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Incubation and nestling periods in hole-nesting passerines in Finnish Lapland

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In northern Finnish Lapland (about 69°03′N, 20°50′E) the mean incubation period was 14.6 days (n = 113) in the Pied Flycatcher *Ficedula hypoleuca*, 14.8 days (n = 47) in the Redstart *Phoenicurus phoenicurus* and 14.8 days (n = 20) in the Siberian Tit *Parus cinctus*. The corresponding figures for the nestling period were 15.6 (n = 50), 13.5 (n = 22) and 18.8 (n = 12). The means did not deviate markedly from published records further south.

The interspecific differences in the relative variability (CV%) of the incubation period were significant and in the Pied Flycatcher and the Redstart the incubation period varied more than the nestling period. CV% of the incubation and nestling period was least variable in the Siberian Tit.

In the Pied Flycatcher and the Redstart, hatching success decreased as the incubation period increased. The main factor affecting the duration of incubation in the Pied Flycatcher and the Redstart was the mean temperature during the incubation period, but in the Siberian Tit it was the laying date. The nestling period was not significantly related to any factor.

1. Introduction

The incubation and nestling phases constitute a central part of the breeding strategy of birds. Despite this, even in the commonest species surprisingly little is known, for instance, about the duration of the incubation and nestling periods in different geographical areas and environments, and about their significance for the breeding success. Prolonged incubation may increase predation pressure and hatching asynchrony (Moreno & Carlson 1989), and in adverse weather the condition of the fledglings may depend on the energy reserves of the female around the time of hatching (Lifjeld & Slagsvold 1986).

In this study I examine some problems connected with the incubation and nestling phases, using mainly my own data on hole-nesting passerine birds in northern Lapland, but also including published records from other areas in Europe. Particular attention is paid to abiotic temperature factors. In harsh environments the physiological constraints on a bird's incubation and feeding capacities apparently manifest themselves more clearly than in less harsh conditions (Mertens 1987). Using interspecific comparisons, I shall try to discover whether the incubation and nestling periods in certain species reveal adaptations to harsh environments.

2. Study area, material and methods

I collected the data in northern Finnish Lapland (the Kilpisjärvi area, about 69°03′N, 20°50′E) in 1973–87. Three hole-nesting passerine birds breeding in nest-boxes in mountain birch forest (alt. 480–600 m) at Kilpisjärvi are included (for details, see Järvinen 1983): the Pied Flycatcher *Ficedula hypoleuca* (a southern migrant and newcomer in northern Lapland), the Redstart *Phoenicurus phoenicurus* (a northern migrant) and the Siberian Tit *Parus cinctus* (a northern resident). In all species the female incubates alone.

Only genuine first clutches in which the duration of the incubation and/or nestling period was known exactly are included in the present analysis. The incubation period is defined as the interval (in days) between the laying of the last egg in the clutch and the hatching of the last egg, and the nestling period as the interval between the hatching of the last egg and the fledging of the last chick. These are the definitions most commonly used in the literature (e.g. Drent 1975). The temperature data are derived from the records of the Kilpisjärvi climatological station of the Finnish Meteorological Institute, situated within the study area (alt. 480 m).

