Developmental asynchrony and onset of incubation among passerine birds in a mountain birch forest of Swedish Lapland

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The onset of incubation and the developmental asynchrony (presumably equivalent to the ensuing hatching spread) were investigated by transilluminating and photographing egg clutches of 14 passerine species in a mountain birch forest of Swedish Lapland. By comparing the visible developmental stages in the eggs (state of yolk swelling, appearance of the embryo and extra-embryonic membranes) with stages of known age obtained from artificially incubated eggs, the time interval between the youngest and oldest stages in each clutch was estimated. Most clutches were asynchronous. The degree of asynchrony ranged from 0.5 to about 2.0 days, with the majority of values ranging between 1.0 and 1.5 days. The pattern of developmental spread among the eggs indicated that a pronounced increase in incubation intensity occurred after the penultimate egg was laid or one day earlier. A minority of the clutches showed developmental synchrony. These were significantly more frequent in the coldest and most rainy of the investigated seasons.

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Introduction

Many passerine species are known to start incubating their clutch well before the last egg is laid. This behaviour results in asynchronous hatching (Clark & Wilson 1981), the adaptive significance of which is still under debate (see Discussion). Years ago, we discovered that the hatching pattern of the passerines in our study area in Swedish Lapland was inconsistent in this respect. We therefore started to collect information on the beginning of incubation by monitoring the progress of embryonic development, as revealed by the transillumination of eggs during the first days after completion of the clutch. In this way we hoped to get an overview of the intraspecific, interspecific, and interseasonal variation, which in turn may contribute to the understanding of the synchrony/asynchrony problem. The method applied and some preliminary results are presented here.

Study area

The field work was carried out each June from 1980 to 1985 as part of the so-called LUVRE project (Enemar 1969) in the mountain birch forest on the south-facing slopes of the mountains of Gaisatjåkke and Valle, Swedish Lapland. The study area extends from the stream of Raurejukke in the west to the stream of Karsbäcken, 8 km to the east. It is bordered in the south by Lake Stora Tjulträsket and the stream of Tjulån. Most of the nests investigated were found in the centre of the area (65°58′N, 16°3′E; about 550 m a.s.l.). The forest vegetation is predominantly of the rich type ("meadow birch forest"). Its bird community has been described by Enemar et al. (1984).

Methods

The transillumination apparatus

The application of the transillumination technique to study the beginning of incubation was introduced by Enemar (1958). A simple transillumination device presented by Enemar & Arheimer (1980) for use in field investigations permitted only one egg to be inspected at a time. For the present purpose, however, a more efficient apparatus was constructed (Fig. 1) with which whole clutches can be transilluminated and

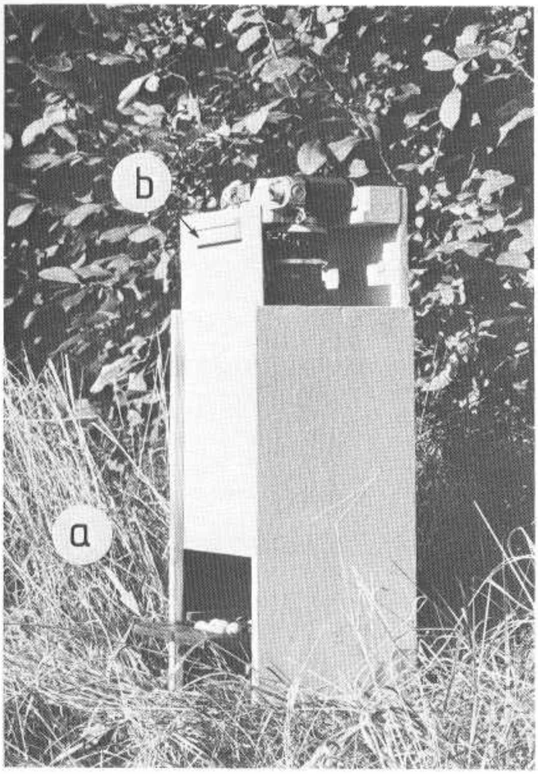

Fig. 1. Apparatus used for transilluminating and photographing whole egg clutches. Six eggs positioned to be photographed are visible on the tray (a). The tray is then pushed into the apparatus and the sliding door (b) is closed. For more details, see text.

