

Combination rules among western European *Parus* species

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The composition of *Parus* assemblages was recorded for 88 local bird communities in western Europe. The number of *Parus* species in a habitat (assemblage size) was found to be most closely correlated with the number of other tree-foraging passerine species, suggesting that the building up of *Parus* assemblages is presumably determined by habitat attributes. Only about one third of all possible combinations with the six available species are found in nature. Mean interspecific difference in bill length (MBD) is significantly higher in combinations which do occur. Among occurring assemblages, MBD values and the number of times combinations have been recorded are positively correlated. Each *Parus* species has a critical threshold value of coexisting congeneric species above which its presence in the assemblage is highly predictable. Species are added to the group in a fairly ordered fashion: smallest assemblages are made up of extreme-billed species, and middle-billed species are added as assemblage size increases. Non-random patterns in the constitution of local *Parus* assemblages are discussed by considering simultaneously the upper limit set on assemblage size by habitat quality and the competitive processes leading to stable, non-invasive configurations.

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1. Introduction

The species pool available over a large geographical area manifests itself in the form of locally assembled subsets. The identity of species in such subsets is determined in a non-random way, and factors like dispersal and competitive abilities of individual species influence the constitution of local species assemblages (Diamond 1975, Cody 1978, M'Closkey 1978). Most previous work on assembly of communities has derived from the analysis of distributional patterns of island birds (Diamond 1975), although the patchy nature of mainland habitats also provides an opportunity to study non-random patterns of species assemblages (M'Closkey 1978). Mainland studies have the advantage of ruling out to a large extent the effects of dispersal and colonizing ability on the assembly of local species subsets, highlighting the influence of competitive factors. Consequently, the study of assembly of mainland species communities is bound to contribute to the understanding of the competitive organization of communities.

Wooded habitats in temperate latitudes of the northern hemisphere almost invariably support a certain number of species of the passerine genus *Parus* L. (Lack 1969). Abundant published information exists on feeding ecology (e.g. Hartley 1953, Betts 1955, Gibb 1960, Royama 1966), population dynamics (e.g. Kluyver 1951, Lack 1966, Krebs 1970) and behaviour (e.g. Hinde 1952, Gibb 1956, Krebs 1973, 1977), to name but a few of the aspects which have been investigated until present. Mechanisms of species coexistence have been a preferred topic of *Parus* studies, and it is now generally accepted that interspecific segregation within this congeneric group is achieved by the stepwise combination of differential selection of habitat and foraging substrate (Snow 1954, Lack 1971). In addition, morphological correlates of habitat and substrate selection have been demonstrated (Snow 1954, Partridge 1976a,b). All these investigations have led to a widely accepted picture of the mechanisms by means of which *Parus* species are able to coexist, based on the simultaneous consideration of morphology, habitat selection and foraging substrate.

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In this paper I deal with one aspect of *Parus* ecology which has not been considered so far, namely the existence of well defined rules governing the constitution of local *Parus* assemblages in western Europe. This finding will hopefully provide a different view of, but not conflicting with, that generally accepted until present about coexistence mechanisms within the genus.

2. Methods

The number and identity of coexisting *Parus* species were recorded for each of 88 local bird communities inhabiting wooded habitats in western Europe (see Appendix for a list and source references). Whenever possible (75 communities), the total number of passerine species and the number of these which usually forage on trees (excluding *Parus* in both cases) were recorded as well. A great variety of habitat types are represented in the sample used, including boreal and temperate deciduous, pure coniferous, evergreen, and mixed forests. This information was originally recorded for each community to be sure that the sample used covered all principal habitat types, but its use has been deliberately avoided in the analyses below, since one of the aims of this paper is to demonstrate that an explanation of the observed assembly patterns does not necessarily require relating them a priori to the qualitative, conventional habitat categories usually considered in the literature on *Parus* habitat selection.

