

Foraging strategy of the Sedge Warbler (*Acrocephalus schoenobaenus*) on migration

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Abstract: CHERNETSOV, N., & A. MANUKYAN (2000): Foraging strategy of the Sedge Warbler (*Acrocephalus schoenobaenus*) on migration. Vogelwarte 40:189–197.

We analysed diet and foraging strategy of migrating Sedge Warblers during spring migration, post-fledging movements, and autumn migration on the Courish Spit (SE Baltic coast). In spring beetles, dipterans, including chironomids, true bugs, and spiders were the most common prey. In late summer and autumn these were plum aphids, chironomids, Hymenoptera, beetles, and spiders. Ecological groups most frequently exploited by Sedge Warblers varied between the seasons. Nevertheless, in both seasons birds tried to use the most common prey. Its taxonomic position is of limited if any importance. The seasonal pattern of arthropod communities in species-specific habitats is crucial for the foraging of Sedge Warblers.

Key words: Sedge Warbler, diet, foraging strategy, ecological complexes of insects.

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1. Introduction

Avian stopover ecology is one of key features of bird migration. The principle aim of migratory stopovers is fuel accumulation, foraging playing a very important role in stopover site selection and shaping stopover behaviour. During migration birds, especially first-year individuals, encounter novel sites which may be poor in preferred food. Migrants not infrequently have to make stopovers at sites that differ from their favoured habitats, and to utilise food items different from those they prefer during their breeding season. In spite of many studies of stopover ecology (for reviews see: LINDSTRÖM 1990, 1995), few papers analyse diets in connection with migration strategy (BIBBY & GREEN 1981, CHERNETSOV 1998a, TITOV 1998). In spite of very good reviews available (BAIRLEIN & GWINNER 1994, BAIRLEIN & SIMONS 1995), detailed studies of species-specific foraging ecology are still needed to understand the complex interactions between foraging and migratory strategies.

Aim of the present study was to investigate the diet and foraging ecology of the Sedge Warbler (*Acrocephalus schoenobaenus*) during migration. This species is reported to utilise plant material in winter quarters (FRY et al. 1970), but within the breeding range fruits are taken very rarely and play a negligible role (BODDY 1991, EGGERS 1996, our data). Nestling diet is well studied (KAZLAUSKAS et al. 1986), data on the diet during autumn migration are available from England, France, and Portugal (BIBBY et al. 1976, BIBBY & GREEN 1981). Sedge Warblers are believed to utilise slow-moving or inactive prey (see also: GREEN & DAVIES 1972), during autumn pre-migratory and migratory period mainly plum aphids (*Hyalopterus pruni*). Aphid abundance is reported to increase and to decline earlier in southerly regions (France, Iberia) compared to northerly regions (England) (BIBBY & GREEN 1981). British Sedge Warblers are believed to accumulate much fat in southern England and northern France when aphids are still available there, and to make a single very long migratory flight to Sahel across the Mediterranean and the Sahara avoiding southern France and Iberia where aphids have already declined (BIBBY & GREEN 1981). Aphids were also reported in Sedge Warbler diet from southern Finland (KOSKIMIES & SAUROLA 1985), Estonia (LEIVITS & VILBASTE 1987, MÄLL 1995), and Kaliningrad Region (CHERNETSOV 1998a). It should be however noted that KOSKIMIES (1991) suggested that the Sedge Warbler is a generalist, not an aphid specialist.

We suggest that insect life histories shape the diet and foraging strategy of this species. Our approach is to combine the studies of avian life history traits with understanding of life history of their prey.

