjälp av den kända medelviktökningen per timme för en unge under första dygnet har dess vikt i kläckningsögonblicket räknats fram.

heavier eggs produce heavier hatchlings at least when a sample of eggs from different clutches is analysed. A crucial question is whether this is also true for the egg/hatchling relation within clutches. This has been tested using intra-clutch pairs of hatchlings from identified eggs. Such pairs scarcely occurred among the 39 investigated clutches. Nine cases could be found with unequal intra-pair egg weights. Five pairs had the same interval, varying from 5 to 24 hours, between the last inspection of the egg and the first inspection of its hatchling. In order to increase the number of pairs, another four pairs were accepted despite the unequal inspection intervals of the siblings, varying from 3 to 12 hours. Thus, all siblings were very likely of different ages when weighed, but because of the many protracted intervals that included both day and night with their differing growth rates, no adjustments of the hatchling weights were made. A statistical test for matched pairs indicated that the heavier egg produces a heavier hatchling also within clutches (t-test: $t = 2.48$; $df = 8$; $p < 0.05$).

Yolk weight in relation to egg weight

The weights of 16 hard-boiled yolk bodies are plotted against their fresh egg weights in the diagram of Figure 2. A positive and significant relation between the yolk and egg weights is evident. The egg pairs from the same clutch are indicated by identical letters in the diagram. The result of a test for matched pairs is that heavier eggs also contain heavier yolk bodies within clutches (t-test: $t = 5.00$; $df = 7$; $p < 0.01$).

Discussion

The weight loss of the fresh egg

The declining egg weight observed during the first day after laying has been estimated in a small number of passerine species. The percentage values are all close to the weight loss of 0.64% shown by the Treecreeper egg: *Hirundo rustica* 0.4%, *Turdus migratorius* and *Quiscalus quiscula* 0.2% (Manning 1979), *Ficedula hypoleuca* 0.2–0.5% (Kern et al. 1992) and *Troglodytes aedon* approx. 0.5% (Styrsky et al. 1999). The only exception is *Parus caeruleus* with a mean weight loss of only 0.0008 g (0.07%) (Nilsson & Svensson 1993). This significant difference might be due to the habit of this species of keeping the eggs carefully covered with insulating nest material, which may reduce the water evaporation rate from the eggs when the female is away from the nest.

The daily weight loss of the eggs increases during the laying period, probably due to the successive

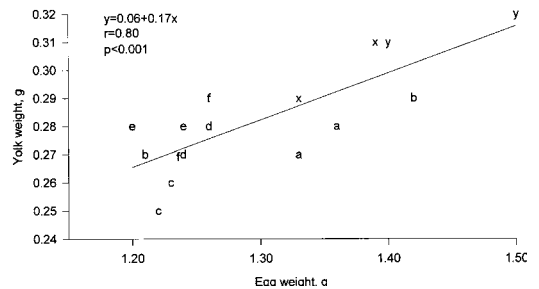


Figure 2. The relation between the weight of the hard-boiled yolk and the weight of the fresh egg. Identical letters indicate pairs of eggs from the same clutch.

Diagram som visar sambandet mellan äggets (horisontell axel) och dess gulas (vertikal axel) vikt. Som synes har de tyngre äggen också en tyngre gula. Diagrammet visar två ägg från varje kull vilka betecknas med samma bokstav.

increase in incubation attentiveness. Manning (1982) found a mean decrease in weight during the whole laying period of $0.9 \pm 0.08\%$ for seven passerine species. The corresponding figure, calculated from 16 clutches of the Treecreeper, is $1.8 \pm 1.9\%$ ($n=57$). The comparisons with other species thus indicate that the Treecreeper eggs suffer the greatest weight (water) loss during the days before the beginning of incubation. The explanation might be (1) that the eggs are small and of the same size as those of *P. caeruleus*, i.e. with a relatively larger surface area than those of the other species referred to above, and (2) that the clutch is left practically uncovered when the female bird is out.