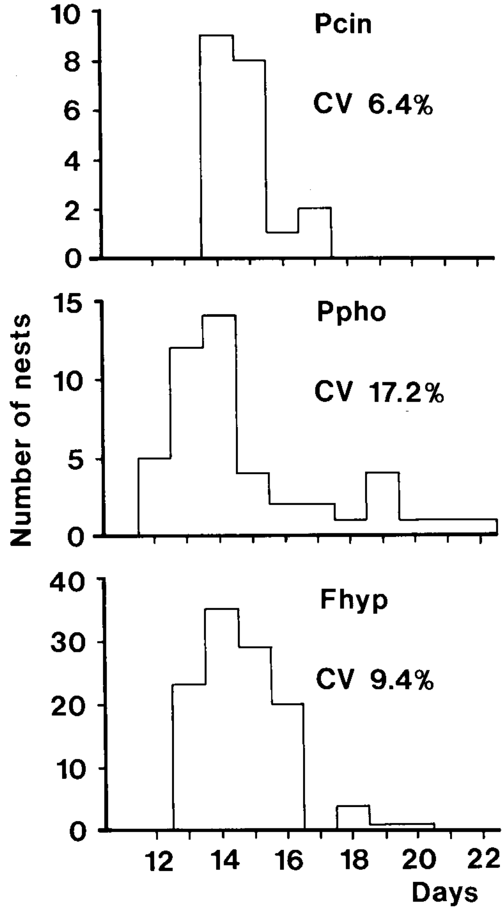

Fig. 1. Duration of the incubation period (days) in the Pied Flycatcher (Fhyp), Redstart (Ppho) and Siberian Tit (Pcin) in northern Finnish Lapland. All pairwise interspecific differences in the coefficient of variation (CV) are significant (t tests according to Sokal & Braumann 1980): Fhyp vs. Ppho $P < 0.001$, Fhyp vs. Pcin $P = 0.02$ and Pho vs. Pcin $P < 0.001$. Descriptive statistics given in Table 4.

3. Results

3.1. Variability of incubation and nestling periods

The Siberian Tit incubated and reared nestlings in the coldest weather and the Pied Flycatcher in the warmest weather (Table 1). In all species the frequency distribution of the duration of the incubation period (Fig. 1) was positively skew but that of the nestling period was more or less normal (Fig. 2). There was no correlation between the incubation and nestling periods in the nests (Pied Flycatcher: $r = 0.019$, $n = 49$, $P = 0.90$; Redstart: $r = -0.139$, $n = 21$, $P = 0.55$; Siberian Tit: $r = 0.158$, $n = 11$, $P = 0.65$).

The interspecific differences in the relative variability (CV%) of the incubation period were all significant but there were no corresponding differences in the nestling period (Figs. 1–2). Both

Table 1. Mean daily air temperature (°C) during the incubation and nestling periods of the Pied Flycatcher, Redstart and Siberian Tit in northern Finnish Lapland. The temperatures were calculated only for those nests in which the duration of the respective periods was known exactly.

Species	Incubation period			Nestling period		
	Mean	SD	n	Mean	SD	n
Pied Flycatcher	8.6	1.9	106	10.0	1.5	50
Redstart	7.0	2.8	47	9.6	1.2	22
Siberian Tit	5.7	2.4	19	7.5	2.2	12

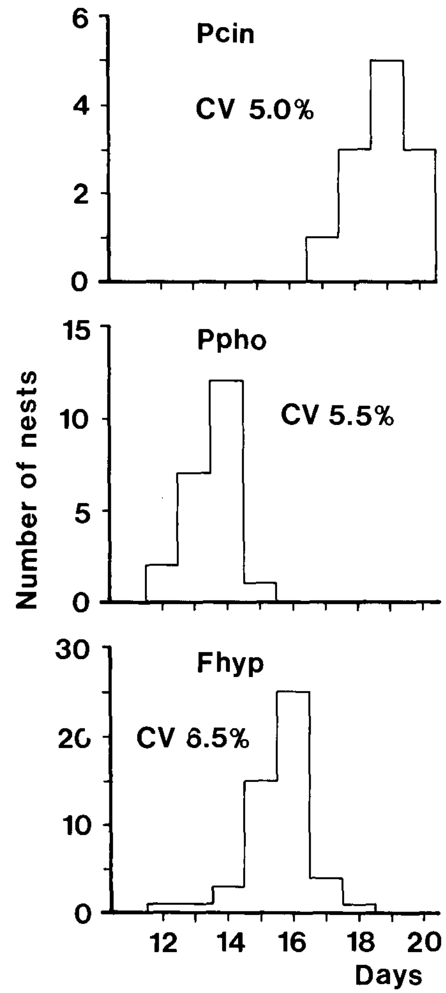

Fig. 2. Duration of the nestling period (days) in the Pied Flycatcher (Fhyp), Redstart (Ppho) and Siberian Tit (Pcin) in northern Finnish Lapland. All pairwise interspecific differences in the coefficient of variation (CV) are clearly nonsignificant. Descriptive statistics given in Table 4.

parameters were least variable in the Siberian Tit. The incubation period varied more than the nestling period in the Redstart (t = 5.74, df = 67, P < 0.001) and the Pied Flycatcher (t = 3.08, df = 161, P = 0.002), but not in the Siberian Tit (t = 0.92, df = 30, P = 0.36; cf. CV% values in Figs. 1–2).