2. Material and Methods

We studied the diet of the Sedge Warbler in spring (between May 1 and June 10), during post-fledging movements and during autumn migration (between July 15 and September 22) in 1997–1998. Diet of Sedge Warblers was studied by flushing stomach contents of mist-netted birds. Some birds were trapped at Rybachy on the Courish Spit, SE Baltic coast, in the trapping programme of the Biological Station Rybachy and Vogelwarte Radolfzell. Ringing routine followed the guidelines of ESF programme (BAIRLEIN et al. 1995). The bulk of Sedge Warblers was however mist-netted at several sites on the Courish Spit by ‘active trapping’. During active trapping, mist-nets are placed in the sample site, then several people walk towards the nets, flushing the birds into the nets (see also: CHERNETSOV 1998b). Birds trapped by this method are handled immediately after capture. When captured all birds were measured (wing-length to the nearest 0.5 mm), weighted by electronic balance, fat score (after KAISER 1993) and moult score were recorded. Stomach flushing was done with a syringe with plastic tube by 1–2 ml of pure water without any emetics (following BRENSING 1977). Samples were conserved in 70% alcohol. A total of 217 samples were taken, 165 from birds captured by active trapping and 52 from birds trapped within the standardised programme (for description of the programme see BAIRLEIN et al. 1995). Sites for active trapping were chosen in reedbeds with willow (*Salix* spp.) and forbs admixed. These sites were distributed along the Courish Spit.

In reedbed, where trapping was conducted, sticky traps placed at different height from the bottom were used for sampling insects throughout the spring collecting period (May 1 – June 10, 1997). We used standard sticky traps that are recommended in forest entomology for studying temporal dynamics of forest pests (MASLOV et al. 1988). Two traps were installed at different locations, each carrying five sticky plates (approx. 10–30 cm) in a vertical row. The traps were replaced every 5 days. Invertebrates were collected and stored following taxa-specific methods (KASPARYAN 1981, KRYZHANOVSKY 1965, SHAPOSHNIKOV 1964; STACKELBERG & NARCHUK 1969, 1970; TOBIAS 1978, 1986, TRJAPITZIN 1978). The same literature, along with special methods (RALPH et al. 1985; MOREBY 1988), was used to identify fragments of invertebrates in samples.

Invertebrate remains were mostly poorly preserved in the stomachs. In most cases it was not possible to determine the exact number of prey items in a sample. In this study we discuss mainly frequency of occurrence (percentage of samples containing remains of certain taxa), which permits only broad comparisons of diets (ROSENBERG & COOPER 1990). Nonetheless, it is possible to characterise the most important features of Sedge Warbler’s diet by this method. We also counted the number of samples in which the given taxon was ‘the main prey item’. ‘Main prey items’ are taxa that comprised over 75% of all prey fragments found in the sample.

When studying taxonomic composition of Sedge Warblers’ food samples we found that various taxa are taken by birds not randomly. Members of certain ecological complexes, e.g. aphids, their parasites, parasites of their parasites, aphids’ predators, parasites of their predators, etc., are very often recorded in a single food sample. The number of such ecological complexes is considerably reduced compared with the overall number of taxa found in birds’ diet. We suggest that this type of analysis allows better understanding of avian diets, and of principles birds follow when collecting food. In detail the ecological complexes of insects taken by Sedge Warblers are described under ‘Results’.

We are most grateful to Dr. C. BOLSHAKOV who inspired us to carry out this research. His constructive criticism was very stimulating throughout the work. Prof. Dr. F. BAIRLEIN made very useful comments on earlier drafts.

3. Results

In spring (between May 1 and June 10) 144 flushing samples were collected (Table 1). These samples refer to both birds on passage and individuals breeding on the Courish Spit. Most frequently occurred dipterans (in 79% of samples), beetles (67%), chironomids (62%), true bugs (40%), and spiders (31%). In early and mid May, Sedge Warblers utilised mostly beetles, butterflies, ‘non-chironomid’ dipterans, and spiders (Table 2). When chironomids started to occur in numbers, these insects became important prey, occurrence of butterflies declined, and beetles and spiders were taken as frequently as before. Over the whole spring, chironomids occurred as main prey item in

Table 1. Occurrence of invertebrate taxa (in % of samples) in Sedge Warbler's diet.
 Tab. 1. Vorkommen der Invertebraten-Taxa (in % der Proben) in der Nahrung der Schilfrohrsänger.

