

A role for female ornamentation in the facultatively polygynous mating system of collared flycatchers

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In a polygynous mating system, females settling with already mated males often experience low mating success due to the reduced parental contribution of the male. However, there are numerous factors that may still make it advantageous for some females to choose this mating status. Facultative polygyny is believed to be dominated by male advertisement and female choice. Although quality differences and competition among females are increasingly recognized as important determinants of polygynous settlement patterns, the importance of signals of female quality in this mating system is largely unknown. Here we examined the relationship of the white wing patch size (WPS) of female collared flycatchers, a phenotypically plastic and age-dependent ornament, with social mating status, while controlling for settlement date and age. At the population level, monogamous, primary, and secondary females did not differ in WPS. However, the primary female of individual males was more ornamented than the secondary female, and this difference declined with increasing distance between primary and secondary nests. Secondary female ornamentation increased, whereas that of the primary female did not change with nest distance. These results suggest a subtle role for female ornamentation at polygynous mating. Future studies should therefore take into account mating status when assessing the costs and benefits of female signals. Moreover, patterns in quality-indicating female traits may contribute to the explanation of differences in reproductive success among females of different mating status. *Key words:* female sexual ornament, individual quality, polygyny, settlement date, territorial distance. [*Behav Ecol* 18:1116–1122 (2007)]

Since Darwin, the classical view of sexual selection has been that of advertising males and choosy females. This view has not seriously been affected by the detailed descriptions of sex-role reversed species (e.g., Owens et al. 1994). Ornamentation in females of species with classical sex-roles has received little attention, in spite of early accounts of mutual sexual selection (Burley 1977). Theoretical models emphasize that the degree to which one sex is competitive and the other choosy depends on sex differences in the costs (Kvarnemo and Ahnesjö 1996) or the benefits of choosiness (Owens and Thompson 1994). However, the predominance of choice by one sex does not preclude choice by the other sex. For example, in spite of the potential difficulties of finding another mate, males may choose among the prospective mates if female quality is sufficiently variable (Johnstone et al. 1996). There has been an increasing number of reports of mutual mate choice for sexual ornamentation (e.g., Johnson 1988; Hunt et al. 1999; Siefferman and Hill 2005). The importance of intrasexual competition in the maintenance of female ornaments has also been emphasized (Whittingham et al. 1992; Irwin 1994; Kraaijeveld 2003). However, female ornamentation has rarely been discussed in the context of polygyny.

In a facultatively polygynous mating system, there is usually a shortage of male parental care, with the single male distributing his parental effort among his mates or choosing to feed the offspring of the first-settled primary female (Slagsvold and Lifjeld 1994). This creates conflicts of interest between the

male and both females and also between the 2 females. Male reproductive success is usually boosted by polygyny (Soukup and Thompson 1998), but the lack of proper paternal help often reduces the reproductive success of females (Johnson et al. 1993), even if they benefit in other ways such as by having attractive offspring (Huk and Winkel 2006). In several species, this conflict has selected for females that prefer unmated to already mated males (Pribil and Picman 1996) and for males that apparently try to hide their already mated status (Alatalo et al. 1981). Another conflict of interest arises between primary and secondary females. This conflict may lead to resident females preventing other females from settling with their mate (Dunn and Hannon 1991) or to secondary females destroying the breeding attempt of the primary female (Hansson et al. 1997).

Polygyny is generally considered a situation where it is predominantly the males that invest in sexual advertisement, whereas the females care for the young (Webster 1992; Cuervo and Møller 1999; Westneat 2006). However, sexual selection on female traits may play important roles in the conflicts outlined above. First, more ornamented members of the limiting sex may be choosier than less attractive individuals (Burley 1977), so they may not settle in a poor quality breeding situation such as a secondary status. Second, analogous to courtship disruptions in lek mating systems (Trail 1990), competition among females for the parental care of polygynous males creates ample opportunity for intrasexual selection on female ornamentation. However, we are aware of only a single study that has examined female ornamentation in relation to facultative polygyny. Pilastro et al. (2003) found that primary females of 11 polygynous rock sparrow males *Petronia petronia* were more ornamented than the secondary females, but they did not examine the ornamentation of monogamous females.

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Here, we use 6 years of breeding data to look for a potential role of female ornamentation in conflicts of interest related to polygyny in the collared flycatcher (*Ficedula albicollis*). In the study population, less than 10% of males attract a secondary female (Garamszegi, Török, Michl, et al. 2004). Both primary and secondary females suffer reduced current reproductive output due to the distribution of parental care by males (Garamszegi, Török, Michl, et al. 2004). Studies on the sister species pied flycatcher (*F. hypoleuca*) show that females prefer unmated over mated males (Slagsvold and Drevon 1999), but some males seem to successfully hide their already mated status when courting a secondary female (Searcy et al. 1991). Moreover, female competition may effectively prevent the settlement of secondary females on nearby territories but not when the secondary territory is further away (Slagsvold et al. 1999). Female aggressiveness may depend on breeding stage (Kral et al. 1996) and the timing of secondary broods relative to primary broods may also affect the distribution of male care (Lifjeld and Slagsvold 1990).