3.2. Factors affecting incubation and nestling periods

In the Pied Flycatcher and the Redstart, but not in the Siberian Tit, the incubation period was inversely related to the mean ambient temperature during that period (Figs. 3–5), and the effects of temperature clearly outweighed the effects of other factors. According to a multiple regression analysis, the Siberian Tit was the only species whose incubation period was affected by the date of laying of the first egg when the effect of temperature was controlled (Table 2).

In none of the species was the nestling period related to the mean temperature during that period (Pied Flycatcher: r = –0.069, n = 50, P = 0.64; Redstart: r = 0.201, n = 22, P = 0.37; Siberian Tit: r = –0.430, n = 12, P = 0.16) and I could not find any other variables to explain the variation in the nestling period, probably due to the fact that it varied comparatively little (see Fig. 2). As explanatory variables, I tried laying date, egg size, brood size, female weight, female wing length, mean temperature during different phases of the nestling period, and many habitat variables determined in the neighbourhood of the nest-boxes (distance from Lake Kilpisjärvi, forest productivity, number of trees and bushes, herb coverage, etc.).

Table 2. Dependence of the duration of the incubation period on the date of laying of the first egg and mean daily air temperature (°C) during the incubation period in the Pied Flycatcher, Redstart and Siberian Tit in northern Finnish Lapland. Standardized partial regression (or beta) coefficients and their t values, degrees of freedom (df) and 2-tailed probabilities are given. The beta coefficients quantify the relative contribution of the x variables to the regression plane. Squaring beta tells how much of the variance of y is accounted for by a particular x variable. The coefficients of determination (R^2, %) for the whole models are also given.

Incubation		Lay date (x_1)			Temperature (x_2)			
period (y)	df	Std. coeff.	t	P	Std. coeff.	t	P	R^2
Pied Flycatcher	103	–0.005	–0.070	0.944	–0.669	–8.767	<0.001	44.9
Redstart	44	–0.021	–0.165	0.870	–0.656	–5.088	<0.001	44.5
Siberian Tit	16	–0.587	–2.959	0.009	–0.148	–0.748	0.465	37.1

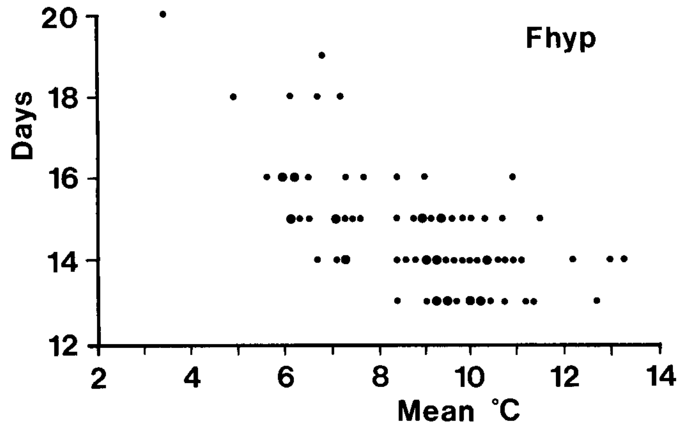

Fig. 3. Relationship between mean air temperature during the incubation period and duration of the incubation period in the Pied Flycatcher in northern Finnish Lapland. Small dots = one observation, large dots = more than one observation. Pearson's correlation coefficient = –0.670, n = 106, P < 0.001.

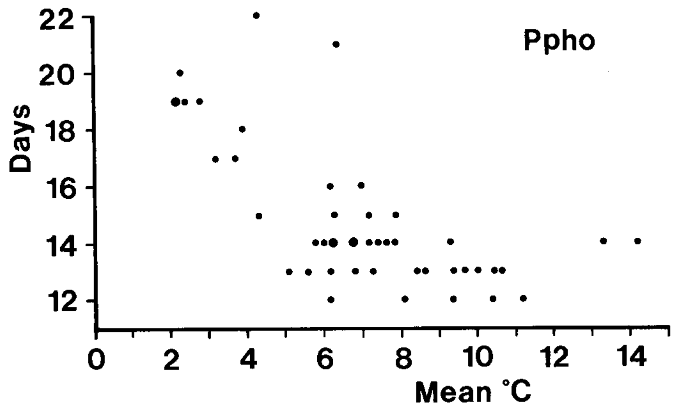

Fig. 4. Relationship between mean air temperature during the incubation period and duration of the incubation period in the Redstart in northern Finnish Lapland. Small dots = one observation, large dots = more than one observation. Pearson's correlation coefficient = –0.667, n = 47, P < 0.001.