	Spring	summer & autumn		spring	summer & autumn
Carabidae	7	3	Tenthredinidae	1,4	0
Curculionidae	27	18	Ichneumonoidea indet.	6	4
Coccinellidae	0,7	7	Ichneumonidae indet.	10	34
Staphylinidae	8	4	Diplazontinae	0	4
Coleoptera indet.	60	37	Aphidiidae	5	23
Coleoptera	67	44	Braconidae	3	0
Cecidomyiidae	0	1,4	Chalcidoidea	0,7	11
Ceratopogonidae	0,7	1,4	Pteromalidae	0,7	10
Chamaemyiidae larvae	0	1,4	Proctotrupeoidea	1,4	1,4
Chironomidae	62	66	“Microhymenoptera”*	3	16
Dolichopodidae	6	22	Formicidae	2	11
Empididae <i>s.l.</i>	0	1,4	Hymenoptera indet.	4	8
Mycetophilidae <i>s.l.</i>	3	3	Hymenoptera	24	67
Psychodidae	1,4	5	Lepidoptera imago	24	12
Sciaridae	0	1,4	Lepidoptera larvae	1,4	1,4
Syrphidae	0	16	Psocoptera	0	1,4
Syrphidae larvae	0	4	Trichoptera	4	5
Tipulidae	0,7	0	Dermaptera	1,4	0
Diptera indet.	17	33	Insecta ind.	6	4
Diptera	79	93	Insecta larvae	2	4
Heteroptera	40	30	Aranei	31	34
Homoptera	12,5	92	Pseudoscorpiones	1,4	8
Cicadinea	1,4	11	Mollusca	0	1,4
<i>H. pruni</i>	9	90	Number of samples	144	73

* Under the entry „Microhymenoptera“ we mean representatives of Chalcidoidea, Proctotrupeoidea, incl. Scelionidae, not further identified.

Als „Microhymenoptera“ werden Vertreter der Chalcidoidea, Proctotrupeoidea, inkl. Scelionidae, gewertet. Weitere Bestimmung war nicht möglich.

37% of samples. The total number of all insects collected by sticky traps increased more than 4-fold from early May to late May, and in early June increased nearly 18-fold compared with early May (Table 3).

In order to distinguish between passage and local birds, we compared diets of fat birds (fat score 3 or more after KAISER 1993) with diets of lean ones (fat score 0–2) (Table 4). Fat Sedge Warblers probably were on migration, whereas lean ones were not necessarily local breeders. Coleoptera, Heteroptera and Hymenoptera were significantly more frequently taken by fat birds – presumably by migrating individuals (Table 2). Dipterans, including chironomids, were equally frequently utilised by both groups.

We compared diet composition of the Sedge Warbler with the pattern of occurrence of invertebrates in reedbeds. We suggest that in spring Sedge Warblers mainly utilise ecological complexes of invertebrates with similar phenology. At least three invertebrate complexes are important for the Sedge Warbler in spring.

Table 2. Pattern of occurrence (in %) of main taxa in Sedge Warbler's diet in spring.

Tab. 2. Verteilungsmuster der wichtigsten Taxa (in %) in der Frühlingsernährung der Schilfrohrsänger.

	May			June
	I	II	III	I
Coleoptera	64	69	60	75
Diptera	57	72	94	79
Chironomidae	14	55	89	60
Heteroptera	7	49	34	46
H. pruni	0	16	6	6
Hymenoptera	7	21	14	37
Lepidoptera	43	60	3	12
Aranei	31	28	23	37
Number of samples	14	43	35	48

Table 3. Pattern of occurrence of main taxa in sticky traps.

Tab. 3. Verteilungsmuster der wichtigsten Taxa (in %) in Klebfallen.

	May			June
	I	II	III	I
Coleoptera	7	2	2	5
Diptera other than Chironomidae	28	24	5	41
Chironomidae	42	70	49	46
Hymenoptera	17	2	3	7
Others	6	2	1	2
Total	104	261	454	1807

Note. Coleoptera includes Cantharidae, Carabidae, Chrysomelidae, Curculionidae, Ipidae, Ptilidae, Staphylinidae. Diptera includes Anthomyiidae, Asilidae, Cecidomyiidae, Ceratopogonidae, Chironomidae, Chloropidae, Conopidae, Culicidae, Dolichopodidae, Drosophilidae, Empididae *s.l.*, Limoniidae, Mycetophilidae *s.l.*, Phoridae, Psychodidae, Scatopsidae, Sciaridae, Syrphidae, Tachinidae, and Tipulidae. Hymenoptera includes Aphidiidae, Braconidae, Ichneumonidae, Chalcidoidea incl. Encyrtidae, Cynipidae *s.l.*, and Tenthredinoidea. Other groups are Thysanoptera, Aphidinea, Psocoptera, Trichoptera, Lepidoptera, and Aranei.