photographed. The eggs are placed on holes in a tray in the apparatus and are illuminated from below by four torch bulbs powered by four 4.5 volt batteries. Unused holes in the tray are masked with opaque tape. The camera is installed above the eggs. When the apparatus is shut the camera lense and the eggs are protected from disturbing daylight. A label, consisting of a piece of transparent adhesive tape on which information about the clutch under study has been written, is placed over a window in the tray and is thus photographed together with the eggs. Photography offers two advantages: 1) The determination of the developmental stages within the transilluminated eggs is more efficient since photos from subsequent days can be directly compared, and 2) photographic prints reveal more details in the transilluminated eggs than can be discerned by visual examination in the field.

The field work

The nests found before or early in the laying period were visited daily to mark the eggs according to their order in the laying sequence. The entire clutch was marked in nest-box species whereas "open-nesting" species were accepted for study as far as at least the last two or three eggs were marked.

Routine photographing started the day after the final egg was laid, a photo being taken once daily for three or four days depending on the rate of development (intensity of incubation). Clutches of the more closely studied species were photographed twice a day at intervals of about 12 h, mostly in the morning and the evening. Sometimes an additional photograph was taken at about noon.

Identification and timing of the developmental stages

The appearance of the transilluminated eggs up to and including the third day after the clutch was completed has been described by Enemar & Arheimer (1980). The key information is provided by the yolk mass (the egg cell). In the fresh egg it appears in the centre of the egg as a dark, circular field surrounded by the translucent albumen (the egg white). In the fertilized egg the yolk mass starts to swell during the second day of steady incubation owing to the uptake of water from the albumen (Romanoff 1960). During this swelling period the yolk mass moves upwards from its original position in the centre and takes on a flattened form by the time it reaches the shell membranes (in this way the early embryo is carried closer to the brood patch of the incubating bird). The dark yolk field thus increases and finally covers the whole aspect of the egg. This process is enhanced by the rupturing of the membrane that envelopes the yolk (the vitelline membrane). As the yolk field approaches the margin of the egg the embryo becomes visible, with its circular field of extra-embryonic, vascularized membranes, the *area vasculosa*, now covering about half of the aspect of the yolk. Blood in the embryo and in the membranes contributes to the growing opacity of the egg. This opacity increases during the following few days as the membranes, which are richly supplied with blood vessels, grow to completely embrace the yolk mass and form the yolk sac. At this point the transilluminated egg is tinged dark red.

Enemar & Arheimer (1980) identified five stages of yolk mass swelling to facilitate describing the developmental state of single eggs inspected in the field.

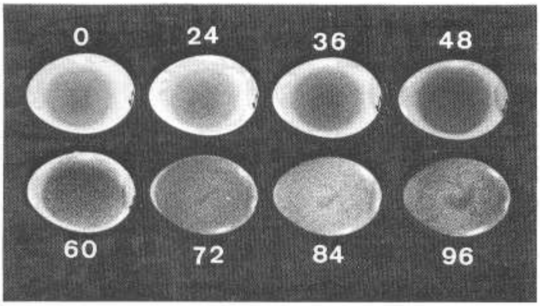

Fig. 2. *Ficedula hypoleuca.* Photos of a transilluminated egg after various intervals of artificial incubation. Incubation times are indicated. An embryo is visible in the 72-h and older stages.