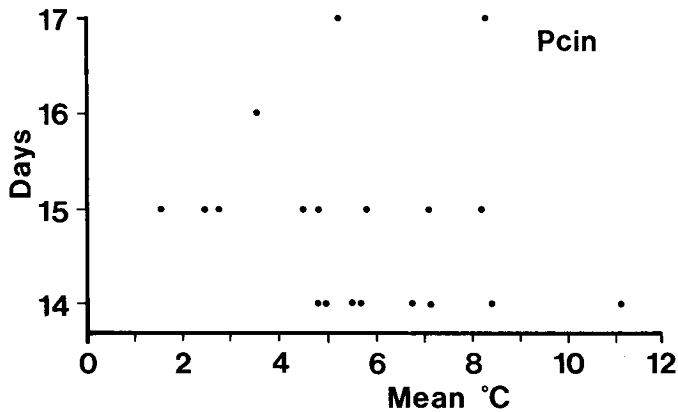

Fig. 5. Relationship between mean air temperature during the incubation period and duration of the incubation period in the Siberian Tit in northern Finnish Lapland. Pearson's correlation coefficient = –0.163, n = 19, P = 0.51.

However, in the Redstart there was some indication that the nestling periods were shorter in nests far from the shore of Lake Kilpisjärvi when the effect of temperature during the nestling period was controlled (partial correlation = –0.427, df = 19, P = 0.05).

3.3. Breeding success

The breeding success of the three species is shown in Table 3, where data are given separately for all cases and for cases in which the incubation or nestling period was known exactly, hatching and/or fledging success being naturally higher in the latter groups. There were no great interspecific differences in hatching or fledging success: on average 80% of the eggs hatched and 70–80% of the hatched young fledged (data on all cases).

In the Pied Flycatcher (r = –0.205, n = 106, P = 0.04) and the Redstart (r = –0.327, n = 47, P = 0.02), but not in the Siberian Tit (r = 0.123, n = 19, P = 0.62), the hatching percentage decreased as the incubation period increased. In the Siberian Tit there was some indication that a long nestling period had a negative effect on the fledging percentage (r = –0.528, n = 12, P = 0.08), but in the Pied Flycatcher (r = –0.059, n = 50, P = 0.69) and the Redstart (r = 0.060, n = 22, P = 0.79) no such relationship existed.

4. Discussion

The incubating Pied Flycatcher female is fed regularly by her mate (up to 100 meals/day; v. Haartman 1958) as is also the female of the Siberian Tit (Haftorn 1973, own observations), but not the Redstart female (Ruiter 1941). The nest of the Siberian Tit is composed of a thick layer of moss and vole hairs and its insulation is apparently better than the insulation of the nests in the other two species. Thus the Siberian Tit seems to be best adapted to breeding in cold conditions.

The difference in male behaviour may explain the fact that the distribution of the duration of the incubation period was most positively skew in the Redstart (Fig. 1). The CV% values in Figs. 1–2 suggest either that the incubation period of the Redstart is most sensitive to cold weather or that the breeding strategy of the species is to leave eggs unincubated during cold spells. Especially in the early incubation phase, long interruptions of incubation do not seem severely to lower the hatching percentage. CV% of the nestling period was very similar in all species. The Siberian Tit was the only species in which CV% of the incubation period did not differ from that of the nestling period. This suggests that the Siberian Tit females are least affected by harsh conditions although they nest in the coldest weather (Table 1).

Table 3. Hatched young as a percentage of the eggs laid (hatching %) and fledged young as a percentage of hatched young (fledging %) in the Pied Flycatcher, Redstart and Siberian Tit in northern Finnish Lapland. The percentages are given separately for all nests, and for nests in which the incubation and nestling periods are known exactly.