3. Spring outside visitors (SOV). These are taxa connected with vegetation other than reed that occur in reedbeds due to their high mobility. They are also sometimes taken by birds when they visit patches of non-reed habitats. These are mainly Lepidoptera (larvae and imagines), Tenthredinoidea (larvae and imagines), some Hymenoptera and Aranei.

1. Insects wintering in reed stems (IWR). In early and mid May Sedge Warblers take insects that are leaving their hibernation hides and accumulate in warm places, usually on their host plants. This complex includes Coleoptera (mainly Carabidae, Staphylinidae, and Curculionidae); more active Hymenoptera and Diptera which do not form aggregations are of secondary importance. In early spring in reed beetle aggregations were found. Later beetles are no longer aggregated, being probably more uniformly distributed across the habitat. This complex is important during early and mid May (Fig. 1), i.e. when bird density is still low. When more abundant ecological complexes develop, the importance of IWR declines.

2. Insects developing in aquatic and/or moist habitats (DAM). This is the most important complex in the Sedge Warbler's spring diet. It includes various families of Diptera, Chironomidae being the most important one. In spring a large spectrum of Diptera was recorded by sticky traps: Cecidomyiidae, Ceratopogonidae, Chironomidae, Chloropidae, Dolichopodidae, Drosophilidae, Empididae *s.l.*, Limoniidae, Mycetophilidae *s.l.*, Psychodidae, Sciaridae, and Tipulidae. Representatives of four families were found in food samples (Table 1). The most abundant group between mid May and early June were Chironomidae, forming the basis of spring diet (Tables 3, 4).

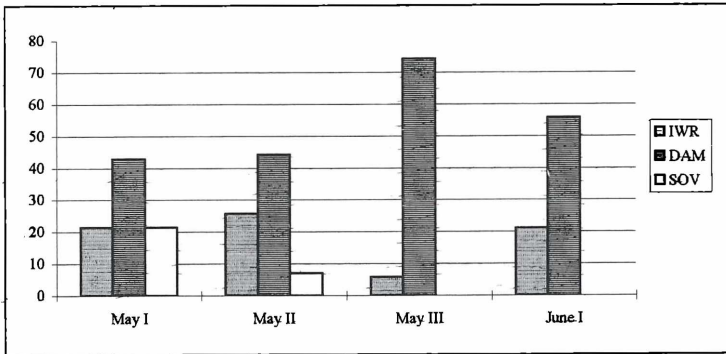


Figure 1. Occurrence of ecological complexes in the diet in spring. Percentage of samples in which the given complex comprised main prey. IWR – insects wintering in reed; DAM – insects developing in aquatic/moist habitats; SOV – spring outside visitors. See text for further explanations.

Abb. 1. Vorkommen der ökologischen Gruppen in der Frühlingsernährung. Prozentsatz der Proben, in denen die gegebene Gruppe die Hauptbeute ausmachte. IWR – im Schilf überwinternde Insekten; DAM – Insekten der Feuchthabitate; SOV – frühjährliche Fremdbesucher. Siehe Text.

Table 4. Occurrence of most important taxa (in %) in spring in lean and fat Sedge Warblers. Only significant ($p < 0,05$) differences are shown.

Tab. 4. Vorkommen der wichtigsten Taxa (in %) in der Ernährung schlanker und fetter Schilfrohrsänger im Frühling (nur signifikante Unterschiede, $p < 0,05$).

	lean	fat	t-test; p		lean	fat	t-test; p
Carabidae	3	8		Tenthredinidae	0	2	
Curculionidae	14	31	0,048	Ichneumonoidea	8	23	0,05
Coccinellidae	0	1		Microhymenoptera	3	6	
Staphylinidae	0	11		Formicidae	3	2	
Coleoptera indet.	42	67		Hymenoptera	0	5	
				indet.			
Coleoptera	42	75	0,0004	Hymenoptera	11	29	0,031
Chironomidae	61	62		Lepidoptera imago	28	22	
Diptera - non	11	10		Lepidoptera larvae	0	2	
Chironomidae							
Diptera indet.	39	22		Trichoptera	0	6	
Diptera	89	76		Dermaptera	0	2	
Heteroptera	25	44	0,045	Insecta ind.	3	6	
Homoptera	11	13		Insecta larvae	3	2	
Cicadinea	0	2		Aranei	28	31	
H. pruni	11	8		Pseudoscorpiones	0	2	
				Number of	36	108	
				samples			

Table 5. The pattern of occurrence of main taxa (in %) in Sedge Warbler's diet in late summer and autumn.