The weight relation between egg and hatchling

The relation between the weight of the fresh egg and its hatchling has been studied in at least 15 passerine species including the Treecreeper. The parameters used are weight or volume of the egg, and weight or size of the hatchling. However, since the egg weight and volume are strongly correlated (Enemar 1997, with references) as are hatchling weight and size (e.g. Richter 1984, Rofstad & Sandvik 1987, Magrath 1992, Ward 1995), the choice of parameter has no significant impact on the calculations. It should be remembered, however, that larger eggs may give rise to heavier chicks due to a large yolk reserve rather than being structurally larger (Williams 1994). The studies differ as regards the amount and precision of presented data, and the analyses are based either on the weights of individual eggs and hatchlings within and among clutches or on the mean values of clutches. As it is troublesome to obtain enough data from hatchlings by following the hatching process closely in the field, sometimes the hatching of eggs brooded in an incubator has been studied. According to the results of these investigations, a positive relation between the weight or size of the passerine egg and the hatchling has been reported for *Parus major* (Schifferli 1973), *Quiscalus quiscula* (Howe 1976), *Iridoprocne bicolor* (De Steven 1978), *Molothrus ater* (Nolan & Thompson 1978), *Delichon urbica* (Bryant 1978), *Pica pica* (Clarkson 1984), *Xanthocephalus xanthocephalus* (Richter 1984), *Ficedula hypoleuca* (Järvinen & Ylimaunu 1984), *Corvus corone* (Rofstad & Sandvik 1985), *Empidonax minimus* (Briskie & Sealy 1990), *Turdus merula* (Magrath 1992a), *Parus caeruleus* (Nilsson & Svensson 1993), *Hirundo rustica* (Ward 1995) and *Troglodytes aedon* (Styrsky et al. 1999).

To my knowledge, apart from the late (second)

clutches of *Troglodytes aedon*, which showed no correlation (Styrsky et al. 1999), no investigation has reported a lack of correlation between egg and hatchling weights. There seems, therefore, to be a general rule among passerine species that larger eggs give rise to heavier hatchlings. This holds at least for comparisons among clutches, although it is generally assumed, rightly or wrongly, that this egg/hatchling relation applies also within clutches, as shown above for the Treecreeper.

The adaptive significance of the egg size and its variation within and among clutches is still under debate (e.g. Nilsson & Svensson 1993, Stoleson & Bessinger 1995, Styrsky et al. 1999). As far as the intra-clutch variation is concerned, the egg weights normally increase in the laying sequence of the Treecreeper (Enemar 1997). As the incubation often starts before clutch completion with asynchronous hatching as a consequence, it follows that the largest eggs hatch last and that the hatchlings are heavier compared to the hatching weight of the siblings. In seven investigated clutches the mean weight of the last chick was $0.90 + 0.06$ g on the day of hatching, which was significantly less than the mean weight, $1.17 + 0.13$ g, of the earlier hatched siblings (t-test: $t = 6.08$; $df = 6$; $p < 0.001$). The hatching weight “surplus” of the last hatchlings has nevertheless been assumed to enhance the prospects of survival and therefore considered to be the selective force resulting in the egg weight hierarchy within clutches according to the “brood-survival”-hypothesis (cf. e.g. Slagsvold et al. 1984). However, this remains to be demonstrated in the Treecreeper.

Nilsson & Svensson (1993) remark that the slope of the regression of nestling weight upon egg weight is close to one in *Parus caeruleus* (regression coefficient $b = 1.01$). This means that every increase in the egg mass results in the same increase in the nestling mass. Their calculation was based on clutch means of eggs and nestlings aged 52 hours. In the Treecreeper the b-values exceed one in all calculations. It is 1.21 in the equation of Figure 1, 1.28 when the regression is based on 39 clutch means with mean nestling age of 12 hours, and 1.42 for the above mentioned four chicks with hatching just finished. This indicates that the weight of the hatchling increases more than the egg weight, consequently resulting in an increasing relative weight. The quotient hatchling-weight/egg-weight, derived from the data sample in Figure 1, is significantly and positively correlated with the egg weight ($y = 0.23 + 0.40x$; $n = 17$; $r = 0.59$; $p < 0.02$).