This is not necessary when analyzing photographs of whole clutches. It is, however, important to know the time elapsed between selected developmental stages when incubation is in full swing. Therefore the timing of the various developmental stages was studied in artificially incubated eggs of the Pied Flycatcher *Ficedula hypoleuca*. Sets of 4, 4, and 9 eggs were sampled from nests with one to three eggs laid (i. e. well before the onset of steady incubation) and continuously incubated at 37±0.5°C, 38±0.5°C, and 39±0.5°C, respectively. The eggs were put into the incubator at 3 h intervals, and whole sets were transilluminated and photographed beginning when the last egg in each set was introduced. The eggs were photographed every 3–4 h during daytime for four subsequent days. In this way photos were obtained of a close series of developmental stages of known age. The results can be summarized as follows (Fig. 2): During the first two days of steady incubation (0–48 h) the shape and size of the yolk sphere remained unchanged. In a few eggs a slight swelling occurred towards the end of the period (a process that was overestimated by Enemar & Arheimer (1980) based only on field data). During the third day (49–72 h) the swelling started and progressed, eventually covering the whole aspect of the egg by the end of that day, give or take a few hours. Many of the photos taken at this point reveal an embryo with an *area vasculosa* having a diameter about half the breadth of the egg. This developmental stage of the embryo, here called the 72-h stage, corresponds with the 72-h embryo in the hen's egg (Hamilton 1952). After 12 to 24 h the membranes lined with blood vessels have grown to such an extent that they cover all aspects of the egg, and the embryo itself is discernible as a dark and relatively large lump.

The rate of development for eggs of the Pied Flycatcher steadily incubated under natural conditions is the same as that found for artificially incubated ones. This has been established by trans-illumination of the last laid egg, which is efficiently incubated from the beginning. We also found that in three other passerine species the 72-h stage is reached within a day of the start of yolk swelling. It is reasonable to assume that the early development, as revealed by transillumination, proceeds according to a similar time schedule in all passerine species belonging to the bird community investigated.

Interpretation of the photographs

Transilluminated eggs usually show different stages of development when inspected during the first few days after completion of the clutch. The photo taken two days after the appearance of the final egg is often highly informative. At this time the yolk of the last-laid egg is generally about to start swelling, provided that steady incubation began once the clutch had been completed or earlier. A case in point is presented in Fig. 4C. The final egg has been incubated for 48 h and still looks fresh. The penultimate egg is still in the yolk-swelling state, indicating that it had not been incubated with full intensity during its three days in the nest. Its developmental stage should therefore be somewhere between the 48- and 72-h stages. The embryos of the first five eggs all appear to be slightly more advanced than the 72-h stage. We can conclude that the incubation intensity increased considerably once the fifth egg had been laid. However, there is still a problem in estimating the developmental age of the final egg since the shape of the yolk mass remains unchanged for about the first 48 h of incubation. The state of the penultimate egg helps in this regard, and suggests that the final egg must be close to the 48-h stage (this was confirmed by the subsequent photo taken 24 h later). It can be concluded that the extent of developmental asynchrony in this clutch is 1 to 1.5 days.

Synchronous development of a clutch is easily established by transillumination (cf. Fig. 3C, D; Fig. 4B). This pattern of development arises when the onset of efficient incubation is postponed at least until the laying of the final egg.

In general, small developmental differences are found between eggs considered to develop syn-

