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Timing of autumn migration in Bluethroats *Luscinia s. svecica* depends on timing of breeding

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In order to test the hypothesis that interannual variations in the timing of breeding can affect the more precise timing of the autumn migration, the northern Red-spotted Bluethroat was investigated. There was a significant correlation between the timing of breeding at Ammarnäs in Swedish Lapland (median date on the first egg laid) and the timing of the autumn migration in eastern Sweden (median arrival dates to stop-over sites). This seems to be a causal relationship and suggests that Bluethroats start their autumn migration as soon as possible after breeding and the moult. The evolutionary significance of an early migration start in this species may, for example, be that it is advantageous to reach suitable stop-over sites as soon as possible.

A clear relationship between the timing of breeding and migration in Bluethroats implies that the onset of migration is not just a consequence of inherited factors and exogeneous influences, but is also affected by annual phase variations in basic events like breeding. However, breeding itself is not to be considered an independent variable since its timing is possibly influenced by both inherited and exogeneous factors.

1. Introduction

An important question for the understanding of bird migration is what factors influence the onset of migration. While exogeneous influences such as photoperiod and climatic conditions for a long time have been known to stimulate migration (e.g. Lack 1960, Alerstam 1978, Richardson 1978, Gwinner 1986), the major role played by endogeneous factors has been demonstrated only recently. The role of an innate circannual rhythm in determining the timing of migration has been shown in elegant experiments that suggest high heritability (Berthold 1975, 1984, Berthold & Querner 1981, see also Sutherland 1988).

Although the genetic basis of circannual rhythms can explain crude intra- and interspecific variations in the urge to migrate, little is known about the effects of the timing of breeding on the timing of migration. A possible relationship between the timing of breeding and migration may, for example, exist within species that normally breed and migrate in close succession, i.e. long-distance migrants. If there is selection for a long-distance migrant to start its autumn migration as soon as possible after breeding and moulting, interannual variations in the timing of breeding should be positively correlated with the timing of the autumn migration.

I have investigated the relationship between breeding and migration in the northern Red-spotted Bluethroat *Luscinia s. svecica*. This subspecies breeds in subalpine localities in Fennoscandia and presumably winters in southwest

Asia (Ellegren & Staav 1990a). Breeding data from Ammarnäs in Swedish Lapland (Arheimer 1982) were analysed together with data on arrival dates at stop-over sites during the autumn migration in eastern Sweden.

2. Material and methods

In the subalpine birch forest at Ammarnäs (65°58′N, 16°17′E), the date of laying of the first egg was recorded during eleven seasons from 1972 to 1982 (Arheimer 1982). The registrations deviated at most ± 2 days from the actual date. From 6 to 29 clutches were observed annually (mean=18, SD=8.3, relayings defined as a laying after a period of ten days without any laying established, were excluded). The average laying date of the first egg is defined as the "timing of breeding". More information on the field work has been given by Arheimer (1982).

Regular ringing of resting Bluethroats was carried out at two stop-over sites in eastern Sweden: 1972–1978 at Angarnsjöängen, N Stockholm (59°33′N, 18°09′E) and 1979–1982 at Inre Fjärden, Gävle (60°41′N, 17°11′E). On average, 413 birds were ringed annually (SD=194). The main migration period of the species was covered by similar activities in all years. Birds were mist-netted in reeds and weedy areas according to schemes that have been described elsewhere (Aspenberg et al. 1980). Age and sex determinations were made according to Svensson (1984). Pooled data from several years reveal a three-day difference in median arrival date between Inre Fjärden and Angarnsjöängen (Ellegren unpubl.), the latter locality being situated 150 km SSE of Inre Fjärden. Since the direction "Inre Fjärden/Angarnsjöängen" approximately corresponds to the general migration direction of Bluethroats, this time difference is thought to reflect the time needed for birds to cover 150 km along the migration route. In order to obtain a uniform time measure on the migration in eastern Sweden, therefore, median arrival dates at Angarnsjöängen have been transformed by subtracting three days. The three-day transformation is further justified by the estimated value of migration speed in Bluethroats during the initial phase of the autumn migration (42 km/day, Ellegren 1990).

3. Results

Annual median dates for breeding at Ammarnäs varied between 2 and 13 June. The variation in annual median arrival dates at the stop-over sites in eastern Sweden was of the same order of magnitude, i.e. 25 August – 5 September (Table 1).