Six species are found in the area considered: Great *P. major* L., Blue *P. caeruleus* L., Willow *P. montanus* Bald., Marsh *P. palustris* L., Coal *P. ater* L., and Crested *P. cristatus* L. tits. They represent a gradient in body size from the smallest *ater* to the largest *major* (mean

body weight 9 and 20 g, respectively, according to Lack 1971). They also show a broad variety of bill sizes, from the shortest-billed *caeruleus* to the longest-billed *major* (means 9.3 and 13.0 mm, respectively, Lack 1971). Bill length has been the morphological character used in the following analyses to determine the ecological bases for the observed combination rules. A representative figure of bill length (measured from the skull) was chosen for each species, taken from Tab. 2 in Lack (1971). As inter-regional differences in bill size are known to occur among western European *Parus* species (e.g. Snow 1954, Herrera 1978), these figures must solely be taken as roughly representative of the involved species, and they are not suited for further detailed analyses of interspecific interactions.

Certain *Parus* species are absent from some marginal areas (e.g. portions of the British Isles and the Iberian Peninsula, Voous 1960) and this undoubtedly affects the observed frequencies of occurrence of some particular species combinations. As no comparison of the kind observed-expected will be attempted, the only effect these absences will have on results is introducing some undetermined amount of irregularity in the composition of smaller-sized assemblages. Some combinations which never occur in the most species-rich regions are represented in impoverished areas. As results will show, this bias falls on the conservative side.

3. Results

In the sample of communities studied, three- and four-species *Parus* assemblages are most commonly found, making up 65.9% of total (Tab. 1). Two- and five-species assemblages are fairly frequent (21.6%), whereas

Tab. 1. Composition of *Parus* assemblages in 88 European passerine bird communities (see Appendix). Figures in parentheses are the number of times a given specific combination has been recorded. Abbreviations for species names are: M, Great tit *P. major* L.; Ca, Blue tit *P. caeruleus* L.; P, Marsh tit *P. palustris* L.; Mo, Willow tit *P. montanus* Bald.; A, Coal tit *P. ater* L.; Cr, Crested tit *P. cristatus* L.

	1-species	2-species	3-species	4-species	5-species	6-species
	Mo (2)	M-Ca (16)	M-Ca-P (19)	M-Ca-P-Mo (13)	M-Ca-P-A-Cr (4)	M-Ca-P-Mo-A-Cr (1)
	Cr (1)	M-Cr (1)	M-Ca-Cr (4)	M-Ca-P-A (5)	M-Ca-Mo-A-Cr (3)	
		M-Mo (1)	M-Ca-A (3)	M-Ca-P-Cr (3)		
		Mo-Cr (1)	M-Ca-Mo (2)	M-Ca-Mo-Cr (1)		
			M-A-Cr (1)	M-Ca-A-Cr (4)		
			M-P-Cr (1)	M-Mo-A-Cr (1)		
				M-P-A-Cr (1)		
Different combinations observed	2	4	6	7	2	1
Total possible combinations	6	15	20	15	6	1

Tab. 2. Correlations between the number of *Parus* species, other passerine species and other tree-foraging species, in a sample of 75 western European localities (see Appendix).

Variables being correlated	First-order correlation coefficient ¹	Partial correlation coefficient ²
Number of <i>Parus</i> species × Number of other passerine species	0.451***	0.126 ^{n.s.}
Number of <i>Parus</i> species × Number of other 'tree-foraging' species	0.561***	0.392***

1. n.s., not significant; ***, $p < 0.001$.

2. Partialled on the variable not included in the correlation.

one- and six-species ones are extremely rare and they will be omitted in all analyses below.

The number of *Parus* species found in a habitat is closely correlated both with the number of other coexisting passerine species and the number of these which forage on trees (Tab. 2), revealing that *Parus* species are progressively added to communities as their overall species richness increases. When partial correlation coefficients are computed, only the correlation between the number of *Parus* and other tree-foraging species continues to be significant (Tab. 2). This suggests that the building up of *Parus* assemblages is presumably determined by the same environmental variable(s) as that of other tree-dwelling species.

It is clear from Tab. 1 that the species combinations actually observed constitute a relatively small subset of all possible combinations which could be formed with the six available species. For all sizes combined, only 22 combinations out of 63 possible ones have been actually recorded (34.9%). No differences exist between assemblage sizes regarding the percentage of possible combinations actually recorded ($\chi^2 = 1.58$, $df = 4$, $p > 0.80$).