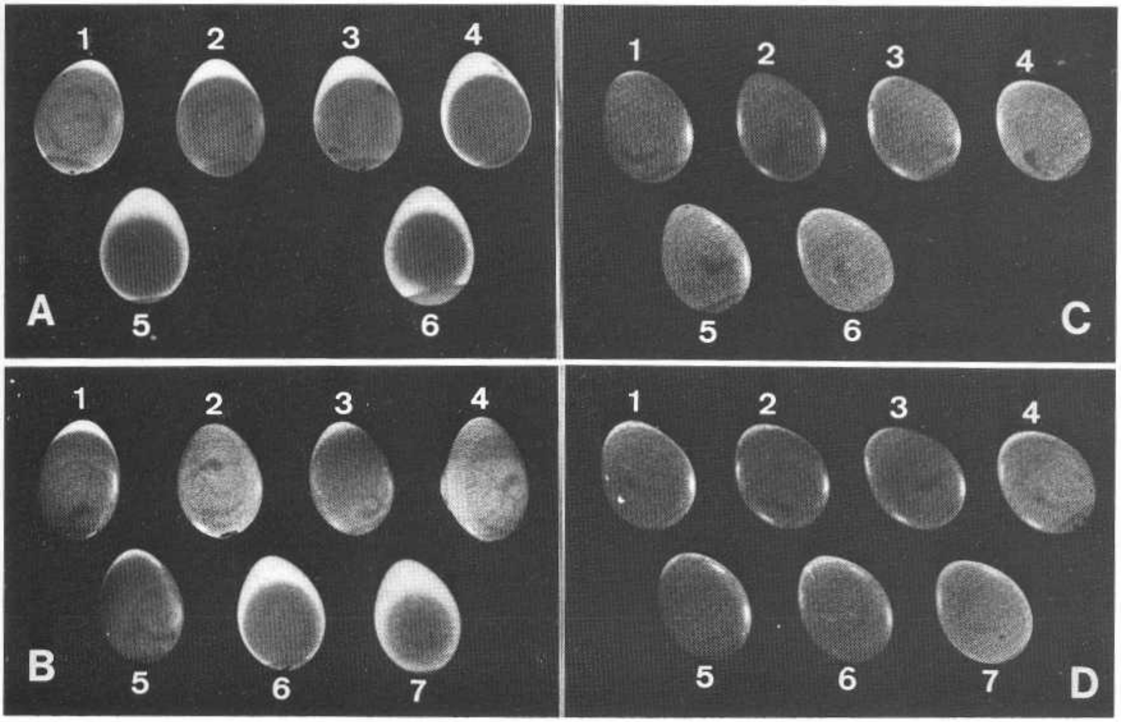

Fig. 3. *Ficedula hypoleuca*. *A* and *B*. Six- and seven-egg clutches photographed 1.5 and 2.0 days after the appearance of the final egg. Both clutches are asynchronous as revealed by the last two eggs which are lagging behind in development. The two and five first eggs in *A* and *B*, respectively, all show embryonic structures. *A* shows a sequence of stages in the development of the *area vasculosa* (eggs 1 to 4), each separated by few hours of incubation time, whereas in B all embryos have progressed to the 72-h stage. The developmental spread was estimated around 1.0 to 1.5 days for both clutches. — *C* and *D*. Six- and seven-egg clutches showing synchronous development; all eggs contain embryos of about the 72-h stage. — Numbers denote the position in the laying sequence.

chronously. This can be attributed to the fact that the older eggs are heated by the female each time she sits on the nest to lay the subsequent eggs. Therefore the eggs laid before the beginning of steady incubation can show a narrow sequence of stages separated by only few hours of developmental time (cf. Fig. 4A).

Interpretation of the photos is sometimes obstructed. This can occur if the egg shell is too darkly coloured, when an egg ceases to develop, or when irregularities occur in incubation behaviour. The two last-mentioned difficulties can be overcome with the aid of photos from a number of subsequent days. After considering all of the limitations inherent in the transillumination technique, we decided to establish a developmental asynchrony scale divided up into 0.5 day (12 h) units. Clutches with less than a 12 h difference in the extent of development between the first and last egg are designated as synchronous.

Results

The developmental asynchrony, as established two to four days after completion of the clutch, is presented for a number of species in Table 1. The time intervals varied from less than 0.5 days (synchronous clutches) to more than 2 days. The majority of clutches were asynchronous, with intervals between first and last laid egg ranging from 0.5 to 1.5 days. Intraspecific variation was considerable in the Pied Flycatcher, Redstart *Phoenicurus phoenicurus* and Reed Bunting *Emberiza schoeniclus*. On the other hand, species

