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Juvenile moult and spatial behaviour of first-year Blackbirds *Turdus merula* on the northeast edge of the range

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A peripheral Blackbird population breeding in Karelia since 1975 was studied in 1978-2005. First captures and subsequent recaptures of 383 birds ringed as nestlings and 490 individuals of unknown origin were analysed. Juvenile moult and spatial behaviour of birds at different stages of moult are characterised. Even though Blackbirds' time of breeding is similar to that of autochthonous thrush species (Redwing and Song Thrush), Blackbirds retain very late juvenile moult and are more sedentary during the postfledging period. Therefore, most first-autumn birds depart very late under adverse weather conditions with uncompleted body moult. The assumption that along with adaptation to northern conditions, juvenile moult should be shifted towards earlier season is confirmed.

Key words: Blackbird, *Turdus merula*, juvenile moult, spatial behaviour

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1. Introduction

The nominotypical subspecies of the Blackbird (*Turdus merula merula*) has expanded its breed range towards the northeast since at least 180 years (Parslow 1967, Spencer 1975). It started to breeding in Leningrad Region in the 1950es, in Karelia in the 1970es (Malchevsky & Pukinsky 1983; Khokhlova 1977, 1986, 1988). After a short pause, its expansion continued: currently Blackbirds have colonised central Karelia and started to breed in Arkhangelsk Region.

This range expansion was accompanied by considerable changes in the annual cycle, in particular by inclusion of regular seasonal migration. Tendency for year-round residency, typical of Blackbirds in their original range (Jackson 1954, Snow 1956), did not hamper this process.

In 1979, Institute of Biology of Karelian Research Centre of Russian Academy of Sciences started a long-term project on population ecology of birds in southern Karelia (Lake Ladoga coast, Mayachino field station) which is continued until now (Zimin et al. 2002, 2003). The Blackbird was one of the original target species. This made it possible to study many parameters of a peripheral population of this species at different stages of its formation. A parallel study of ecologically similar other thrush species, the Song Thrush *Turdus philomelos* and the Redwing *T. iliacus*, and large dataset on the Blackbird's biology in the core part of its range available in literature (Snow 1958, 1969, 1988; Ribaut 1964; Stephan 1985 etc.), allowed us to identify certain population-specific features related to breeding in an area with a short window of favourable conditions (Khokhlova 1988, 1994a, b, 2001; Khokhlova & Yakovleva 1991, 1995).

Already in the first years nearly all reproductive parameters of Blackbirds became very similar to the parameters of other locally breeding thrushes. At the same time, this species retained its late post-breeding and post-juvenile moult, which are probably under genetic control, and more sedentary habits in the post-breeding and post-fledging period, typical of this species in the core part of its range (Jackson 1954, Snow 1956). As a result, most Blackbirds leave their northern breeding quarters very late when the environmental situation sharply deteriorates and with unfinished moult (Khokhlova 1983, 1994a, 1995a). This cannot remain without consequences for the survival rate of the peripheral population. It may be hypothesised that this is one of the reasons of the stepwise range expansion towards the northeast: during the pauses changes are accumulated that facilitate further range expansion and establishing itself in the new areas.

Data of a long-term study in Karelia made it possible to test this hypothesis by analysing population parameters of Blackbirds at the initial and more advanced stages of adaptation to northern conditions. This study is devoted to postfledging period of Blackbirds from a peripheral population which has formed in southern Karelia. Most attention is given to post-juvenile moult and spatial behaviour at different stages of formation and replacing juvenile plumage.

2. Study area, material and methods

This paper is based on the results of visual observations of individually marked Blackbirds and captures of birds in mist-nets at several south Karelian sites in 1972-2004. Collection of biometric data followed the protocol of Gaginskaja & Rymkevich (1973).

Most data were collected at the Mayachino field station of the Institute of Biology, Karelian Research Centre of Russian Academy of Sciences which is situated on the eastern coast of Lake Ladoga near the border between Russian Karelia and Leningrad Region (60°46' N, 32°48' E; Zimin et al. 1993, 2002, 2003). At the permanent

study plot with an area of ca. 2 km² a total of 379 nestlings from 98 nests and 406 juveniles of unknown origin were ringed in 1979-2005. All nestlings were marked by a unique combination of colour rings.

I also used the data on birds ringed in Kivach Nature Reserve (central Karelia, 1981-2004), Pedaselga field station of Karelian Research Centre (Prionezhsky district, 1974-1977) and Ladoga Ornithological Station (Gumbaritsy, 1970-1981).

Apart from visual observations, I used 911 descriptions of plumage conditions at (re)captures of 490 birds of unknown origin and 60 descriptions of 40 first-year birds ringed as nestlings, and the data on plumage formation and moult of seven birds raised in captivity.

3. Results and discussion

3.1. Some features of the species' biology in Karelia

The Blackbird colonised Karelia which lies north of 60°30' N, just several decades ago. The first nest was found in Gumbaritsy on the border to Leningrad Region in 1971 (Noskov et al. 1981). In 1975, when spring was unusually early and warm, nests were found simultaneously in three southern Karelian districts: Prionezhsky (Pedaselga field station), Kondopoga (Kivach Nature Reserve) and Medvezhegorsk (Great Klimenetsky island in Lake Onego). By the mid 1980s, a sustainable population had already formed in southern Karelia, on the northeastern edge of the range of this mainly sedentary species (Khokhlova 1986, 1988). However, its breeding density remains vary low even in optimal habitats. In 1979-2005, it varied at Mayachino between 3.1-10.0 pairs·km⁻², in Kivach Nature Reserve it did not exceed 4 pairs·km⁻². For comparison, in western European parks it may be as high as 246 pairs·km⁻² (Batten 1973).

Karelian Blackbird population is nearly completely migratory, only singular birds sometimes remain in winter in southern parts of Karelia. The stay in the region varies between seven and nine months in different years. In spring, first individuals (usually old males) arrive in late March – early April, in autumn the last birds disappear in November – early December. When in Karelia, Blackbirds manage to raise 1-2 broods and to undergo the main stages of post-breeding and post-juvenile moult (Khokhlova 1988).