Within each of the most commonly found combination sizes (2 to 4 species), there is a particular combination among those observed which occurs disproportionately more frequently than the remaining ones. For two- to four-species combinations, the three commonest ones (M-Ca, M-Ca-P and M-Ca-P-Mo; see Tab. 1 for abbreviations) have been found as many as 48 times, whereas the remaining 14 were observed only in 29 instances. All this suggest the existence of a highly non-random pattern in the specific constitution of *Parus* assemblages in western Europe.

To elucidate whether this pattern has some obvious ecological correlates, interspecific differences in mean bill length (larger minus smaller) were computed for every possible species pair. For two-species combinations, these figures were used as estimates of overall morphological discrepancy. For combinations of more than two species, a species-x-species half-matrix was obtained whose elements were the corresponding figures for binary differences. Then, the average of the elements in the matrix was used as the measure of overall morphological discrepancy. This was done for all possible species combinations ranging in size from two

to five species, irrespective of whether they were actually observed or not.

The distribution of mean bill length differences (MBD) for the differently-sized species combinations is shown in Fig. 1. As combination size increases, the

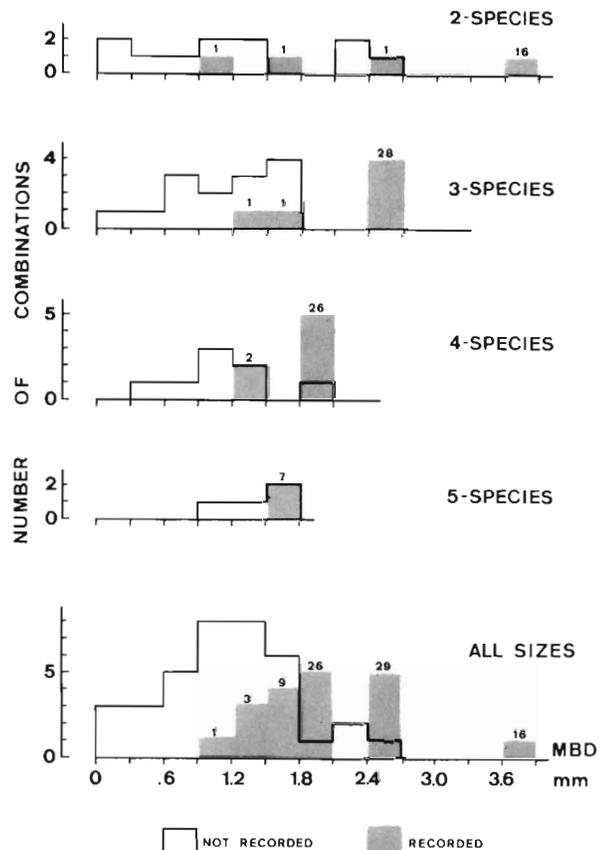


Fig. 1. Frequency distributions of mean bill size difference (MBD, see text) of differently-sized *Parus* assemblages. Combinations have been divided into observed and not-observed ones, and represented as separate histograms. Figures above the columns of shaded histograms (combinations actually observed) represent the number of times combinations falling in a given MBD class have been recorded. For all combination sizes, those combinations which actually occur tend to show larger bill differences than those never recorded. Among combinations recorded, the most frequent are invariably those with the highest MBD values.

range of MBD values becomes narrower, but this effect must simply be attributed to the averaging procedure followed which tends to amortigate the effects of extreme binary differences in the largest matrices. Specific combinations which actually occur tend to fall consistently in the upper zone of the range of MBD values. For all sizes combined, this difference is highly significant ($H = 17.03$, $df = 1$, $p \ll 0.001$, Kruskal-Wallis analysis of variance), demonstrating that species combinations which actually occur are characterized by larger interspecific differences in bill size than those which were not observed. For particular assembly sizes, differences in MBD between observed and not-observed combinations are significant for three- and four-species assemblages ($H = 7.41$, $p < 0.01$ and $H = 6.48$, $p < 0.02$, respectively). Five-species combinations are too few for statistical comparison, and two-species ones do not show significant differences ($H = 2.06$, $p > 0.20$).

Combinations showing the highest MBD values occur with disproportionate frequency with respect to other combinations of lower MBD, as can be appreciated in Fig. 1. There exists a significant, positive correlation between the number of times a given combination has been recorded and its MBD value (r_s corrected for ties = 0.572, $n = 19$, $p = 0.01$, all sizes combined, only combinations actually occurring), revealing that those with larger differences in bill length are the most likely to occur.