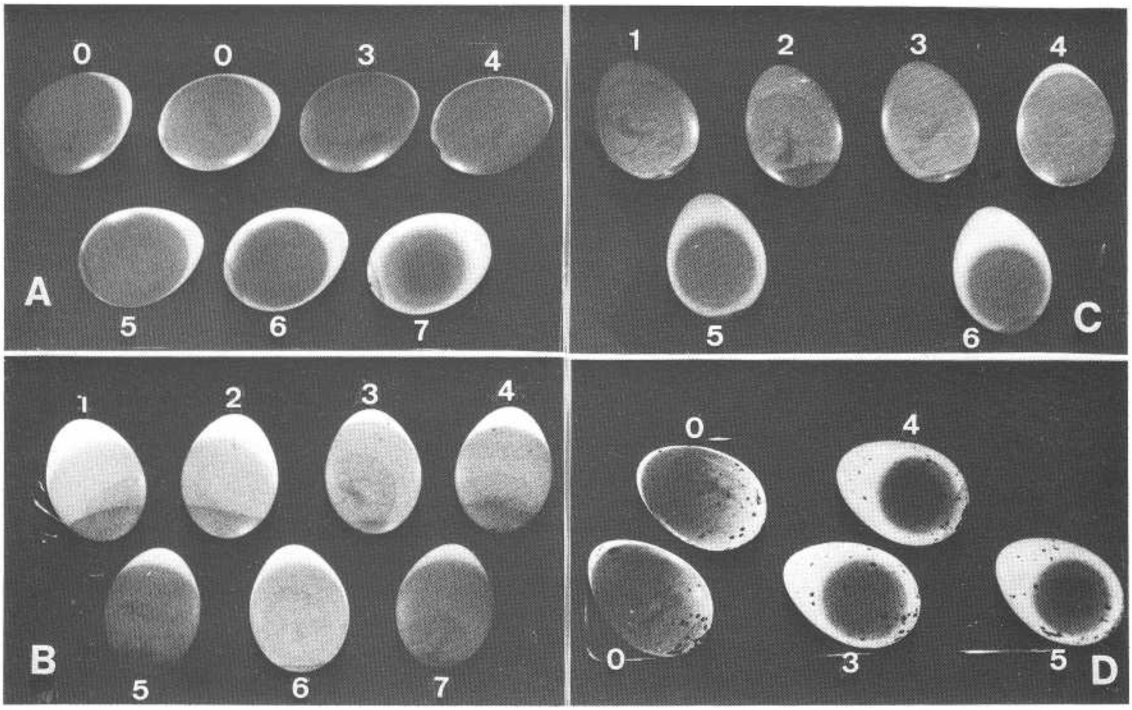

Fig. 4. *A* and *B*. *Phoenicurus phoenicurus*. Clutch *A* was photographed 1.5 days after the appearance of the final egg, which, accordingly, still looks fresh, whereas the yolk is in the process of swelling in the penultimate egg. The first four eggs show 72-h embryos whereas the embryo of the fifth egg is younger. The developmental asynchrony was estimated to be 1.0 to 1.5 days. — Photo *B* shows a synchronous clutch three days after completion. All eggs contain embryos in different positions. They are all of about the 72-h stage, except for the penultimate egg, which is a little younger. — *C*. *Luscinia svecica*. Clutch photographed 48 h after completion, with the yolk of the final egg about to start swelling. It is evident that a sharp rise in incubation intensity occurred after the fourth egg was laid. Developmental asynchrony = 1.0 to 1.5 days. — *D*. *Turdus philomelos*. The developmental spread of this clutch indicates that the female had already increased incubation intensity considerably after laying her second egg. The developmental asynchrony, estimated with the aid of photos taken 12 and 24 h later, amounted to nearly 2 days. — Numbers denote the egg's position in the laying sequence. 0 indicates more than one egg present in the nest when first inspected.

Table 1. The distribution of clutches according to estimated degree of developmental asynchrony for 14 passerines in the mountain birch forest.

Species	Developmental asynchrony, days				
	0–<0.5	0.5–<1.0	1.0–<1.5	1.5–2.0	>2.0
Ficedula hypoleuca	7	3	6	–	–
Phoenicurus phoenicurus	3	3	3	1	–
Luscinia svecica	–	–	6	–	–
Phylloscopus trochilus	1	1	6	–	–
Emberiza schoeniclus	3	–	2	–	–
Carduelis flammea	–	–	4	1	–
Prunella modularis	–	1	–	–	–
Fringilla montifringilla	–	1	–	2	1
Motacilla flava	–	1	–	–	–
Anthus pratensis	–	–	2	–	–
Muscicapa striata	–	1	–	–	–
Turdus pilaris	–	–	–	1	–
Turdus iliacus	–	1	2	1	–
Turdus philomelos	–	–	–	1	–
Total clutches	14	12	31	7	1

Table 2. Numbers of synchronous and asynchronous clutches in wet, cold seasons and in normal seasons for those species investigated in both types of years ($\chi^2 = 16.9$, $P < 0.001$).