The upperparts of male collared flycatchers are black, with white forehead and wing patches and collar. Females are brown, lack the collar and the forehead patch but have a wing patch of similar size to yearling males. The 2 white plumage ornaments of males (forehead and wing patch) have been intensively studied in our population. These studies have revealed a difference in phenotypic plasticity between the 2 ornaments, and several lines of evidence for a role of these traits in sexual selection (Hegyi et al. 2002; Michl et al. 2002; Török et al. 2003; Garamszegi et al. 2006; Hegyi et al. 2006). In females, on the other hand, white wing patch size (WPS) has recently been shown to reflect age both among and within individuals. Furthermore, within-individual changes in female WPS were correlated with climate during the summer molt, and changes in WPS also predicted differences in the attractiveness of mates acquired by a female in 2 consecutive years (Hegyi et al. 2007). Female WPS may therefore be a condition- and age-dependent trait with a role in mate acquisition. Here we examine whether this ornament is also important at the formation of polygynous pair-bonds. First, we investigate whether any consistent difference in ornamentation exists among the groups of monogamous, primary, and secondary females at the population level, when controlling for age and breeding date. Second, we compare the ornamentation of 2 females settling with a single male, also taking into account female age, the relative breeding date of the 2 nests, and the distance between them.

There is no single expected pattern in the difference in female ornamentation among mating status groups at the population level, and the complete lack of previous studies also makes it difficult to outline predictions. For example, if high-quality males become polygynous and they also acquire high-quality females (e.g., Møller 1991), primary and secondary females may both be more ornamented than monogamous females. A similar pattern is expected if only high-quality females can afford the risk of infection from an attractive, promiscuous male (Thrall et al. 2000). Alternatively, female competition may cause primary females to be more ornamented than either secondary or monogamous females. We expect the same pattern if there is mutual mate choice early in the season, but not later on, when secondary or late monogamous females are settling (see Qvarnström et al. 2000). Finally, female ornamentation may indicate quality but may not be sexually selected in the context of polygyny. In this case, if only high-quality females can afford the secondary position (also see Forstmeier et al. 2001), we may find secondary females being more ornamented than primary or monogamous females. The comparison between the 2 females of the same polygynous male is expected to yield the same results as

population-level comparisons, but with much more power, because variation in male quality is controlled for. Moreover, we expect that any WPS difference between the primary and the secondary female will diminish with nest-box distance if direct female interactions or deception play a role. Finally, competition for paternal care may lead to an effect of settlement date differences on the relative ornamentation of the 2 females.

METHODS

Field data

The study was conducted in Pilis Mountains, near Szentendre, Hungary, where a nest-box breeding population of collared flycatchers has been monitored since 1981 (see Török and Tóth 1988 for details). The total number of nest-boxes is approximately 800, which form several plots in different parts of the same oak woodland. In the period of pairing and egg laying, the nest-boxes were checked several times a week, and the date of nest initiation, stage of nest building, laying date, and the number of eggs laid were noted. The nests were again frequently visited around the expected time of hatching. Most parents were caught while feeding 8- to 12-day-old nestlings. Female WPS was measured as the sum of lengths of white on the outer vanes of primaries 4–8 on the right wing (see Török et al. 2003). Female ages were accurately determined for recruited nestlings and estimated as 1 year at first capture for individuals first caught as breeders. The error introduced by the age estimation has previously been found to be small (Hegyi et al. 2007). Body size, as measured by tarsus length, explains very little variation in WPS ($r^2 < 0.0001$; Hegyi et al. 2007), so body size is not considered in this paper.

Mating status was assigned based on the identity of the male feeding the young. Of 2 nests of the same male, that with the earlier date of egg laying was termed primary, whereas the other secondary. In case of the same laying date, we could always unambiguously determine status based on records of nest building. Broods where no male was caught were handled as a separate group in the population-level analyses. Capture effort was high throughout, and approximately 90% of females were caught at nests where at least one egg hatched. Therefore, if there was no substantially sex-biased adult mortality, the majority of nests without males were probably secondary broods without male feeding assistance, as confirmed by genetic data in pied flycatchers (Huk and Winkel 2006). We therefore had 4 nest categories: primary nests, secondary nests with male assistance, secondary nests without male assistance, and monogamous nests. The latter category also contains the primary broods of unidentified polygynous males, which makes our analyses conservative. Pooling unassisted nests with monogamous ones or removing them from the analyses did not change the conclusions. Distance between the primary and secondary nest-boxes of the same male was measured on digitized maps of the main plots, or directly in the field, if the nest-boxes were outside the main plots. The 2 ways of measurement gave very similar results, as shown by measuring a subset of the nest-box pairs both on the map and in the field (log-transformed data; Pearson $r = 0.980$, $n = 10$, $P < 0.001$). The data presented here were collected in 6 breeding seasons from 2001 to 2006.