	Pied Flycatcher		Redstart		Siberian Tit	
	Mean	n	Mean	n	Mean	n
All nests						
Hatching %	79.3	306	80.1	170	79.4	45
Fledging %	76.1	305	79.5	169	70.1	46
Incubation period known						
Hatching %	87.4	106	87.3	47	88.0	19
Fledging %	83.1	105	85.3	47	71.0	20
Nestling period known						
Hatching %	87.2	50	93.1	22	93.8	12
Fledging %	95.5	50	95.6	22	84.3	12

However, the nesting success of the Siberian Tit was relatively low, too (Table 3). Breeding early is hazardous since the parents have difficulties in finding food for themselves and the young (Järvinen 1982a, 1983), and cold spells during the time of hatching may be disastrous (own observations). In early spring, when there is still snow on the ground, the male Siberian Tit may not feed the incubating female as frequently as later on, which may explain the fact that in the Siberian Tit the laying date affected the incubation period (Table 2).

For 209 Pied Flycatcher nests in southern Finland, the mean daily temperature during the incubation period was 13.0°C (SD = 1.6; calculated by me from Table 3 in v. Haartman 1956), which is about 4.5°C higher than in northern Lapland (Table 1). Thus, in the north the birds must be able to tolerate remarkably low temperatures during the whole incubation period. Cold weather almost invariably lengthens attentive periods (v. Haartman 1956, Haftorn 1973, White & Kinney 1974). However, in extremely cold weather birds leave the nest and cease to incubate for their own survival (Pied Flycatcher, Redstart; own observations; for the Willow Warbler *Phylloscopus trochilus* in Swedish Lapland, see Arvidson & Nilsson 1983). A long incubation period may reduce the viability of the embryos, which lowers the hatching success (for the Pied Flycatcher and the Redstart, see Results; cf. White & Kinney 1974, Drent 1975).

The incubation periods shorten as the season advances, possibly because the average air temperature is higher, preventing the eggs from losing heat when the incubating bird is off the nest (e.g. Armstrong 1955, v. Haartman 1956). For instance, the mean incubation period of the Pied Flycatcher in southern Finland was 14.6 days in May but 14.0 days in June and there seemed to be a negative correlation between the incubation period and the mean daily air temperature (v. Haartman 1956, present study). Haftorn (1983) showed a similar inverse relationship for the Great Tit *Parus major* in central Norway

In central Norway, Slagsvold (1986) found a negative correlation between the incubation period and the laying date in the Pied Flycatcher. In the present study the laying date did not affect the incubation period of this species, but the mean air temperature did (Table 2). This may be partly due the fact that in northern Lapland cold spells often occur relatively late (end of June or July) and the mean daily air temperature does not necessarily rise with the progress of the season. However, there may be other reasons than temperature for the shortening of the incubation period, such as an increased and more available food supply later in summer, enabling the incubating female to spend less time in foraging and more time in the nest. Slagsvold (1986) suggests that for many early nests full incubation does not start until some days after the termination of egg-laying.

The negative correlation between the nestling period and distance from the lake shore in the Redstart is possibly due to retarded plant phenology near the shore, caused by the cooling effect of melting ice and cold water (see Järvinen 1982b).

Incubation and nestling periods are usually calculated for the last egg. However, some authors have calculated the incubation period from the laying of the last egg to the hatching of the first egg (Meidell 1961, Menzel 1971, Zang 1975, Winkel 1986; cf. Table 4) and the nestling period from the hatching of the last egg to the fledging of the first chick (Menzel 1971) or to the fledging of 50% of the young (Pied Flycatcher, v. Haartman 1956, 1969). These methodological differences cause only minor differences in the mean values of the variables, but they should be kept in mind when comparing the figures in Table 4.

In northern Lapland the Redstart has the shortest and the Siberian Tit the longest night-rest in nestling feeding (Hannila & Järvinen 1987). The short night-rest apparently promotes rapid growth of the Redstart nestlings. There is some evidence that the nestling period shortens from the tropics northwards (Armstrong 1954, Oakeson 1954, Lack 1968:227), possibly due to the prolonged daily parental feeding in the north (Armstrong 1954; for the Pied Flycatcher, the Redstart and the Siberian Tit in northern Lapland, see Hannila & Järvinen 1987). Since the northern summer is short, it would be advantageous to shorten the incubation and/or nestling period (e.g. Moreno & Carlson 1989). However, as pointed out by Irving (1960) and demonstrated in Table 4, embryonic or nestling development cannot be modified appreciably

Table 4. Incubation and nestling periods of the Pied Flycatcher, Redstart and Siberian Tit in different European study areas. Sources: 1) mountain area, Pulliainen 1977, 2) Haftorn 1971, 3) mountain area, Meidell 1961, 4) v. Haartman 1969, 5) mountain area, Zang 1975, 6) Glutz von Blotzheim, 7) Menzel 1971, 8) Winkel 1986, 9) Ryhtä & Näyhä 1983, 10) Haftorn 1973.