Table 1. Breeding data from Ammarnäs, Swedish Lapland and migration data from Angarnsjöängen and Inre Fjärden in eastern Sweden, for the Red-spotted Bluethroat.

	Breeding data			Migration data	
Year	Number of broods	Range	Median date	Number ringed	Median date
1972	6	4–15.6	6.6	232	2.9
1973	29	3–11.6	7.6	389	30.8
1974	26	1–17.6	8.6	270	4.9
1975	12	4–14.6	9.6	289	3.9
1976	19	30.5–16.6	3.6	529	31.8
1977	17	6–15.6	13.6	244	5.9
1978	18	2–12.6	7.6	341	2.9
1979	12	2–19.6	6.6	263	1.9
1980	7	3–13.6	7.6	841	3.9
1981	24	29.5–19.6	2.6	617	25.8
1982	23	4–17.6	9.6	527	31.8

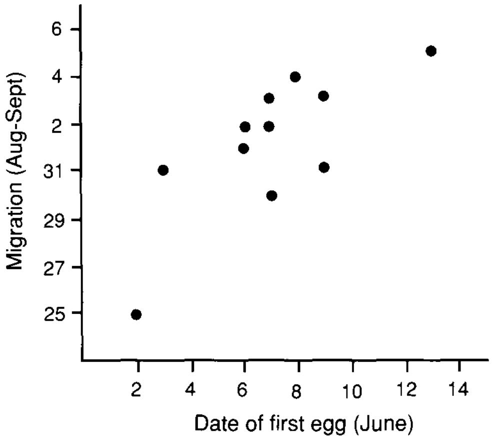

Fig. 1. The relationship between annual median date of the first egg layed at Ammarnäs, Swedish Lapland, and annual median arrival date to two stop-over sites in eastern Sweden during the autumn migration of the Bluethroat.

The earliest (1981) and the latest (1977) breeding season coincided with the year of the earliest and latest arrival at the stop-over sites, respectively. Overall, there is a positive relationship between the timing of breeding and the timing of autumn migration (Fig. 1, Spearman rank correlation, $r_s = 0.65$, $P < 0.025$). When breeding was tested against the migration of juvenile males separately (mean=217, SD=111), the correlation was still significant ($r_s=0.60$, $P<0.05$), but it was not significant in the test against juvenile females (mean=128, SD=66, $r_s=0.43$, $P>0.05$). Too few adults were ringed annually to be sufficient for a meaningful analysis (mean=54, SD=34).

4. Discussion

The northern Bluethroat is a suitable species for ecological studies on migration. It is common in certain resting places and can easily be trapped. It can also be aged and sexed easily. Most importantly, the subspecies breeds in a well-defined, northern area, and thus birds appearing in southern Fennoscandia are evidently migrants. Consequently, actual migration can be distinguished from post-breeding dispersal and local movements. This situation is necessary for accurate determinations of the timing of migration at stop-over sites. Another attractive feature is that birds migrating through eastern Sweden seem to originate from a homogeneous Swedish/Norwegian population (Ellegren & Staav 1990a). Compare, for example, the complex migration pattern of the Robin *Erithacus rubecula* (Pettersson & Lindholm 1983, Gezelius & Hedenström 1988), the Willow Warbler *Phylloscopus trochilus* (Hedenström & Pettersson 1987) and the Great Tit *Parus major* (Pettersson 1981) in southern Scandinavia.

Bluethroats breeding in Ammarnäs and the surrounding areas may not migrate precisely over the part of Sweden where Inre Fjärden and Angarnsjöängen are located. In fact, ringing recoveries indicate that birds appearing in eastern Sweden have their main recruitment areas somewhat south of Ammarnäs (Ellegren & Staav 1990a). Here it is assumed, however, that data on breeding times at Ammarnäs constitute a fairly representative measure of the average timing of breeding in the southern part of the Fennoscandian mountain chain.

Data provided in this study show that there is a positive correlation between the timing of breeding and migration in the northern Bluethroat. Since the migration pattern of adults and juveniles may differ, however, it is important to point out that the material consists of 90% juveniles and that, due to the small sample size, it was not possible to analyse adults separately. To be able to test this relationship four criteria have to be fulfilled:

1) the timing of laying of the first egg should be an appropriate measure of the timing of breeding,
2) the timing of the post-juvenile moult should depend on the timing of breeding,
3) the timing of departure from the breeding areas should depend on the timing of the moult and
4) the timing of arrival at stop-over sites should depend on the timing of departure from the breeding areas.