The period of possible egg-laying and thus of fledging is extended for 2.5 months. Depending on the progress of spring, onset of breeding may vary within three weeks (26.04.1990–16.05.1978). The latest clutches are laid in late June – early July (09.07.1980). In different years, early broods fledge between 24 May and 13 June, the late ones in late July – early August (02.08.1980, 05.08.2003). Fledging of the first broods is usually well synchronised. Most fledglings appear in the first 10-day period of June (Fig. 1). Not all pairs are double-brooded, but due to replacement clutches the proportion of late broods fledging in July and August exceeds 35%.

Breeding territory protected by a male is in Karelia usually some 10 ha. Territories are usually odd-shaped and always border to an area rich in earthworms, which are the main prey: lake shores, streams, stubble fields, reclamation dykes etc.

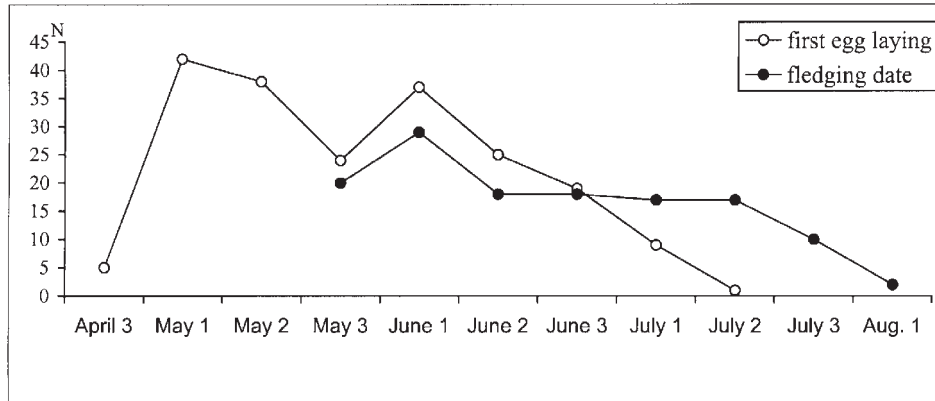


Figure 1. Time of starting clutches (1) and fledging (2) in 200 Blackbird nests in the Ladoga area in 1978-2004.

Nest site is probably selected by the criteria relevant during the nest construction period. Therefore, nests not infrequently appear in the territory's end opposite of the foraging site, so that the birds have to fly 300-400 m to get earthworms. However, even if the nest is located within the foraging area, birds very seldom forage less than 50-100 m from the nest.

If disturbed, Blackbird nestlings may fledge on the ninth day of their lives, but usually they remain in nest until the youngest ones are 10-11 days old. Most fledge when 10-13 days old, but some do not fledge until the age of 14-15 days. Brood size varies between two and six nestlings. Incubation of even small clutches rarely starts with laying the last egg, therefore hatching in one nest may occur within 3-3.5 days. Difference in nestling mass remains until fledging and may even increase under poor conditions because of retarded growth of the younger ones. Nevertheless, even large broods usually fledge within one day. Only if fledging is early and induced this process may extend for 2-3 days, even though the parents actively stimulate the remaining nestlings to fledge. The first fledglings are nearly always taken away by the male, whereas the female waits for the late ones.

Many pairs are double-brooded. Time window between fledging of the first brood and the onset of laying the second clutch rarely exceeds one week. Therefore the first brood is usually fed by the male, whereas the female switches her activity to the second nest. If the breeding attempt is the last one in this season, the partners share their care. They may care for the whole brood together or split it, as has also been reported from other parts of the breeding range (Snow 1958, 1988; Ribaut 1964, Edwards 1985).

Across the whole range, Blackbirds switch their diet seasonally. In autumn and winter, they feed on fruits: rowan, aronia, haw, viburnum, shadberry etc., start to attend garbage bins (Snow 1956, 1988). Of all these fruits, only rowan is common in Karelian forest, but it is patchily distributed and does not yield good crops annually. The main Blackbird food in autumn are fruits of low shrubs, e.g. bilberries, cowberries, bog whortleberries etc. Therefore the first snow which covers the ground for at

least for one day forces the birds to leave the forest habitats and move searching for available food, often covering considerable distances.

3.2. Formation and replacement of juvenile plumage

3.2.1. Formation of juvenile plumage

Formation of juvenile plumage starts in Blackbirds, like in other passerines, during the first week upon hatching. Most pterilia are formed in nestlings, with feathers growing since 3rd-4th day (ventral, dorsal pterilia) or 6th-7th day (middle auxiliaries). At fledging (13-17 days old) plumage is already enough developed that the birds can fly gaining altitude. However, formation of juvenile plumage is not completed until much later. Body feathers that start to grow in nest complete growth and are free from shafts when the birds are 38-43 days old. It is not until fledging that feathers start to grow on flanks, inner greater coverts and inner primary coverts, on the upper row of lower marginal coverts, and on lower arm coverts. Around this time naked areas in the upper proximal part of propatagium and in outside upper thigh are covered with feathers, additional feather rows grow on ventral, dorsal, scapular, head (ear coverts) and anal pterilia.

Of all the aforementioned feather tracts, only inside greater coverts and primary coverts grow within a definite time window. They start to grow when the birds are 17-27 days old and finish growing at the age of 32-43 days, simultaneously or just a little later than remiges and rectrices. In some individuals, isolated inner coverts may emerge later and not finish to grow until mid moult. Time and sequence of growing feathers in other feather tracts are variable, but with a general trend towards shorter period of growing the first generation of feathers towards the end of season. Juveniles hatched early in the season or in mid season show a gap between growing inner greater coverts and primary coverts and other feather tracts: at the age of 40-50 days when inner greater coverts and primary coverts are grown there is a period when no feathers are growing. Late hatched juveniles have no such gap.

Just a fraction of birds compete formation of juvenile plumage before onset of moult. Most overlap this process with "stages 1 and 2" of moult, few birds even with "stages 3 and 4" (Fig. 2). No clear relationship between the degree of overlap and timing of moult exists. The process of covering apteria with feathers is most variable. It usually starts short before moult or soon after its onset. In some cases dorsal and side apteria may remain naked until the middle of "stage 2", and ventral apteria until "stages 3 and 4" of moult. Most typically, down first grows on back and flanks and later on the belly. Side apteria may be covered by down already in the middle of moult "stage 1", dorsal apteria in the beginning of "stage 3", ventral apteria only at "stage 5". In all other areas down grows until the end of moult.