Among the passerine species listed above, seven

regression coefficients are reported (based on hatchling weights), which are all clearly less than one, ranging from 0.50 to 0.87. This indicates that the larger eggs of the Treecreeper are supplied with proportionally more nutrients to produce the most pronounced hatchling weight hierarchy among the investigated passerines.

The weight relation between the egg and its yolk body

Even if a positive correlation between the weights of yolk and egg is highly significant in the Treecreeper (Figure 2), there is no relative increase of the yolk body corresponding to that of the hatchling. The proportion of the yolk weight probably decreases with increasing egg weight. A test of the data presented in Figure 2 indicates a negative although insignificant relation ($r = -0.39$; $n = 16$; $p < 0.2$). Available information regarding other passerine species is diversified, to say the least. A positive relation is found in *Parus major* (Schifferli 1973, Perrins 1996), with a negative trend of the relative yolk weight (Ojanen 1983a). Positive correlations are reported also for *Delichon urbica* (Bryant 1978), *Molothrus ater* (Ankney & Johnson 1985), *Agelaius phoeniceus* (Muna & Ankney 1987), and *Quiscalus major*, where the weight increase is said to be due to inclusion of more water (Bancroft 1985). *Corvus corone* is special in that the relative yolk sac weight increases with egg weight (Rofstad & Sandvik 1987). No definite trends are found in *Sturnus vulgaris* (Ricklefs 1977, 1984), *Tyrannus tyrannus* (Murphy 1986), *Ficedula hypoleuca* (Ojanen 1983a), and *Parus caeruleus* (Kunz 1999). The relative yolk weight decreases with increasing egg weight in *S. vulgaris* (Ricklefs 1977) and *F. hypoleuca* (Ojanen 1983a).

Nevertheless, as demonstrated above, larger eggs seem to give rise to heavier hatchlings generally in passerines, but it does not follow that a larger yolk body is necessary for the weight increase. Although the yolk mass might be of decisive importance for the amount of nutritive reserve in the yolk sac of the hatchling, the total egg weight is the best indicator of the resources (calories, lipids, proteins) available to the embryo (Carey et al. 1980). Larger eggs with their relatively smaller yolk bodies contain proportionally more protein-rich albumen (Arnold 1992, with references), which might further the embryonic growth rate and/or weight increase. The proportionally smaller yolk bodies in the larger eggs also means

that more space is available for the growing embryo. These relationships may reasonably apply also to the Treecreeper.

Concluding remarks

As documented in a previous study (Enemar 1997), the size or weight of the Treecreeper eggs increases significantly from first to last egg in the clutch, rising from 96 to 104 %, on average, when size is expressed as a percentage of the clutch mean. It was hypothesised that this tendency and ability of the female to successively increase her investment in the egg is of adaptive value from at least two aspects: 1. Under favourable breeding conditions when incubation starts before the clutch is complete and hatching becomes asynchronous, the then presumed increased weight of the last hatchlings increases the prospects of survival in competition with the older siblings (cf. Howe 1976, Rydén 1978). 2. Under constraining conditions, the mentioned quality of the female may enable her, at the expense of the successive increase in egg size and the early incubation start, to go on laying without gaps and to keep even the last eggs of a size and quality to give rise to viable and normally fit and synchronously hatched chicks (Enemar 1997). Moreover, Magrath (1992b) writes that "the tendency to lay relatively large eggs later in the clutch might be selected for in order to counter the effects of an increasing risk of unfavourable conditions".