This non-random pattern shown by the constitution of local *Parus* assemblages is in some manner summarized by Fig. 2. Each *Parus* species has a critical threshold value of coexisting *Parus* species above which its presence is highly predictable, and species are added to the group in a fairly ordered fashion. *Parus major* and *caeruleus* form the basic initial pair, and they constitute the extremes of bill length (13.0 and 9.3 mm, respectively). *Parus palustris* is usually the third to enter, with bill length near the middle of the range set by the two former species (10.4 mm). *Parus montanus* is normally a component of either four- or five-species assemblages, and its bill size falls between *major* and *palustris* (10.6 mm). *Parus ater* and *cristatus* are the last to be added, and both fall in between *major* and *montanus* (bill length 10.8 and 11.5 mm, respectively). In this way, the 'combination rules' suggested by Fig. 2 represent another view of the pattern suggested by Tab. 1, and they may be readily related to the pattern of differences in bill size shown in Fig. 1.

Summarizing, only about one third of all possible combinations of western European *Parus* species are found in nature, and there are combination rules which determine those assemblages which are permitted and the order in which species are added as size increases. Divergence in bill size is maximized in species combinations, and combinations which remain unrecorded showed the closest morphological packing as measured by bill length differences.

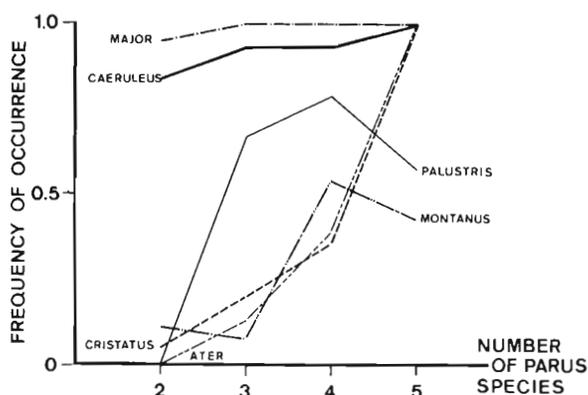


Fig. 2. Frequency of occurrence of the six *Parus* species in assemblages of increasing size. Based on data in Tab. 1.

4. Discussion

Bill length is not more than a single character within the whole set of morphological attributes which configurate the position of a species in the space determined by environmental variables (Karr and James 1975). In general, however, bill size appears to be an ecological trait which is very sensitive to competitive interactions (Brown and Wilson 1956, Schoener 1965), and spacing of coexisting species along the bill size gradient has been usually related to mechanisms of alleviating competition (Hutchinson 1959, Schoener 1965). Among *Parus* species, bill size has been variously related to prey size, habitat type and foraging methods (e.g. Snow 1954, Betts 1955, Partridge 1976a), but this morphological variable can not easily be related in this genus to any single ecological gradient (e.g. prey size, habitat). It rather represents an adaptive compromise in response to a combination of diverse environmental gradients. In any case, however, a close relationship between bill size and patterns of resource utilization has been repeatedly documented for the genus *Parus* (Snow 1954, Higuchi 1975, Partridge 1976a,b, Herrera 1978), and thus bill size may properly be used as an ecologically relevant parameter in depicting putative competitive interactions between species.

Patterns derived from observations of nature at points in time inevitably reflect only an instantaneous, static view of a highly dynamic system. However, if a sufficiently large number of such instantaneous observations are gathered of systems in different states of temporal evolution, some inferences can be drawn about the likely pathways followed by the system under study. The information on *Parus* assemblages analyzed in the present study may thus be used to assess the dynamics of their constitution and, in general, of rich insectivore guilds. Some of the observed patterns can also be used to assess some aspects of the competitive relations underlying these processes.