3.2.2. Sequence of plumage replacement

Sequence of plumage replacement in juvenile Blackbirds generally follows the pattern typical of turdids (Rymkevich et al. 1990, Khokhlova & Yakovleva 1991). Moult usually starts in abdominal and dorsal pterilia when the first generation of feathers is

still growing in their periphery in many individuals (Fig. 2). Start of replacement of feathers in different tracts may be divided into three stages on the basis of several main pterilia that start to moult in a clearly defined sequence, unlike other tracts where the pattern is variable. Feather growth is subdivided into two further stages. Besides, within each stage a beginning and an end may be distinguished if necessary.

“*Stage 1*”: since the onset of moult in the dorsal pterilia and ventral part of abdominal pterilia until the beginning of feather replacement of lower and upper tail coverts. During this stage, thigh and shin start to moult, in many individuals also neck and post-ventral part of abdominal pterilia, upper propatagium and inside scapular coverts. Very few birds also start to replace feathers in the pectoral part of abdominal pterilia, outside and inside wing coverts, inside propatagium covers and the upper row of inside marginal coverts.

Stage duration is 10-12 days. Its final part is indicated by half-grown feathers in abdominal and dorsal pterilia (days 6-7).

“*Stage 2*” extends since losing juvenile lower and upper tail coverts until the beginning of feather replacement in intermandibular and mandibular parts of the head pterilia. In the end of “*stage 2*”, all birds start to moult neck, post-ventral part of abdominal pterilia, upper propatagium coverts, inside scapular and wing coverts. Many individuals start to moult pectoral feathers, greater primary and secondary coverts, allula, upper wing coverts, middle inside primary and secondary coverts, inside propatagium and marginal coverts. Some birds also moult the forehead, occipital and ear parts of head pterilia, middle primary and secondary coverts, carpal feather, inside tertiary coverts. Few individuals complete the growth of lower tail coverts.

This stage lasts 9 to 18 days. Its advancement is easily determined on the basis of lower and upper tail coverts condition: the shafts open on the 4th-5th day and reach one-half of length of a full grown feather after the 7th day.

“*Stage 3*” extends from the start of feather replacement in intermandibular and mandibular feather tracts until the end of growth of greater coverts. During this stage, all the remaining pterilia start to moult. Just a few individuals do not start to moult their anal pterilia, shin and eye feathers until the beginning of the next moult stage. All birds finish growing their lower tail coverts, most also middle primary and secondary coverts, carpal feathers, allula, upper wing coverts, middle inside primary and secondary coverts, inside marginal coverts. Some individuals complete moult of pectoral feathers, lesser coverts, upper and lower propatagium coverts, inside scapular coverts.

This stage lasts for 12-20 days. Its final part is characterized by the condition of intermandibular and mandibular feathers and by the fact that fans of all lower and upper tails coverts reach more than 50% of their definitive length.

“*Stage 4*” is the period between the end of growth of greater coverts and all inside wing coverts which lasts 9 to 17 days. By the end of this stage, upper and lower tail coverts and wing coverts are replaced, except for a few cases when some upper propatagium coverts are still growing. Many individuals also completed moult in many tracts in body and head, and just ventral and interscapular parts and head still have moulting feathers until the end of next stage.

“*Stage 5*” is defined as the period with no moult of lower wing coverts, or lower and upper tail coverts. Plumage formation is nearly completed at this stage, just a

fraction of feathers are completing growth. Duration of this stage is 11-14 days. Its final part starts when the feathers of head and shin which are the last to moult reach one-half of their definitive length.

In cases when moult progress description on the basis of all key pterilia is problematic (e.g. under poor visibility conditions) it may be advisable to use of upper and lower tail coverts which start to moult at "stage 2" and are completely renewed by the beginning of "stage 5". With an average extension of feather loss period (up to one week), new feathers grow in these feather tracts during 33-38 days.

Skin peeling may start in some individuals before feather replacement. However, in most birds it does not start in earnest until moult "stages 3-4" and finishes after completing moult. In birds in new plumage skin peeling suggests a recent moult and may be considered "stage 6" of juvenile moult.

3.2.3. Extent of juvenile moult

Juvenile plumage of Blackbirds, especially of males, differs in colour from the feathers of the next generation. It makes it possible to estimate the extent of moult quite accurately.

In this species, like in most other passerines in Karelia, juvenile moult is not a complete one. It does not include rectrices, primaries and secondaries. Most birds also retain juvenile primary coverts, greater inside primary coverts, contour feathers on flanks, the lower row of inside marginal coverts and some greater coverts. Many individuals do not moult carpal coverts and lesser, some also medium secondary coverts, lower row of marginal coverts, feathers in the distal part of shin and some contour feathers, especially in tracts that grow after fledging. In cases when moult extent is most complete all body feathers are replaced, except of some greater inside primary and secondary coverts. We have recorded one case of replacing the innermost secondary feather (a tertiary). Moult extent shows a clear tendency to be reduced towards the end of the season.

The most popular proxy of moult extent is the number of retained juvenile greater coverts. First-autumn Blackbirds retain in Karelia 0-9 feathers ($n = 258$). Most birds (75%) retain 3-5 juvenile feathers, on average 3.9. Asymmetries in numbers of greater coverts retained were recorded in 7.4% birds, but in many such cases the reason could have been accidental feather loss. As mentioned earlier, late in the season moult extent is reduced and the number of retained old greater coverts increases (Tab. 1). However, certain variation occurs: a bird which replaced not only all greater coverts and carpal coverts, but also the innermost tertiary feather, still retained the 2nd and 3rd lesser coverts. Reversely, some birds that retained five or six old primary coverts moulted all allula feathers.

Moult extent of Blackbirds in Karelia is significantly smaller than in southwestern parts of their breeding range, not only as recorded in breeding birds of those areas, but also in winter visitors (Snow 1988, Richter 1972, Svensson 1975, Baillie & Swann 1980, Khokhlova 1994b). Reduction of moult extent towards the northeast across the species' range is quite regular (Fig. 3) and runs in parallel with increasing proportion of late moulting birds in northern populations. However, comparison

Table 1. Number of retained juvenile greater coverts in relation to time of juvenile moult.