This study confirms that the heavier eggs are of higher quality, judging from their heavier yolk bodies, and that they produce heavier hatchlings, also proportionally, in the Treecreeper. The comparatively large span between the smallest and largest eggs within clutches and the even larger span between their hatchlings indicate that the intra-clutch egg size variation is instrumental in the breeding strategy of this double-brooded species. To save time and be able to produce several broods, females regularly start to incubate before the last egg is laid. This selects for the evolution of a distinct egg size hierarchy in the Treecreeper. However, the survival and fitness of small and large young early and late in the hatching row remain to be investigated. In fact, there are few studies that strongly support the view that egg size and offspring fitness are positively related in passerines (Williams 1994). It should also be remembered that there are other egg qualities of survival value that are not related to size, among them, for example, the concentration of maternal antibodies (Kunz 1999).

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References

- Ankney, C. D. & Johnson, S. L. 1985. Variation in weight and composition of Brown-headed Cowbird eggs. *Condor* 87:296–299.
- Arnold, T. W. 1992. Variation in laying date, clutch size, egg size, and egg composition of Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*): a supplemental feeding experiment. *Can. J. Zool.* 70:1904–1911.
- Bancroft, G. T. 1985. Nutrient content of eggs and the energetics of clutch formation in the Boat-tailed Grackle. *Auk* 102:43–48.
- Birkhead, T. R. 1991. *The Magpies*. T & A D Poyser, London.
- Bonnier, G. & Tedin, O. 1940. *Biologisk variationsanalys*. Svenska Bokförlaget, Stockholm.
- Bryant, D. M. 1978. Establishment of weight hierarchies in the broods of House Martins *Delichon urbica*. *Ibis* 120:16–26.
- Briskie, J. V. & Sealy, S. G. 1990. Variation in size and shape of Least Flycatcher eggs. *J. Field Ornithol.* 61:180–191.
- Carey, C., Rahn, H. & Parisi, P. 1980. Calories, water, lipid and yolk in avian eggs. *Condor* 82:335–343.
- Clarkson, K. 1984. *The breeding and feeding ecology of the Magpie Pica pica*. Unpubl. Ph.D. Thesis, University of Sheffield. (Cited after Birkhead, T.R. 1991.)
- De Steven, D. 1978. The influence of age on the breeding biology of the Tree Swallow *Iridoprocne bicolor*. *Ibis* 120:516–523.
- Enemar, A. 1992. Laying and clutch size of the Treecreeper *Certhia familiaris* in south-western Sweden. *Ornis Svecica* 2:93–102.
- Enemar, A. 1995. Incubation, hatching, and clutch desertion of the Treecreeper *Certhia familiaris* in south-western Sweden. *Ornis Svecica* 5:11–24.
- Enemar, A. 1997. The egg size variation of the Treecreeper *Certhia familiaris* in south-western Sweden. *Ornis Svecica* 7:107–120.
- Fowler, J. & Cohen, L. (printing year lacking). *Statistics for Ornithologists*. BTO Guide 22.
- Howe, H. F. 1976. Egg size, hatching asynchrony, sex, and brood reduction in the Common Grackle. *Ecology* 57:1195–1207.
- Järvinen, A. & Ylimaunu, J. 1984. Significance of egg size on the growth of nestling Pied Flycatchers *Ficedula hypoleuca*. *Ann. Zool. Fennici* 21:213–216.
- Kern, M. D., Cowie, R. J. & Yeager, M. 1992. Water loss, conductance, and structure of eggs of Pied Flycatchers during egg laying and incubation. *Physiol. Zool.* 65:1162–1187.