Let us assume a wood which at a given time is

occupied only by species A and B in the same guild, and that these two species can coexist there indefinitely provided no alterations in the resource space take place. Assume also that no barrier to colonization exists. At certain time, a third species C colonizes the habitat. If long-term coexistence of all three species is possible, then a three-species guild is formed. But if coexistence is not permitted by the resource space inherent to the wood, at least one species will become extinct. If either A or B is eliminated, a new configuration emerges, which is in turn open to further invasions. But if C is eventually eliminated, the combination A–B is resistant to invasion by C in that wood. The former process may take place many times as a sequence of trial-error events, and only two possible outcomes are to be expected eventually in ecological time:

(a) An increase in the number of species in the guild takes place. Obviously, this situation is another departure point for the trial-error sequence. The process will eventually stop in option (b) below when the upper limit to species richness set by habitat quality has been reached.

(b) A non-invadable (in that habitat) species configuration is eventually reached, without changing the initial number of species. Presumably, there will be only a few of such stable configurations among the set of possible ones, provided that the number of species in the assemblage is not very large.

I suggest that the patterns observed in the composition of *Parus* assemblages reflect simultaneously the two former processes. Outcome (a) is related to observed variation in the size of assemblages, and outcome (b) is to combination rules and non-random pattern of species assortment.

The different habitats included in the present study represent a great variety of the so-called 'habitat types' but, nevertheless, they are ideally orderable along a gradient of physical complexity. The observed variation in the number of passerine species occupying these habitats must be closely related to changes in habitat complexity, as it has been repeatedly demonstrated in the literature for many geographical locations (MacArthur and MacArthur 1961, MacArthur et al. 1966, Karr and Roth 1971, Blondel et al. 1973). Consequently, correlations found between *Parus* species richness and either total or tree-dwelling passerine species number tend to suggest that the size of *Parus* assemblages is largely determined by the vegetational complexity of the habitat. Specifically, results suggest that it is the diversity of arboreal vegetation volumes (or size of their 'ecological space') what must be most closely related to *Parus* species richness, and a similar relationship has been demonstrated by Ulfstrand (1975) during the non-breeding period (see also Hertz et al. 1976). It is perhaps irrelevant in the present context to speculate about whether the gradient of increasing *Parus* richness is related to 'habitat type' – or 'habitat complexity' – related gradients, for any of them

would be probably seen by late-arriving species to the assemblage as one of increasing ecological opportunities. Nevertheless, literature on European *Parus* is plenty of statements about the habitat types selected by each species, along with fairly numerous exceptions in which species are found in the 'wrong' habitat type (see reviews in Snow 1954 and Lack 1971). My results do not conflict with the 'habitat type' view of *Parus* assemblage organization, but rather constitute and extension of it which inserts exceptions into a more general framework. Raw data I have used include both 'right' and 'wrong' cases of habitat selection (e.g. *P. cristatus* in broad-leaved forests, Herrera 1978), probably in proportions close to those found in nature. If neat interspecific differences in habitat type selection were to exist on a continent-wide basis, curves in Fig. 2 would not show regular shapes, but rather sharp discontinuities. Their appearance suggests that 'exceptions' also fit to a general pattern of combination rules governed by bill size. The essential difference between the two approaches lies probably in my consideration of a continuous gradient of ecological opportunities instead of the conceptually discrete one inherent to the habitat type view, and a partial interpretation of assembly rules in terms of habitat-type selection is feasible (Herrera unpubl.).

Outcome (b) mentioned above and related to non-randomness of species combinations is exemplified by the existence of a few combinations which largely predominate over the rest. These 'permitted' combinations are presumably the least invadable in most habitats, and they constitute the common end of all trial-error processes. Importantly, in addition to these dominant combinations, there are several other less common ones which presumably represent either pre-equilibrium situations or stable configurations in certain rare habitats or impoverished regions. It must be noted that the commonest combinations (M–Ca, M–Ca–P, M–Ca–P–Mo) form an ordered sequence of self-contained subsets, demonstrating that a combination is stable and closed to invasion only under some specified circumstances, but may hold further species if the resource space available increases. Many unobserved combinations (e.g. Ca–P, Ca–Mo, Ca–P–Mo) are part of common combinations of larger size, suggesting again that invadability is strongly dependent on the capacity of the habitat. These aspects of results tend to support the dynamic model outlined above for the building up of *Parus* assemblages.