Species and area	Incubation period Mean	SD	Range	n	Nestling period Mean	SD	Range	n
Pied Flycatcher								
This study	14.6	1.4	13–20	113	15.6	1.0	12–18	50
1) NE Lapland	13.9	–	12–18	96	14.7	–	12–19	84
2) Norway	14.4	–	13–18	24	–	–	15–17	12
3) Norway	14.2	0.9	13–16	21	–	–	–	–
4) S Finland	14.2	–	–	209	16.0	–	–	–
5) W Germany	14.7	2.1	12–23	102	–	–	–	–
6) Switzerland	14.7	0.9	14–17	10	15.1	0.7	14–16	21
Redstart								
This study	14.8	2.5	12–22	47	13.5	0.7	12–15	22
1) NE Lapland	13.7	–	12–20	23	13.3	–	9–16	24
2) Norway	–	–	11–13	5	–	–	14–17	4
3) Norway	12.9	0.9	12–14	9	–	–	–	–
4) S Finland	14.3	0.8	13–15	7	13.7	0.9	12–15	9
7) Central Europe	12.9	1.5	11–17	58	13.9	1.5	11–18	50
8) W Germany	13.6	1.4	12–18	20	–	–	–	–
6) Switzerland	13.3	1.3	11–17	29	14.6	1.3	12–17	20
Siberian Tit								
This study	14.8	1.0	14–17	20	18.8	0.9	17–20	12
1) NE Lapland	16.8	1.2	15.5–17.5	3	19.5	–	19–20	2
9) N Finland	13.7	–	–	10	18.7	–	–	7
2, 10) Norway	14.7	0.6	14–15	3	–	–	–	–

as a climatic adaptation (the nestling period of 9 days for the Redstart in NE Finnish Lapland is remarkably short and probably erroneous).

In contrast, apparently due to direct temperature effects, the incubation period is likely to be longer in cold than in warm conditions, since in cold conditions it is difficult to maintain the eggs at the proper temperature (+34°C appears to be the lower temperature limit for successful hatching; White & Kinney 1974). At very cold temperatures all or almost all the time is spent in foraging, which results in a decline in the mean egg temperature and extends the incubation period (White & Kinney 1974).

According to Lack (1968:182), if food is scarce, the nestlings appear to grow their feathers at about the normal speed and so fledge at about the normal time, but with much smaller food reserves. My data on the Pied Flycatcher from northern Lapland indicate that heavy and long-winged nestlings leave the nest young, and that wing length at fledging is positively correlated with the mean temperature during the nestling period (Järvinen & Ylimaunu 1986). The effect of the ambient temperature on the duration of the incubation period was very clear in the Pied Flycatcher and the Redstart (Figs. 3–4). This result is important, since it suggests that the breeding success of passerines is also influenced by factors operating during incubation (see also Moreno & Carlson 1989).

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Selostus: **Koloissa pesivien varpuslintujen haudonta- ja pesäpoikasajat Kilpisjärvellä**

Kirjosiepon haudonta-ajan keskiarvo (113 pesää) oli 14.6 vrk ja pesäpoikasaika 15.6 vrk (n = 50). Leppälinnun vastaavat arvot olivat 14.8 vrk (n = 47) ja 13.5 vrk (n = 22) sekä lapintiaisen 14.8 vrk (n = 20) ja 18.8 vrk (n = 12). Keskiarvot eivät poikenneet eteläisten tutkimusalueiden keskiarvoista.

Kirjosiepon ja leppälinnun haudonta-ajan pituuteen vaikutti eniten haudonta-ajan lämpötila.

Kirjosiepon ja leppälinnun munien kuoriutumisprosentti laski haudonta-ajan pitenemisen myötä.

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