	Synchronous	Asynchronous
Wet and cold	10	7
Normal	1	26

such as the Bluethroat *Luscinia svecica* and the Redpoll *Carduelis flammea* showed relatively little variation in the degree of asynchrony. Too few clutches were examined, however, to detect interspecific differences.

The 1981 breeding season stood out as very wet and cold compared with the other years of the investigation. Therefore the results of that year are presented separately in Table 2 for those species investigated in both 1981 and in at least one other season. The proportion of synchronous clutches during the harsh season of 1981 was significantly higher than that of the remaining five years.

Discussion

The transillumination method

Although information on the developmental progress among the eggs of a clutch is of little value in itself, it does serve to predict the degree of the subsequent hatching spread, namely that component of the spread attributable to the female's incubation behaviour during the laying period. Other factors, such as differences in egg quality (Bryant 1978) and various accidental events, may also influence the hatching spread. It follows that the extent of the initial developmental spread and that of the hatching spread can differ, although this remains to be determined. It has, however, commonly been observed that the last egg to be laid is usually the last one to hatch, indicating that the way in which the female starts to incubate is the main factor generating the hatching spread. Moreover, the variation in the hatching spread of the Redwing *Turdus iliacus* and of the Bluethroat reported by Arheimer (1978, 1982) is similar to our estimate of the developmental asynchrony in this species (Table 1).

The degree of hatching asynchrony has usually been measured by directly observing the hatching process. Repeated visits to the nest are required, which often disturb the bird considerably during a delicate phase of the incubation. This might in turn affect the timing of the hatching process under study. Frequent visits should therefore be avoided. Consequently, only rough and often contradictory measurements are available for many species. Slagsvold (1986) mastered the problem by deriving the hatching spread in the Pied Flycatcher from the weight increase curves of the nestlings. The transillumination method might be helpful in this context. Apart from the information provided on hatching spread the following advantages of the method deserve to be mentioned. (1) The estimated developmental asynchrony is mainly based on a single factor: the behaviour of the sitting bird. (2) The "chronometer" used is the egg cell and the embryo itself, both of which pass through easily identifiable stages of development during the first few days of incubation, following a fixed, heat-dependent time schedule. The "clock-work" is the same for all eggs of the clutch: the sitting bird. Therefore, under optimal conditions the time intervals between the developmental stages in the clutch can be determined using transillumination on a single occasion (see below). (3) Information is simultaneously obtained on the beginning of incubation in relation to the appearance of the eggs.

To minimize disturbances, the transillumination work should not be started until two days after the clutch is completed, at which time the yolk of the final egg is about to start swelling. In synchronous clutches the remaining eggs are also in the swelling stage, and no further inspections are required. Although the developmental spread in asynchronous clutches can sometimes be determined conclusively on this first occasion, one or a few more inspections at intervals of 12 to 24 h are often required. We strongly recommend checking the nest during laying in order to mark at least the last few eggs with their ordinal numbers. The transillumination of initially unmarked clutches should be repeated on two or three consecutive days to avoid misinterpretations due to the occurrence of eggs that are unfertilized or that fail to develop normally for other reasons. In such cases it is necessary to mark the eggs on the occasion of the first transillumination. In this way the development of each individual egg can be followed, thereby facilitating interpretation.

The onset of incubation

Haftorn (1981) discusses the concept of "incubation start". He defined "incubation" as every brooding behaviour raising the egg temperature above the threshold value for embryonic development. This implies that incubation always starts before the clutch is complete, since a certain amount of heat is transmitted to the eggs in connection with laying. According to Haftorn it is reasonable to discriminate between this first stage of incubation and "steady incubation", during which time the egg temperature is constantly kept above the threshold value necessary for maintaining *optimal* developmental rate. For most clutches in our investigation steady incubation began when the final egg was laid. This is demonstrated by the condition of the final egg three days after completion of the clutch. At that time the developmental stage of this egg often corresponds to that of eggs incubated artificially for 72 h (the 72-h stage).