For any given combination size, the trend towards a stable configuration is one of maximizing the divergence in bill size and thus, presumably, minimizing ecological similarity between species. With decreasing combination size species are eliminated if they are too packed in the morphological space, leading to a decrease in similarity of bill sizes. The enrichment of *Parus* assemblages takes place by adding species with middle-sized bills and species-poor combinations are dominated by species

with extreme bill sizes. If interspecies competition is actually responsible for the observed patterns, they suggest the existence of diffuse competition along a continuous resource gradient (MacArthur 1972). Fretwell (1978), testing predictions emanated from two competition models (discrete vs. continuous resources, MacArthur and Levins 1964, 1967), has shown that when the resource base exploited by a guild is continuous, species-poor guilds are dominated by extreme-sized species. On the contrary, when the resource base is discrete, species-poor guilds are dominated by middle-sized species. In other words, continuous resources promote increasing (ecological) divergence with decreasing species richness, whereas discrete resources originate decreasing divergence with decreasing guild size. Results therefore suggest that *Parus* species are competing along a continuous resource gradient.

Consideration of the type of resource may serve to explain the striking discrepancy between my results and those of M'Closkey (1978) in his analysis of assembly rules in Sonoran Desert rodent communities. In contrast with *Parus*, niche separation among Sonoran rodents increases with species diversity and, for a given species richness, species combinations permitted are those minimizing niche separation. One is tempted to relate this difference to the equally contrasting patterns shown by Fretwell (1978) for woodpecker and sparrow communities. The former, based on a continuous resource, behaves much like European *Parus* assemblages whereas the latter, depending on a discrete resource base, shows a pattern similar to that of Sonoran rodents. It may thus be suggested that differences in combination rules of *Parus* and rodent species originate from substantial differences in the type of resource exploited by each group.

The MacArthur and Levins (1964, 1967) competition models tested by Fretwell (1978) assume species are competing along a single resource gradient. 'This' resource is not readily identified, at least from our conventional, man-centered eyes. In the case of *Parus*, it is difficult to infer the nature of this resource from bill size information alone, as it has been stated previously in this paper. Most likely, the continuous, single resource in question must represent some sort of complex combination of prey size, prey type and microhabitat. As it has been made clear by Cohen (1978), underlying dimensional properties of ecological systems may usually be difficult to interpret in simple, conventional terms, but this by no means imply that some simple dimensionality structure does not occur.

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Appendix. Summary of material used in the present study.

Authority	Number of bird communities ¹	Location
Amat (unpubl.)	1(1)	Sevilla, Spain
Constant et al. (1973)	3	Bretagne, France
Eybert (1973)	3	Bretagne, France
Frochot (1971)	13	Bourgogne, France
Garnica (1978)	1	León, Spain
Głowacinski (1975)	7	Niepolomice, Poland
Głowacinski and Weiner (1975)	1	Ispina, Poland
Hartley (1953)	1(1)	Oxford, England
Herrera (1977)	2	Huelva, Spain
Herrera (unpubl.)	4(4)	Andalusia, Spain
Hogstad (1967)	2	Oslo, Norway
Irvine (1977)	1	England
Joensen in Cody (1973)	1	Denmark
Moksnes (1972)	1(1)	Nord-Trøndelag, Norway
Moksnes (1973)	1(1)	Nedal, Norway
Moksnes (1974)	1(1)	Nord-Trøndelag, Norway
Møller (1975)	1	Denmark
Mrugasiewicz (1974)	5	Milicz, Poland
Parsons (1976)	1	England
Pikula (1968)	9	Brno, Czechoslovakia
Purroy (1972)	1	Pyrenees, Spain
Purroy (1974)	1(1)	Pyrenees, Spain
Purroy (1977)	3(1)	Pyrenees, Spain
Røv (1975)	1(1)	western Norway
Saemann (1973)	9	Karl-Marx-Stadt, eastern Germany
Tomialojc (1974)	8	Legnica, Poland
Ulfstrand (1976)	1	southern Sweden
Ulfstrand (1977)	1	southern Sweden
Ulfstrand and Nilsson (1976)	1(1)	Denmark
Williamson (1974)	1	Mid-Argyll, Scotland
Williamson and Williamson (1973)	1	Sussex, England
Zollinger (1976)	1	Cossonay, Switzerland

1. Composition of *Parus* assemblages was recorded for all these communities. Figures in parentheses represent the number of communities at a given location for which no detailed data on total passerine species composition were available.

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