- Kunz, C. 1999. Effects of egg size and maternal antibodies on nestling growth and health in Blue Tits. In *Genetic variation and phenotypic plasticity in body traits of nestling Blue Tits*. Thesis, University of Uppsala.
- Magrath, R. D. 1992a. The effect of egg mass on the growth and survival of Blackbirds: a field experiment. *J. Zool. Lond.* 227:639–653.
- Magrath, R. D. 1992b. Seasonal changes in egg-mass within and among clutches of birds: general explanations and a field study of the Blackbird *Turdus merula*. *Ibis* 134:171–179.
- Manning, T. H. 1979. Density and volume corrections of eggs of seven passerine birds. *Auk* 96:207–211.
- Manning, T. H. 1982. Daily measurements of variation in weight loss of seven passerine species before and during natural incubation. *Can. J. Zool.* 60:3143–3149.
- Muma, K. E. & Ankney, C. D. 1987. Variation in weight and composition of Red-winged Black-bird eggs. *Can. J. Zool.* 65:605–607.
- Murphy, M. T. 1986. Body size and condition, timing of breeding, and aspects of egg production in Eastern Kingbirds. *Auk* 103:465–476.
- Nilsson, J.-Å. & Svensson, E. 1993. Causes and consequences of egg mass variation between and within Blue Tit clutches. *J. Zool. Lond.* 230:469–481.
- Nolan, V. Jr. & Thompson, C. F. 1978. Egg volume as a predictor of hatchling weight in the Brown-headed Cowbird. *Wilson Bull.* 90:353–358.
- Ojanen, M. 1983a. Composition of the eggs of the Great Tit (*Parus major*) and the Pied Flycatcher (*Ficedula hypoleuca*). *Ann. Zool. Fennici* 20:57–63.
- Ojanen, M. 1983b. Effects of laying sequence and ambient temperature on the composition of eggs of the Great Tit *Parus major* and the Pied Flycatcher *Ficedula hypoleuca*. *Ann. Zool. Fennici* 20:65–71.
- Perrins, C. M. 1996. Eggs, egg formation and the timing of breeding. *Ibis* 138:2–15.
- Ricklefs, R. E. 1977. Variation in size and quality of the Starling egg. *Auk* 94:167–168.
- Ricklefs, R. E. 1984. Variation in the size and composition of eggs of the European Starling. *Condor* 86:1–6.
- Richter, W. 1984. Nestling survival and growth in the Yellow-headed Blackbird *Xanthocephalus xanthocephalus*. *Ecology* 65:597–608.
- Rofstad, G. & Sandvik, J. 1985. Variation in egg size of the Hooded Crow *Corvus corone cornix*. *Ornis Scand.* 16:38–44.
- Rofstad, G. & Sandvik, J. 1987. Morphology of hatchling Hooded Crows and its relation to egg volume. *Condor* 89:494–499.
- Rydén, O. 1978. Egg weight in relation to laying sequence in a South Swedish urban population of the Blackbird *Turdus merula*. *Ornis Scand.* 9:172–177.
- Schifferli, L. 1973. The effect of egg weight on the subsequent growth of nestling Great Tits *Parus major*. *Ibis* 115:549–558.
- Slagsvold, T., Sandvik, J., Rofstad, G., Lorentsen, Ö. & Husby, M. 1984. On the adaptive value of intraclutch egg-size variation in birds. *Auk* 101:85–697.
- Stoleson, S. H. & Beissinger, S. R. 1995. Hatching asynchrony and the onset of incubation in birds, revisited. When is the critical period? *Current Ornithology* 12:191–270.
- Styrsky, J. D., Eckerle, K. P. & Thompson, C. F. 1999. Fitness-

- related consequences of egg mass in nestling House Wrens. *Proc. R. Soc. Lond. B* 266:1253–1258.
- Ward, S. 1995. Causes and consequences of egg size variation in Swallows *Hirundo rustica*. *Avocetta* 19:201–208.
- Williams, T. D. 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. *Biol. Rev.* 68:35–59.

Sammanfattning

Sambandet mellan äggets, äggulans och den nykläckta ungens vikt hos trädkryparen Certhia familiaris.