Tab. 5. Verteilungsmuster der wichtigsten Taxa (in %) in der Spätsommer- und Herbsternährung der Schilfrohrsänger.

	July	August	August	September
		1 st half	2 nd half	
Coleoptera	79	22	19	67
Diptera	100	100	94	83
Chironomidae	50	89	74	56
Heteroptera	36	22	16	56
<i>H. pruni</i>	100	89	94	78
Hymenoptera	79	56	61	78
Lepidoptera	50	22	6	11
Aranei	71	33	10	44
Number of samples	14	9	31	18

Table 6. Occurrence of main ecological complexes in autumn diet. DAM – insects developing in aquatic/moist habitats; ICR – insects connected with reed; ICA – aphid consumers; AOV – autumn outside visitors. See text for further explanations.

Tab. 6. Vorkommen der wichtigsten ökologischen Gruppen in der Herbsternährung. DAM – Insekten der Feuchthabitate, ICR – Schilfinsekten, ICA – Blattlaus-Konsumenten; AOV – herbstliche Fremdbesucher. Siehe Text.

Ecological complex	occurrence, %
Chironomidae	66
DAM apart from Chironomidae	59
ICR	45
<i>H. pruni</i>	90
ICA-1 (consumers of <i>H. pruni</i>)	59
ICA-2 (attracted by <i>H. pruni</i>)	40
AOV	18
Number of samples	73

Between July 15 and September 22, which refers to the post-fledging and post-breeding period and to autumn migration, 73 diet samples were collected, 66 from first-year birds and 7 from adults. Frequency of coleopterans, Heteroptera, and spiders declined from June towards August, but rose again in September. The frequency of butterflies declines in September nearly 5-fold. High occurrence of Diptera and Hymenoptera was recorded during the whole summer and autumn (Table 5).

For autumn diet high taxonomic diversity and high abundance of different ecological groups are typical. In this period dominating ecological groups change in reed communities, and taxa are re-distributed over ecological complexes. During post-fledging period and autumn migration Sedge Warblers usually take invertebrates that are directly or indirectly (via food chains) connected with reed (*Phragmites australis*).

Food items taken in autumn may be classified in the following way (Table 6):

1. Insects developing in aquatic/moist conditions (DAM) are mainly the same as in spring. These items are collected from reed leaves, where concentrations may be found at the lower

surface. Due to great importance of chironomids in Sedge Warbler's diet and their high abundance two sub-complexes may be distinguished in autumn: (1) family Chironomidae; (2) other taxa of DAM.

2. Invertebrates connected with reed (ICR). This complex includes animals that use reedbeds as their habitat: coleopteran families (but for Coccinellidae), spiders, and invertebrates foraging on reed. Among them plum aphids (*Hyalopectus pruni*) are the most important element.
3. Invertebrates connected with plum aphids via food chains (ICA). This complex includes the following groups:

- 3.1. Aphid consumers, including (a) aphids' primary parasites, Aphidiidae (Hymenoptera); (b) aphids' secondary parasites, i.e. parasites of Aphidiidae: some Pteromalidae and other Chalcidoidea; (c) aphids' predators: Syrphidae, larvae and imagines; Chamaemyiidae (the only species found in reed stands is *Leucopis argentata*); (d) parasites of predators (parasites of Syrphidae): Diplazontinae, Ichneumonidae (mainly *Diplazon laetatorius*), Pteromalidae (*Asaphes vulgaris*).
- 3.2. Taxa attracted by aphids. These insects are connected with aphids only as imagines. They use aphids' carbohydrate-rich excretes as supplementary imaginal food. In dense reedbeds with few other plants these insect form considerable aggregations near aphid colonies. This group includes some Diptera (except Chironomidae), Ichneumonidae and other Hymenoptera.
4. Autumn outside visitors (AOV), taxa connected with vegetation other than reed.