Сроки	Number of retained juvenile greater coverts at "moult stage"			
	3	4	5	moult completed
1-15 August	3.50 ± 0.742 (5) 1-5.5			
16-31 August	3.56 ± 0.235 (18) 2-6	3.71 ± 0.486 (7) 2-6		
1-15 September	4.29 ± 0.224 (33) 2-7	3.82 ± 0.206 (38) 1-6	3.22 ± 0.306 (16) 1-5	
16-30 September	5.18 ± 0.349 (19) 2.5-9	4.46 ± 0.194 (42) 2-7	3.61 ± 0.197 (62) 2-9	3.36 ± 0.237 (7) 2.5-4
1-30 October	5 (1) 5	4.71 ± 0.184 (7) 4-5	4.85 ± 0.249 (13) 4-7	3.17 ± 0.391 (12) 1-5

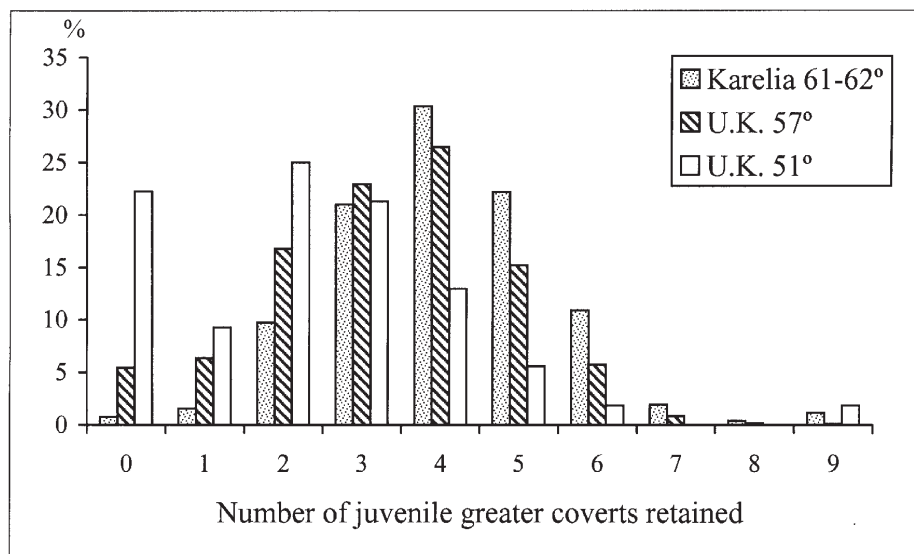


Figure 3. Number of retained juvenile greater coverts in Blackbirds in Karelia and in the U.K. (from Baillie & Swann 1980).

of other moult parameters in these populations shows variation that at least partly could have a genetic basis. Blackbirds breeding in Britain at 57°N (Baillie & Swann 1980) on average replace many more greater coverts than their Karelian conspecifics, but proportions of birds moulting carpal coverts (38% vs. 40% in Karelia) and especially lesser coverts (1% vs. 12%) were surprisingly low in this population.

3.2.4. Timing of moult

Early hatched juveniles start to moult in late July when late hatched juveniles are still in nests (Tab. 2). Birds just starting moult were recorded between 22 July (Mayachino, 1983 and 1993) and 16 September 1985 (Kivach). When late-hatched birds just start to lose juvenile feathers, some early birds have already finished moult (Mayachino, 16 September 1992). However, even juveniles from early broods often complete moult in adverse environmental conditions due to poor weather and foraging opportunities.

Table 2. Timing and progress of juvenile moult in Blackbirds captured at Mayachino in 1979-2004. 01 for flight feathers not fully grown; 02 for full grown flight feathers, growing body feathers; 03 juvenile feathers not growing; 1-5 – “stages of moult”; mc – moult completed.

Time period	Number of birds captures with plumage condition coded as (total / ringed as nestlings / unknown origin stopped over for >2 days)										N captures	% stopped over
	Stages of growth of juvenile feathers and of moult											
	01	02	03	1	2	3	4	5	mc			
beg July	1/1/-	1/1/-									2/2/-	100,00
mid July	7/4/-	1/-/-	5/-/-								13/4/-	30,77
end July	24/12/-	14/-/1	32/2/4	17/-/2	1/-/-						88/14/7	28,38
beg Aug	11/3/3	14/1/2	20/1/6	19/-/7	11/-/5	3/-/-					78/5/23	35,90
mid Aug	8/1/1	13/1/4	13/1/3	24/1/6	21/-/11	7/-/3					86/4/28	37,21
end Aug	3/-/-	10/-/4	4/1/2	11/-/4	19/2/9	12/-/4	6/-/4				65/3/27	46,15
beg Sep		3/-/1		7/-/2	9/-/3	13/2/4	16/1/2	5/-/-			53/3/12	28,30
mid Sep				4/-/1	4/-/2	19/1/6	24/1/8	31/-/3	2/-/-		84/2/20	26,19
end Sep						8/-/4	23/1/9	40/1/8	4/-/1		75/2/22	32,00
beg Oct						1/-/1	1/-/-	4/-/1	4/-/		10/-/2	25,00

3.2.5. Age of starting moult

Age of starting juvenile moult varies in Karelian Blackbirds between 45 and 70 days. Moult start at the age of 42 days was recorded in a juvenile hatched vary late and kept in an aviary, which still had shafts at the base of its primaries. Generally, late-hatched juveniles moult at younger age. This relationship is however less pronounced in Blackbirds than in thrushes better adapted to boreal conditions, e.g. in the Red-wing and Song Thrush, and is only apparent when comparing extreme cases.

3.2.6. Individual duration

Individual duration of moult is estimated to vary between 55 and 70 days, recaptures suggest the duration of 60-65 days (Fig. 4).