According to breeding data given by Järvinen & Pryl (1980) and Arheimer (1982) the first statement is correct. Statements 2–4 are questions concerning whether four sequential events are correlated with respect to timing. At Ammarnäs juveniles leave their nests, on average, on 5–10 July (calculated from Arheimer 1982), with still poorly developed remiges. Just three weeks later their remiges are fully grown and usually the post-juvenile moult is in an advanced state (Lindström et al. 1985). This suggests that the moulting event is closely linked to the time of juvenile independence, although there are no data available showing a correlation based on interannual variations. Similar arguments can be used for statements 3 and 4. Juveniles leave Ammarnäs about 10 August and later while the post-juvenile moult may still not be complete (Lindström et al. 1985), and migrating birds start to appear in eastern Sweden about 15–20 August (Aspenberg et al. 1980). There is also a lack of data on interannual variations in these two events. However, the very restricted time this species spends in its breeding grounds indicates that all the events are performed in close succession. I have therefore interpreted my data as demonstrating that the timing of migration depends on the timing of breeding.

The connection between the timing of breeding and migration suggests that Bluethroats start their autumn migration as soon as possible (but strictly speaking the data only show that when breeding is early, migration is early and vice versa). In this context two related observations are particularly interesting. Firstly, the fact that some juveniles leave their birthplaces and start to migrate before the body moult is completed (Lindström et al. 1985) is well in accordance with the results presented here, since it may imply that the urge to migrate becomes so intense that migration starts before the moult is finished. Normally, the energy-consuming moult and migration do not overlap (Ginn & Melville 1983). Secondly, the fact that some adult Bluethroats undergo a moult migration to southern and eastern Sweden in July (Ellegren & Staav 1990b) can also be interpreted as a manifestation of the importance of starting the autumn migration early. The evolutionary significance of an early start of the autumn migration in Bluethroats can only be speculated on (cf. Ellegren & Staav 1990b). Two alternative reasons would be either to reduce the risk of becoming exposed to adverse alpine weather, or to reach stop-over sites where temporal feeding territories are probably defended (Aspenberg et al. 1980).

The present study constitutes the first example of how interannual variations in breeding time can affect the more precise timing of the autumn migration. Thus, another variable can be added to the mixture of endogenous factors and external stimuli governing the onset of migration. However, it must be emphasized that the timing of breeding itself can be affected by endogenous factors, as well as by external stimuli. For example, since Bluethroats' nests are situated right down on the ground, the timing of nest construction is highly dependent on the degree of snow cover (Järvinen & Pryl 1980). Due to annual variations in the time when the ground becomes free of snow, therefore, this variable can influence the whole schedule, including the timing of the autumn migration.

My finding is based on observations on the population level. Recently, Rees (1989) has shown that there is an individual consistency in the timing of migration in the Bewick's Swan *Cygnus columbianus*, a pattern that is acquired either genetically or by learning from one generation to another. Rees suggests that the individual consistency acts on the basis of different threshold levels for photostimulation. Whether this kind of variation exists in a species where the timing of migration depends on the timing of breeding, remains to be elucidated.

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Sammanfattning: **Tidpunkten för blåhakens *Luscinia s. svecica* höstflyttning påverkas av tidpunkten för häckningen**

I denna studie undersöktes huruvida tidpunkten för blåhakens häckning styr tidpunkten för artens höstflyttning. 11 års häckningsdata från Ammarnäs i svenska Lappland jämfördes med ankomsttider till rastlokaler i östra Sverige under höstflyttningen. Sträckmaterialet utgjordes huvud-

sakligen av ungfåglar. Ett signifikant positivt samband erhölls mellan tidpunkten för häckning och flyttning. Detta antyder att blåhaken startar sin höstflyttning så snart som möjligt efter häckningen. Den bakomliggande orsaken till mönstret kan t.ex. vara att det är viktigt för fåglarna att tidigt anlända till vissa rastplatser under flyttningen. Sambandet mellan tidpunkt för häckning och flyttning innebär att ytterligare en variabel kan läggas till den komplexa blandning av endogena faktorer och yttre påverkan, som styr tidpunkten för fåglars flyttning.

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