The time spent incubating increases gradually during the laying period, with an accelerated rise in intensity occurring towards the end of this period. The transillumination photos usually reveal that one or two eggs in any given clutch lag considerably behind the rest in development. This indicates that incubation increased substantially after the penultimate egg was laid or one day earlier, which coincides with the beginning of steady incubation of a large number of passerine species (cf. Clark & Wilson 1981). Thus it appears that asynchronous hatching occurs regularly among the passerines in the investigated mountain birch forest. There are exceptions to this "asynchrony rule", however. These are commented on below.

Interseasonal variation in developmental asynchrony

In this investigation 14 of 65 clutches were synchronous, i.e. they had less than 12 h spread in degree of development. Ten of these clutches were recorded in 1981, the four exceptions being one Redstart clutch (1980) and three Reed Bunting clutches (1983, not investigated in 1981). Since the 1981 breeding season was exceptionally wet and cold we presume that this synchrony was a consequence of the harsh weather during laying. Five species were investigated in 1981: Pied Flycatcher (11 clutches), Redstart (2), Bluethroat (2), Willow Warbler *Phylloscopus trochilus* (1), and Redpoll (1). Seven clutches of the Pied Flycatcher, both of the Redstart clutches and the Willow Warbler clutch were synchronous while both of the Bluethroat clutches and the Redpoll clutch were asynchronous.

Descriptions of the hatching pattern have been included in many studies on the breeding biology of various passerine species during the last few decades. These studies contain some information regarding the effects of environmental factors on hatching pattern. Ylimaunu & Järvinen (1987), studying the Pied Flycatcher in northernmost Finland, also reported a tendency toward synchrony in a year characterized by unusually cold weather. This result was considered "unexpected". Slagsvold (1985, 1986) established that hatching spread in the Pied Flycatcher was more pronounced in rich habitats than in poor ones and that it was positively correlated with the air temperature during the five days prior to the start of laying. He therefore suggested that "birds may hatch the eggs rather synchronously under unfavourable conditions". This hypothesis gains substantial support from our results.

It seems reasonable to assume that constraints on food availability, whether or not they are induced by inclement weather, during the egg-laying period force the female to forage more intensively, leading to a delay in the onset of steady incubation. In fact, in the harsh season of 1981 some of our nesting females did not start incubating until 0.5 to 1.5 days after the appearance of the final egg. It is easy to understand why such a situation leads to synchronous development.

The House Martin seems to be an exception: its hatching spread increases in response to food shortage during laying (Bryant 1978). This fact need not contradict the above-mentioned interpretation since the asynchrony in the House Martin, according to Bryant, is rather caused by the differential quality of the eggs than by the brooding behaviour of the female. On the other hand, it has been demonstrated in some species that hatching asynchrony increases as the breeding season progresses (Gibb 1950, van Balen 1973, Neub 1979, Haftorn 1981). This tendency has been proposed as being an adaptation to the decline in food resources that occurs towards the end of the season. In this case, early incubation has been interpreted as an effort by the parent birds to produce at least a few fledglings before resources disappear (Clark & Wilson 1981).

Theoretical analyses as well as interpretations based on experiments in the field or in the laboratory have been conducted to determine the ultimate value of hatching asynchrony. Lack (1954) hypothesized that asynchronous hatching should facilitate the quick elimination of the smallest young when competing with larger siblings during a period of food shortage. As a consequence, fewer fledglings of better quality would be produced. This so-called "brood-reduction hypothesis" has recently been questioned, and a number of other hypotheses have been proposed, resulting in a growing consensus that a diversity of selection pressures contribute in shaping the hatching pattern (cf. Hussell 1972, 1985, Clark & Wilson 1981, 1985, Richter 1982, Mead & Morton 1985, Slagsvold 1986, Skagen 1987). The current discussion should not be reviewed in this context. Nevertheless, we want to call attention to the fact that most of the synchronous clutches in the mountain birch forest occurred during a period of bad weather, i.e. in a food shortage situation. If food was still in short supply during the ensuing nestling period, asynchronous clutches would be favoured according to the brood-reduction hypothesis. Moreover, asynchrony has also been suggested as being an adaptive response to bad weather because it reduces the time between the first egg and the first fledgling (Tyrväinen 1969, Hussell 1972). The predominance of synchronous clutches during the cold, wet 1981 season in our study is incompatible with these views. Perhaps these clutches simply represent failures by the females in their efforts to generate developmental asynchrony, whatever the driving and ultimate selective force(s) of the latter might be.