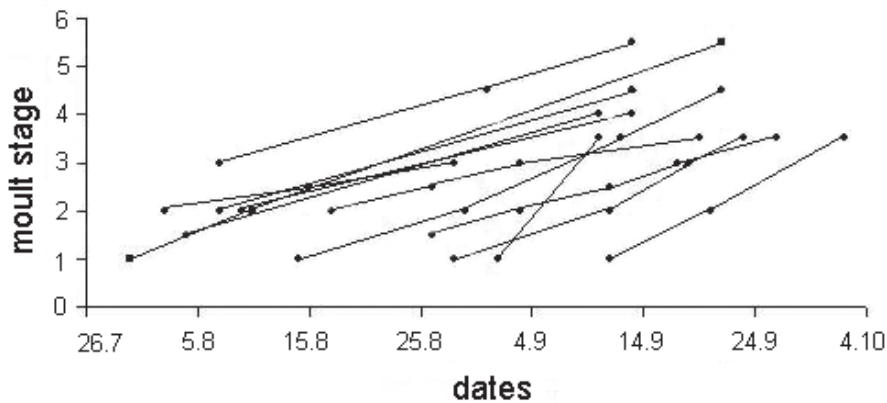


Figure 4. Juvenile moult of Blackbirds in relation to time of moult beginning.

The whole plumage is involved in moult during 35-45 days, formation of the new generation of feathers lasts for 20-25 days more. Start of moult in different feather tracts is usually more synchronised when moult is late. However, birds that replace their plumage early also may lose juvenile feathers within a relatively short period of time. Lower and upper tail coverts that start to moult later than other feather tracts may be indicators. In August, they do not reach one-half of their definitive length until greater coverts are full grown (*“stage 4”*) in 90% of birds. In two-thirds of late moulting birds tail coverts are half-grown when greater coverts are still growing (*“stage 3”*). However, synchronised start of moult in small feather tracts has a weak impact on the total moult duration which is mainly dependent on the duration of feather replacement in large dorsal and abdominal pterilia. Therefore, if moult is late, *“stages 2 and 3”* are usually short and *“stages 4 and 5”* are long. This influences the occurrence of birds even at early stages of feather replacement in captures (Fig. 5).

3.3. Spatial behaviour

As in other birds, intensity and range of movements of juvenile Blackbirds change along the postfledging period. Movements are more restricted before juvenile plumage is formed, and then during active moult.

3.3.1. Period before brood disintegration

Juveniles fledged when 8-9 days old spend first 2-3 days upon fledging on the ground and chirp loudly which may attract the attention of predators. Birds that fledge when 12-14 old are already able to fly to the nearest tree and to settle on its branches. Blackbird fledglings are more energetic than other thrushes and rarely remain stationary for a long time, but follow the old birds. Sometimes they seem to be chasing the parents that try to give a portion of food to their young and to break away from them to collect a new portion. As long as flight capabilities of fledglings

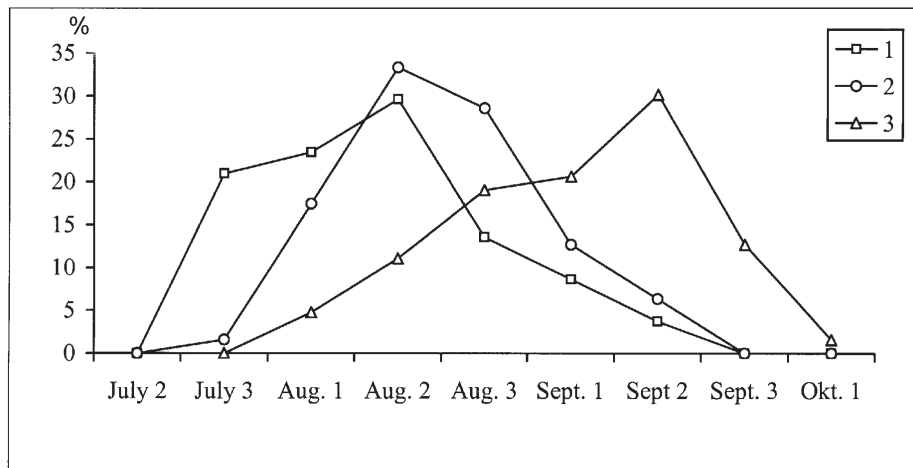


Figure 5. Dynamics of juvenile Blackbird captures at "stages 1, 2, and 3" of plumage replacement (Karelia, 1972-2004).

improve, home range area visited by the brood get larger and expands to the territories of neighbours. However neighbours do not show aggression towards birds accompanying their broods to any degree comparable to other situations, even in regions with much higher breeding density (Ribaut 1964).

After fledging, adults usually continue to use their usual foraging sites and visit them together with fledglings. Early broods appearance in wet fields, on Lake Ladoga shores and on the banks of streams in Mayachino is quite synchronized: it usually occurs in mid and late June. Habitat use is different in mid July when the abundance of earthworms in upper layers of soil declines due to dry weather, but bilberries and other berries start to ripen. During this time broods of all ages spend time at bilberry bushes and move to new patches as berries ripen, with less time spend in the aforementioned habitats. In the very end of summer the birds mainly forage on cowberries.

Depending on local conditions during fledging, the brood may remain near the nest (this however happens infrequently), move 200-400 m, or move further and thus disappear from the study plot (Tab. 3). Some of the vanished fledglings reappear after brood disintegration, but many probably die. This is suggested by leg rings from Blackbird fledglings found in Sparrowhawk (*Accipiter nisus*) nests (four cases), frequently found remains of juveniles, observed cases of attacks by Goshawks (*Accipiter gentilis*) and by Ural Owls (*Strix uralensis*) on freshly fledged Blackbirds, and captures of adults whose behaviour suggests that they had lost their offspring soon after fledging.

3.3.2. Period of brood disintegration

Parents care of their offspring quite intensively during just 7-10 days, until the young are 21-25 days old. Even though both parents or just the male may remain with the young for 1-2 weeks more, until they are 41 days old, they are mainly connected by the joint foraging area.

Table 3. Distance from nest at which Blackbird fledglings are found before brood disintegration in Mayachino.