Inledning

I en tidigare uppsats (Enemar 1997) visade jag hur äggen i varje kull blir större och tyngre under värpningen förlopp hos trädkryparen. Som regel är de båda sist värpta äggen kullens största. Då betydelsen av detta förhållande diskuterades, förutsattes att de tyngsta äggen också gav upphov till de tyngsta ungarna hos denna art. Eftersom de sista äggen i regel också kläcks sist, skulle dess nykläckta ungar stå sig bättre i konkurrensen med de äldre kullsyskonen, bl.a. därför att de sista ungarna var försedda med en större matsäck i form av gula från tiden i ägget. Det fanns alltså alla skäl att ta reda på om dessa förmodade samband existerar i verkligheten. Det gällde då inte bara att utreda om de tyngre äggen kläcker ut tyngre ungar utan även om de tyngre äggen också har en tyngre gula. Dessa spörsmål har nu utforskats med metoder och resultat som redovisas i denna uppsats.

Metoder

Undersökningarna genomfördes i Gunnebo utanför Mölndal på det bestånd av trädkrypare som där bygger sina bon i speciella häckningsfickor av takpapp (se Enemar 1992). Värpningen följdes upp genom dagliga besök, då varje nytt ägg vägdes med en för fältbruk anpassad elektronisk våg. Äggen försågs med ett nummer motsvarande platsen i värpföljden. För vissa kullar vägdes de äldre äggen flera dagar under värperioden för att utröna hur stor viktnedskningen var per dygn.

Vid tiden för kläckningen återupptogs bokkontrollerna för att väga de nykläckta ungarna. Ofta gjordes fler besök dagligen i förhoppning om att endast en nykläckt unge tillkommit efter föregående inspektion. Ungen kunde då skiljas ut från ev. tidigare

kläckta syskon, eftersom varje nykläckt och vägd unge märkts med färgpenna på kroppen eller med nagellack på några klor. För en ensam nykläckt unge kan man därmed avgöra från vilket vägt ägg den härstammar. Fältarbetets mål var att erhålla många sådana fall där både äggets och dess nykläckta unges vikt kunde bestämmas. Ett antal ungars viktökning registrerades med timmars mellanrum det första dygnet för att bestämma den genomsnittliga viktökningen per timme. Med hjälp av detta värde kunde en unges ungefärliga kläckvikt beräknas även om vägningen kraftigt försenats i förhållande till kläckningsögonblicket.

För studiet av gulornas vikt insamlades två ägg från sex bon. Till dessa fogades två par ägg från en nyligen övergiven kull. Äggens vikt registrerades i fält i samband med insamlandet. Efter det att äggen hårdkokats kunde gulorna lätt skiljas från vitan och vägas.

Resultat

Under första dygnet efter värpningen minskade äggets vikt (genom avdunstning) i genomsnitt endast 0,008 g av sin medelvikt på 1,26 g, d.v.s. endast 0,64%. Hos 14 ungar ökade vikten under första dygnet genom tillväxt i genomsnitt 0,023 g per timme.

För 17 vägda ägg blev ungens kläckvikt känd antingen direkt genom vägning i nära anslutning till kläckningen eller efter korrektion av vikten i de fall då ungen vägts inom max. 12 timmar efter kläckningen. Som framgår av diagrammet i Figur 1 föreligger ett säkert samband mellan vikterna hos ägg och unge. Tyngre ägg producerar tyngre ungar. I fyra fall var de nykläckta ungarna alldeles färska vid vägningen, eftersom den ena äggskalshalvan fortfarande satt kvar på kroppen eller låg strax intill i boet. Även dessa ungar visar klart på sambandet, vilket framgår av följande viktpar i gram (ungens vikt först): 0,80/1,15; 0,86/1,21; 0,87/1,24 och 1,02/1,30. I nio fall kunde sambandet prövas inom syskonpar, alltså för ägg och ungar i samma kull. Resultatet blev att även inom samma kull gäller att tyngre ägg producerar tyngre ungar.