Acknowledgements. In the hope that the present study will interest Professor Lars von Haartman, it is dedicated to him on the occasion of his 70th birthday. A.E. still reveres his very first and most excellent supervisor in ornithology (cf. Vår Fågelvärld 8 (1949):74–80). We thank Åke Norberg and Bengt Svensson for help in constructing the "ootransilluminograph" and David Tilles for his scrupulous linguistic revision. The investigation was supported by the Swedish Natural Science Research Council and the Royal Society of Arts and Sciences of Göteborg.

Sammanfattning: **Om asynkron fosterutveckling och ruvningens igångsättande hos tättingar i en lappländsk fjällbjörkskog**

Ruvningens gångsättande och spridningen i fostrens utvecklings-stadier i äggkullen studerades genom att analysera den bild av tillståndet i äggen man erhåller genom att genomlysa och fotografera äggen med hjälp av en apparat som visas i Fig. 1. Ett tidsschema över utvecklingsförloppet, såsom det kan urskiljas i det genomlysta ägget, erhölls genom att med jämna tidsintervall fotografera ägg av svartvit flugsnappare som hållits under kontinuerlig ruvning i en äggkläckningsmaskin. Resultatet framgår av Fig. 2 där siffrorna anger ruvningstid i timmar. Med hjälp av detta "facit" kunde alltså spridningen i utvecklingstid mellan äggen, såsom de framstår på fotografierna av de genomlysta kullarna (Fig. 3 och 4), skattas på ett halvt dygn när. Därvid spelade äggulans svällning och uppträdandet av synligt foster med omgivande blodkärlsmönster den största rollen.

Resultatet av genomlysningarna redovisas i Tabell 1. De flesta kullarna uppvisade en spridning i fostrens utvecklingsstadier som motsvarar en skillnad i utvecklingstid mellan äldsta och yngsta ägg på 0,5 till omkring 2 dygn med 1,0 till 1,5 dygn som vanligaste intervall. Den konstaterade asynkronin i utvecklingen inom kullen beror på att ruvningen börjar innan sista ägget är värpt, ett sedan länge känt förhållande. Den bild av spridningen i fosterutvecklingen som fotografierna ger är alltså på samma gång en bild av hur ruvningsbeteendet utvecklats under äggläggningsperioden. Oftast har en avsevärd höjning i ruvningsintensiteten skett när det näst sista eller näst-näst sista ägget värpts.

Ett mindre antal kullar uppvisar synkron utveckling (tidsintervall < 0,5 dygn, Fig. 3 C and D, Fig. 4 B) med klar koncentration i förekomst till den säsong som var extremt regnig och kall (Tabell 2).

Den asynkroni i utvecklingen inom en kull som kan konstateras med genomlysning kommer att följas av en ungefärligen motsvarande spridning mellan äggen vad gäller tidpunkt för kläckningen. Den huvudsakliga biologiska betydelsen av utvecklingsasynkronin är att söka i de kläckta ungarnas olikåldrighet. Flera tolkningar har föreslagits. Den här redovisade tekniken erbjuder en möjlighet att relativt snabbt införskaffa kunskap om kläckningsspridningens inom- och mellanartsvariation samt dess omgivningsberoende. Detta krävs säkerligen för att förklara anpassningsvärdet i det förhållandet att effektiv ruvning så ofta utvecklas långt innan sista ägget är värpt.

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