4. Discussion

In the end of April and in early May invertebrates start to appear in patches of reed stands warmed by the sun. During this period aggregations of beetles occur in developing vegetation and on dry reed. Inside dead reed stems we found wintering Coleoptera, also Hymenoptera (mainly Ichneumonidae) and some Diptera. In late May and early June insects wintering in humid conditions, mainly in decomposing plant material, start to appear in numbers. At the same time Chironomidae begin to emerge in abundance.

It is noteworthy that the complex of spring occasional visitors (SOV), though recorded in nearly one-third of samples, formed the main prey only in 5% of cases. This suggests that it is of secondary importance for Sedge Warblers in spring. The basis of the diet of this species is formed by two other complexes (Fig. 1).

Comparison of autumn vs. spring diet (Table 1) reveals that nearly all taxa recorded in spring were also found in autumn samples. In autumn, occurrence of beetles and butterflies in samples decreases by half compared to spring. Occurrence of Homoptera increases 7-fold, and of Hymenoptera – nearly 3-fold. Occurrence of aphids rises by an order of magnitude.

During post-fledging movements and autumn migration the importance of aphids is growing. Aphids were main prey in 75% of samples taken in July – September. It should however be noted that birds take not only aphids themselves. Of certain importance is the whole arthropod complex connected with aphids – their invertebrate primary and secondary consumers, and insects attracted by them. Autumn diet is mainly formed by reed consumers, direct or via food chains. We recorded very small Hymenoptera (Aphidiidae, Chalcidoidea, Proctotrupeoidea, other 'Microhymenoptera') which are only ca. 1 mm large. Aiming taking these insects seems to be energetically unfavourable. These invertebrates are probably taken together with aphids, many of the latter being 2–3 mm long, and other larger members of respective ecological complex.

Occurrence of various Diptera, especially Chironomidae, remains high during the whole summer and autumn. Chironomids constituted main prey in 20–27% of samples. This is another argument against the exclusive role of aphids in Sedge Warbler's diet. Until now doubts in the hypothesis of exclusive importance of aphids were based on theoretical considerations, e.g. that too narrow specialisation may be evolutionary disadvantageous, and that Sedge Warblers must survive and migrate also in years with low aphid numbers (ORMEROD et al. 1991, MÄLL 1995). Our study provides evidence for this viewpoint.

Our data suggest that Sedge Warblers are more flexible in diet selection than thought earlier. This species can utilise very different prey items abundant in species-specific habitats, including e.g. beetles. Sedge Warblers frequently take any abundant prey, incl. chironomids and hymenopterans (Table 1), not necessarily plum aphids as suggested by some authors (BIBBY & GREEN 1981, KOSKIMIES & SAUROLA 1985). Sedge Warblers search for good foraging sites where food necessary

for energy-consuming tasks, as moult and fuel accumulation, can be collected. When birds find prey aggregations, they usually do not hold territories (BIBBY & GREEN 1981). Such behaviour is typical to animals utilising superabundant but non-uniformly distributed prey (BAIRLEIN 1996).

At migration Sedge Warblers tend to use the most common, available and aggregated prey. Its taxonomic position is of limited if any importance. The seasonal pattern of arthropod communities in species-specific habitats is thus crucial. Seasonal shifts in Sedge Warbler's diet follow the phenology of invertebrate ecological complexes in these habitats.

5. Zusammenfassung

In dieser Arbeit werden Nahrungszusammensetzung und Ernährungsstrategie von ziehenden Schilfrohrsängern während des Heimzuges, der nachbrutzeitlichen Ortsveränderungen und während des Wegzuges auf der Kurischen Nehrung analysiert. Im Frühling sind Käfer, Dipteren (inkl. Chironomiden), Heteropteren und Spinnen die häufigste Beute. Im Spätsommer und im Herbst sind dies Blattläuse, Chironomiden, Hymenopteren, Käfer und Spinnen. Die ökologischen Gruppen, die die Schilfrohrsänger am häufigsten nutzen, sind in den Saisonabschnitten unterschiedlich. In beiden Jahreszeiten spielen die häufigsten Beutetiere die wichtigste Rolle, dabei ist ihre taxonomische Position kaum von Bedeutung. Das saisonale Muster der Arthropoden-Gemeinschaften in artspezifischen Habitaten ist von entscheidender Bedeutung für die Schilfrohrsänger.

6. Literature

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