Days elapsed between fledging and last encounter	Number of broods	Maximum distance from nest where the brood or some fledglings were found, m				
		<100	100-200	200-300	300-400	>400
< 1	11	11	–	–	–	–
1-3	5	2	3	–	–	–
4-7	5	2	1	–	2	–
8-14	3	–	–	3	–	–
15-25	24	–	7	3	8	6
Total	48	15	11	6	10	6

Juvenile Blackbirds gain independence of their parents gradually, usually during the fourth week of their lives. Fledglings kept in captivity with their parents ($n = 3$) and without them ($n = 4$), try to peck already when 11-13 days old and were often successful since the age of 15-16 days. Were the food superabundant, they could have foraged themselves since the age of three weeks. Since juveniles start to feed themselves, they chase their parents without the former enthusiasm. Off-periods of adults become more frequent and longer. At the age of 20 days juveniles may be often encountered without the supervision of adults. The brood breaks up and gathers together several times. Some juveniles get lost, and at the age of 25-40 days they may follow intact broods of Redwings or Song Thrushes. Later they join the groups of independent juveniles and travel across patches of berry bushes in temporary groups.

Before flight feathers finish to grow (at the age of 38-43 days), fledglings are seldom found far from their parents' home range. In captures in Mayachino the proportion of birds ringed as nestlings is the highest just in this cohort (>40%). Most of them originate from nests located <500 m from the recapture site (Tab. 4), but some birds aged 32-42 days had covered at least 600-1200 m. Quite many birds from this group (42.9%) were subsequently recaptured at later stages of plumage formation (Tab. 5).

When remiges are free from the shafts, the disposition of juveniles to move peaks. Most birds are captured 500-1000 m from natal nests, but they usually do not remain here for long and are not recaptured after the age of 43-46 days. Most birds of unknown origin that have immigrated just after brood disintegration disappear, too. Many birds with fully grown flight feathers appear, 80% also leave before starting juvenile moult (Tab. 5).

Movements of juveniles during this period are habitat-related. If large areas with relatively homogenous distribution of bilberries are available, the birds may quickly cover large distances. In Gumbaritsy a 40-day-old fledgling was captured 2 km from its natal place. Two Blackbird siblings were found 1.5 km from their natal nest when 37-day-old and 200 m from the nest when 62-day-old. At Pedaselga field station which

Table 4. Distance from natal nests at which juvenile Blackbirds were captured in mist-nets in Mayachino, 1979-2004.

Distance between the natal nest and capture site, m	Nestlings ringed	Of the recaptured (first/repeat recaptures)											Total		
		16-25	26-35	36-45	46-55	56-65	66-75	76-85	86-95	96-105	106-115				
<250	57	1/-	3/-	7/1										1/-	12/1
251-500	88	1/1	3/-	2/3	-/3	-/2	-/1	-/1	1/1					1/-	8/12
501-1000	110	-		2/1	1/-	1/-				1/-				-	5/1
1001-2000	46		1/1	2/1	-/1	-	-	-	-	-	-	-	-	-	3/3
>2000	38									1/-				1/-	2/1
Total	339	2/1	7/1	13/6	1/4	1/2	1/1	1/1	1/2	1/1	1/1	1/2	1/-	2/-	30/18

Table 5. Plumage condition of juvenile Blackbirds at first capture and at recapture (Mayachino, 1979-2005). Plumage conditions code as in Table 2.

Number ringed		Of them recaptured (last recapture)												
Plumage condition code	N	Plumage condition code										Total	stopped over, %	
		01	02	03	1	2	3	4	5	mc	N/A			
0.1	36	5	5	2	2	1							15	41.7
0.2	49		6	2	3	3	4	1					19	38.8
0.3	55			9	6	4	2	3					24	43.6
1	63				5	6	6	5	1	–	3		26	41.3
2	36					2	3	2	–	–	2		9	25.0
3	38						3	4	3	–	–		10	26.3
4	48							6	3	–	2		11	22.9
5	71								8	–	–		8	11.3
6	10									1	–		1	10.0
N/A	3											1	1	
Total	409	5	11	13	16	16	18	21	15	1	8		124	30.3
Ringed as nestlings	339	21	2	3	1	2	2	3	1	–			35	10.3

is surrounded by pine and deciduous stands at early stages of succession, the pattern of Blackbirds' movements is different. Isolated Blackbird pairs breed here in small patches of old stands along the creeks. In autumn, they mainly feed on cowberries growing in young stands, which do not ripen until August. Therefore, broods remain near their nests in creek valleys for a long time. In 1977, fledglings aged 47-58 days were still captured in the home ranges of their parents and did not disappear until second half of July. Since mid August, immigrant birds were captured. Most variable are young Blackbirds' movements near Mayachino where habitat variability is high.

Between late June and early August, all species of thrushes in the Ladoga area perform summer nocturnal movements (Bolshakov & Rezvyi 1975, 1981; Rezvyi & Bolshakov 1987). However, they are least pronounced in the Blackbird, as reported by these authors: only some juveniles before starting moult participate. During the given time window, only birds fledged before late June could migrate. It should therefore be expected that among late-fledged Blackbirds and birds moulting late, the proportion of individuals that remain in the natal area after brood disintegra-

tion should be higher than among early-hatched juveniles. No significant pattern was found, even though in the very late birds that started moult in September, such a tendency was apparent. It seems that in Karelia most juvenile Blackbirds do not move large distances before starting moult, like their conspecifics in the core part of the range.

3.3.3. Juvenile moult period

Since the beginning of juvenile moult, mobility of juveniles and range of their movements decrease, the number of new birds in captures gets smaller. One-third of birds captured in mist-nets were recaptured after 1-59 days, birds marked as nestlings were captured until the age of 17-117 days. Among birds captured during most heavy moult ("*stage 2*"), previously ringed individuals comprised nearly 50% (Tab. 2), and their subsequent stay was the longest one, >3 weeks (Tab. 6). This parameter was gradually decreasing with the progress of moult.

Composition of birds in the study plot was changing during all the season. However, the proportion of transients was not very variable (Tab. 2).

Before the onset of moult, young Blackbirds settle in defined home ranges that may be situated within the territories of adult pairs. Adults are known to pay no attention to the presence of juveniles within their territories, so up to six juveniles territorial towards each other may settle within one territory of an adult (Jackson 1954; Snow 1956, 1988). Juveniles that are lucky enough to settle in an area rich in food may remain there until migratory departure, whereas birds that found themselves in a poor area have to change a territory up to several times, irrespectively of their moult status.