De tyngre äggen innehåller också en tyngre gula. Sambandet visas med diagrammet i Figur 2. Det innebär att de större och tyngre äggen också innehåller mer näring. Sambandet gäller också för äggpar inom en och samma kull. Detta kan också utläsas av diagrammet, där de två äggen från samma kull betecknas med samma bokstav.

Diskussion

Den viktminskning om drygt en halv procent som trädkryparäggen genomgår per dygn i avvaktan på ruvningsstarten, säkerligen genom avdunstning av vatteninnehållet, överensstämmer i stort med vad man funnit hos fyra andra tättingarter. Enda undantaget är blåmesen, vars ägg minskar med obetydliga 0,07% per dygn. Detta kan förklaras av att blåmes-honan så omsorgsfullt håller äggen täckta med isolerande bomaterial, då hon är frånvarande. Så sker ej hos trädkryparen, vars bobale innehåller obetydligt med fjädrar, ull eller annat värmeisolerande material.

För 14 undersökta tättingarter har det visats, att större eller tyngre ägg resulterar i tyngre ungar, ett resultat som oftast baserats på jämförelse mellan medelvärden för hela kullar. Inget undantag från denna "regel" har så vitt känt hittills rapporterats. För trädkryparens del innebär det att den sist kläckta ungen från det stora och sist värpta ägget också är tyngst. I sju kullar kunde det konstateras att medelvikten för den nykläckta ungen var 0.90 g medan motsvarande vikt för de tidigare kläckta syskonen var 1,17 g och alltså hade ett försprång om 0.27 g eller 30%. Det är möjligt att den högre kläckvikten hos de sista ungarna hjälper dessa att klara den konkurrenssituation de kläckts in i, en rimlig hypotes som dock fortfarande är under diskussion.

Trädkryparen är unik i så måtto att den nykläckta ungens vikt ökar mer än vad man kunde förvänta av ökningen i äggvikt. Hos blåmesen ligger de båda viktökningarna ungefär i takt med varandra, medan hos sju andra tättingarter ungens viktökning släpar betydligt efter äggviktökningen.

En jämförelse med andra arter vad gäller sambandet mellan äggets och gulans vikt ger en minst sagt förvirrad bild. Exempel finns på samma förhållande som hos trädkryparen men även på frånvaron av samband eller på att gulevikten minskar, då äggvikten ökar. Även om trädkryparens gula ökar klart med äggvikten, så släpar den dock efter något, alltså tvärtemot vad som gäller för ungen. Man skall dock komma ihåg att det tyngre äggets ökning i äggvita inte är betydelslös. Denna är rik på bl.a. proteiner som främjar embryots tillväxt. (Dock finns forskare som påvisat att de större äggens viktökning beror endast på ett större vatteninnehåll, vilket i något fall skall gälla även för de nykläckta ungarna!)

Sammanfattningsvis, som tidigare visats har trädkryparen normalt en jämförelsevis stor skillnad mellan de tidigare lättare och de senare tyngre äggen i sina kullar. Denna skillnad är ännu större för motsvarande nykläckta ungars vikter. De sista tyngre ungarna har haft en tyngre gula till förfogande i ägget, vilket rimligen bidragit till tillskottet i ungens storlek och/eller vikt, det senare helt eller delvis i form av en rikligare gulereserv i tarmen. Vad allt detta betyder för trädkryparens fortplantningsframgång och de sist kläckta ungnas överlevnadsmöjligheter kan inte avgöras i nuläget. Man saknar framförallt en jämförelse mellan de äldsta och de yngsta syskonens överlevnad till häckningsålder, något som ter sig minst sagt knepigt att utforska för en glest förekommande art som trädkryparen med sin tidiga häckning och sina regelmässigt(?) dubbla kullar.