Just a few Blackbirds manage to get into optimal conditions in the Ladoga area. This is especially problematic for late-hatched juveniles, as best patches are already occupied when they settle. In Mayachino the same pattern repeated in different years in the same 200 × 200 m study plot. One bird remained within a 100 × 100 m square adjacent to the garbage bin during the whole period of moult. Several other birds stayed in the periphery for variable periods of time, depending on abundance of bilberries and cowberries and left when food was depleted, irrespectively of their moult status (Tab 7). Other individuals were transients in the area.

This rather strict, even temporary, territorial behaviour might explain the low prevalence in captures of birds ringed as nestlings nearby. They comprised only 8.1% of birds trapped during the postfledging period, and just 5.3% of those that remained for some time. Only four such birds stopped for a week or more in the study plot. It seems that in most cases at the moment of brood disintegration all suitable patches within the parents' territory are occupied by earlier-hatched juveniles. It forced the birds to leave their natal site. Later they could reappear when changing their temporary suboptimal territories (Tab. 5).

In the core part of the breeding range juvenile Blackbirds remain near their natal territories during several months. They seldom cover more than 2.5 km, and the range of their foraging trips in summer usually does not exceed 3 km (Werth 1947, Snow 1988, Greenwood & Harvey 1975). The same trend is observed in the northern

Table 6. Period of stay of juvenile Blackbirds that were first captured in a given plumage condition (Karelia, 1972-2004). Plumage condition code as in Table 2.

Plumage condition at first capture	Number of birds that stayed for the given number of days														Length of stay, days																	
	1	2	3	4	5	6	10	11	20	21	30	31	40	41	50	51	60	61	70	71	80	81	90	91	100	101	110	Total	Mean	Min	Max	
0.1	2	5	5	4	3	1	1	1	2																		23	16.5	1	57		
0.2	7	5	7	2	5	1	3																				26	15.5	1	47		
0.3	2	3	7	5	4	6	1	2																			30	20.5	1	59		
1	2	5	8	9	7	6	1	1																			39	18.4	1	54		
2	-	2	2	4	3	5	-	-																			16	22.1	2	40		
3	-	2	6	2	2	2	-	-																			13	15.2	2	38		
4	1	7	3	3																							14	6.6	1	17		
5	1	5	1	1																							8	4.8	1	14		
mc	-	1																									1	2			2	
Total	11	35	41	31	24	21	6	5																			172					
Ringed as nestlings	1	2	3	5	13	9	1	2	-	2	1	3	1	43																		

Table 7. Period of stay of juvenile Blackbirds that were last captured in a given plumage condition (Karelia, 1972-2004). Plumage condition code as in Table 2.

Plumage condition at last capture	Number of birds that stayed for the given number of days														Length of stay, days																	
	1	2	3	4	5	6	10	11	20	21	30	31	40	41	50	51	60	61	70	71	80	81	90	91	100	101	110	Total	Mean	Min	Max	
0.1	2	3	6	3	2	1																					6	4.0	1	14		
0.2	3	6	12	3	3	5	2	1																			16	8.4	1	40		
0.3	2	3	6	3	3	5	2	1																			20	7.5	1	18		
1	2	2	4	4	5	5	2	-																			22	15.2	1	43		
2	-	2	4	4	5	5	2	-								1											19	19.2	2	51		
3	-	2	4	4	5	6	5	4	1																		27	25.6	2	57		
4	1	6	4	4	4	5	9	1	2																		32	22.7	1	59		
5	1	5	2	3	2	1	-	1																			15	14.6	1	54		
mc	-	1																									1	2				
N/A	-	5	4	3	2	1																					14	11.3	4	40		
Total	11	36	39	40	24	21	6	5																			172					

periphery of the range. In Mayachino most juveniles in moult were recorded within 1.5 km from the natal site. Just two siblings were captured on 13, 19 and 28 September 1980 2.5 km from their natal nest aged 85, 91, and 100 days, respectively, at moult “*stages 3 and 4*” (Tab. 4). In Gumbaritsy just one juvenile Blackbird was captured at such distance from its natal nest. The bird was completing moult (“*stage 5*”) and aged 117 days. Another evidence for short range of postfledging movements in this species is the complete lack of recaptures between Mayachino and Gumbaritsy in 15 years, even though the sites are just 13 km apart.

Thus, Blackbirds from northern populations retain all basic features of spatial behaviour typical of the core part of the species’ range where this species is mainly sedentary, even though these northern birds are migrants.

3.3.4. Migratory departure

Time of migratory departure is dependent on the weather in autumn. In southern Karelia the first night frosts are recorded between mid August – mid September. Mean daily temperatures usually drop below +5 °C in the latter half of September, and they may drop below freezing point as early as late October (Anon. 1959). Low temperatures *per se* do not bother Blackbirds much, as they regularly overwinter in the parks of St. Petersburg and its vicinity (Malchevsky & Pukinsky 1983) where winter temperatures may be as low as in Karelia. A much more important factor is food shortage.

Weather in Karelia strongly varies between years. First snowfalls may occur in September, but may not happen until only November. Snow cover in some years (e.g. 2002) may form in mid October, but more often it is not formed until late November – December. Therefore, berries may disappear under snow when Blackbirds are in the midst of their moult. In western Europe juvenile Blackbirds in such situations leave their foraging areas only temporary and gather in orchards and parks. As such habitats are widespread, the birds do not need to cover large distances (Snow 1956, 1988). On the northeastern edge of the range Blackbirds have to leave their preferred habitats and often to depart for migration before completing moult.

Captures in funnel traps in 1970-1982 suggest that in the Ladoga area the peak on autumn passage and the last captures of local breeders occur in late September – first half of October (Khokhlova 1988). In Leningrad Region Blackbird movements finish in early November (Malchevsky & Pukinsky 1983). During this period, most Blackbirds are still in moult. Nearly all juveniles that have not completed moult, both transients and residents, have small subcutaneous fuel stores. Only among the few birds that have completed moult some individuals had medium fuel stores.

Judging on plumage condition and lack of fuel stores, Karelian Blackbirds are not yet prepared for migration when they depart, and do so only because they are forced to by extreme environmental conditions. The situation is especially difficult for late-hatched juveniles that moult late and are energetically stressed by overlap of growing the first set of feathers, moult, and autumn migration.

3.4. Long-term changes in the timing of juveniles moult

Plumage condition of recaptured birds suggests a large variation in age of starting moult by birds that fledged at the same time, and in moult rate. As most Blackbirds seem to replace plumage in the natal area, individuals that complete moult early should be advantaged in Karelia. One can expect that the timing of moult in this northern population should be shifted towards earlier season with time. This tendency was indeed recorded when moult progress in birds captured in September was compared between periods 1979-1990 and 1991-2005.

The earliest captures of migrating juvenile Blackbirds that had completed moult before 1990 occurred on 26 September 1973 and 28 September 1980 (captures in funnel traps in Gumbaritsy). In Mayachino in habitats where Blackbirds moult, birds with completed moult had not been captured until 4 October in 1981 and 1983. In later years, they were captured earlier and earlier: 29 September 1988, 17 September 1990, 16 September 1992. The proportion of birds in moult "stage 5" and those having completed moult in September was correspondingly growing (Fig. 6), the difference being significant (Fisher test, $p < 0.01$). In mid September this proportion was 33.0% of all birds captured in 1979-1990 ($n = 45$) and 42.1% in 1991-2005 ($n = 46$). The respective figures for late September were 50.0% ($n = 34$) and 66.7% ($n = 42$).

Analyses of spring temperatures and timing of breeding of birds in Mayachino (Artemyev 2002, Nazarova & Filatov 2004, Both et al. 2004) showed that variation in the time of breeding is not explained by weather factors. Of the early period (1979-1990) early, warm and stable springs were generally typical, which caused early onset of breeding in many birds, thrushes including. The earliest dates of onset of egg laying by Blackbirds recorded until 1990 ($n = 102$) were 26 April 1990 and 27 April 1989. The earliest dates after 1990 were 29-30 April 2001 ($n = 84$). Mass occurrence of fledglings was also later on average by one week. It should however be mentioned that an analysis of timing of breeding in Blackbirds, Redwings and Song Thrushes showed a small shift in Blackbirds towards phenologically earlier season. In the first years of study, all three species started clutches practically at the same time. Since the late 1980s Blackbirds start clutches consequently earlier than the two other species.

Our observations on a peripheral Blackbird population in Karelia showed a tendency of a gradual shift of juvenile moult towards earlier season along with the species' adaptation to a narrow window of favourable conditions on the northern edge of its range.

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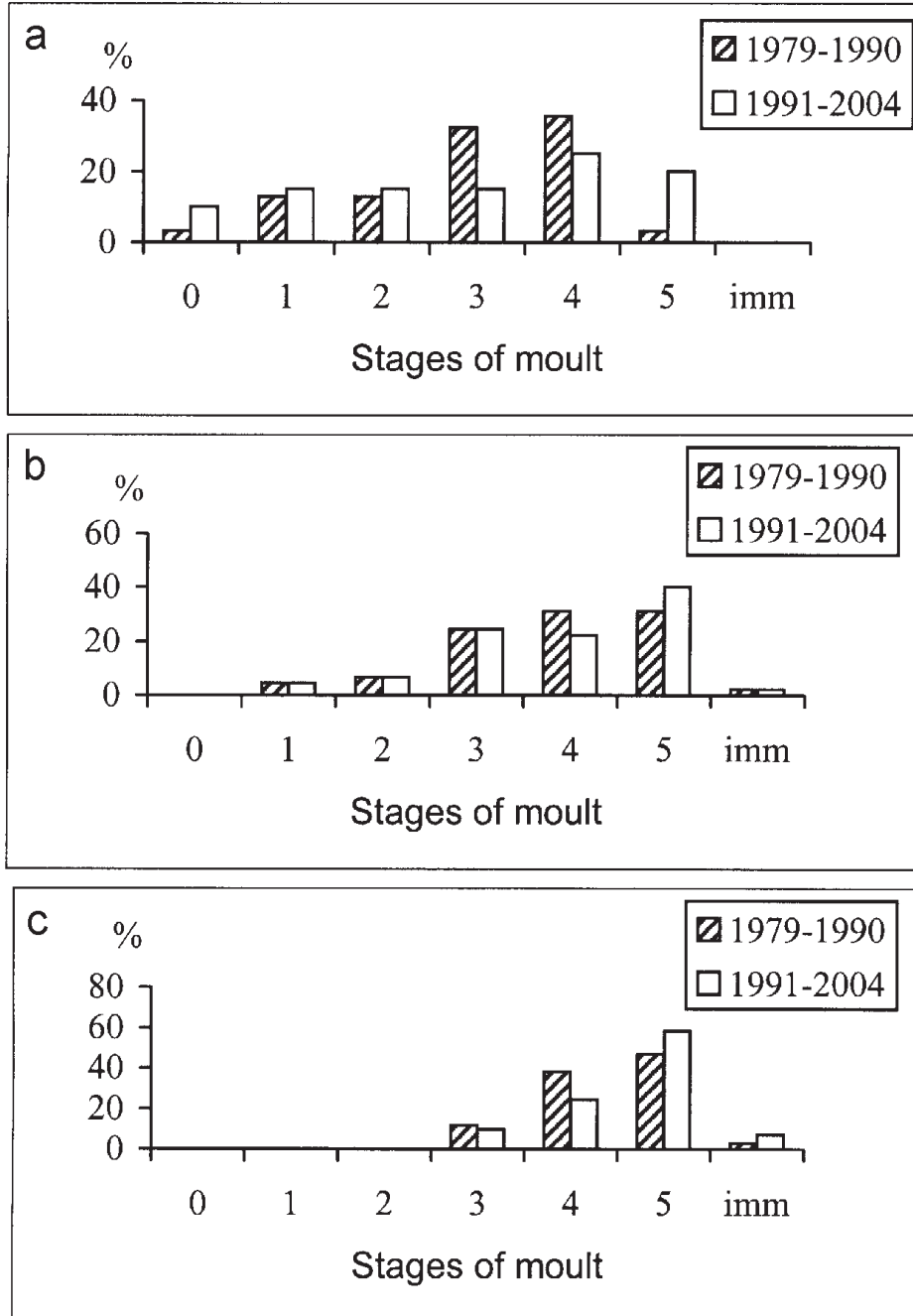


Figure 6. Frequency distribution of Blackbirds in different plumage condition in Mayachino in early (a), mid (b) and late (c) September in 1979-1990 and 1991-2004.

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