Statistical analyses

Laying date was given relative to the overall yearly median and $\log(x + \min(x) + 1)$ transformed before analyses, where $\min(x)$ is the smallest relative value in the whole dataset. Differences in laying date within nest pairs were not transformed.

Table 1
Female ornamentation in relation to mating status at the population level

	<i>F</i>	df	Variance explained	Effect size (<i>r</i>)	CI lower	CI upper
Year	7.13***	5737	0.046	0.215	0.165	0.264
Female binary age	74.60***	11024	0.068	0.261	0.211	0.309
Mating status	0.15	3727	0.001	0.025	-0.027	0.077
Laying date	2.11	1861	0.002	-0.049	-0.101	0.003
Year × age	1.32	5944	0.007	0.083	0.031	0.135
Year × status	0.65	15 752	0.013	0.113	0.061	0.164
Year × laying date	0.83	5738	0.006	0.075	0.023	0.126
Age × status	1.28	3858	0.004	0.067	0.015	0.118
Age × laying date	3.82	1899	0.004	0.065	0.013	0.117

General linear mixed models with Satterthwaite correction and backward stepwise selection. Female identity as a random factor ($P < 0.001$) is not shown here. Terms in the final model are shown in bold face. *** $P < 0.001$; df, degrees of freedom; CI, 95% confidence interval.

Nest-box distance was also log transformed to achieve normality. Female WPS increases between 1 and 2 years of age, but does not change thereafter (Hegyí et al. 2007), so we entered binary age into the analyses. We used general linear mixed models with restricted maximum likelihood parameter estimation and Satterthwaite correction, as implemented in the MIXED procedure of SAS 8.02 (SAS Institute, Cary, NC). Differences in female ornament size among the 4 groups of females of different mating status were analyzed with female WPS as dependent variable; year, binary age, and status as factors; laying date as a covariate; and female identity as a random factor. We also calculated all 2-way interactions. The difference in female ornamentation within polygynous nest pairs was assessed with age-standardized WPS as a dependent variable, status (primary or secondary) as a repeated measures factor, year as a fixed factor, nest distance and difference in laying date as covariates, and the identities of the 2 females as random factors. We also assessed all 2-way interactions involving year or status. Finally, the relationship between nest-box distance and the WPS of primary or secondary females was examined with distance as dependent variable, year and the binary age of the 2 females as fixed factors, difference in laying date and the year- and age-standardized WPS of the 2 females as covariates, and the identities of the 2 females as random factors. We also calculated the interactions of primary and secondary female WPS with year and the age of the respective female. All models were subjected to backward stepwise model selection, and results reported here for non-significant terms reflect their reintroduction to the final

model one by one. All statistical tests are 2-tailed, and we use $P < 0.05$ as the criterion of significance.

RESULTS

At the population level (Table 1), female WPS was significantly related to year and binary age. WPS was unrelated to mating status category or laying date, and all interactions were non-significant. At the level of individual polygynous males (Table 2), the age-corrected WPS of the primary female was significantly larger than that of the secondary female. However, there was a significant interaction between nest-box distance and the repeated measures factor (Figure 1). The effects of year, difference in laying date, and all other interactions were not significant. Analyzing the ornamentation of the 2 females separately (Table 3) revealed no relationship between nest-box distance and the WPS of the primary female. The WPS of the secondary female, however, was significantly positively related to the distance between her nest and the primary nest-box of the male (Figure 2). All other effects and interactions were non-significant.

DISCUSSION

Polygynously mated males generally enjoy higher reproductive success than monogamous males (Kempnaers 1995; Hasselquist 1998; Parish and Coulson 1998), but secondary, or even primary, females often experience impaired current reproduction (Westneat 1988; Wheelwright et al. 1992; Smith

Table 2
Correlates of the difference in ornamentation between the primary and secondary females of the same polygynous male

	<i>F</i>	df	Variance explained	Effect size (<i>r</i>)	CI lower	CI upper
Year	1.07	5101	0.050	0.224	-0.044	0.462
Mating status (repeated)	4.79*	1106	0.043	0.208	-0.061	0.449
Distance	0.89	1106	0.008	0.091	-0.178	0.348
Laying date difference	1.45	1105	0.014	-0.117	-0.371	0.153
Year × status	1.04	596	0.051	0.227	-0.041	0.464
Year × distance	0.89	596	0.044	0.211	-0.058	0.451
Year × date difference	0.69	496	0.028	0.167	-0.103	0.414
Status × distance	4.02*	1106	0.036	0.191	-0.078	0.435
Status × date difference	1.12	1104	0.011	0.103	-0.167	0.359

Repeated measures general linear mixed models with Satterthwaite correction and backward stepwise model selection. The identities of the 2 females as random factors are not shown here (both nonsignificant and removed from the final model). Terms in the final model are shown in bold face. * $P < 0.05$; df, degrees of freedom; CI, 95% confidence interval.

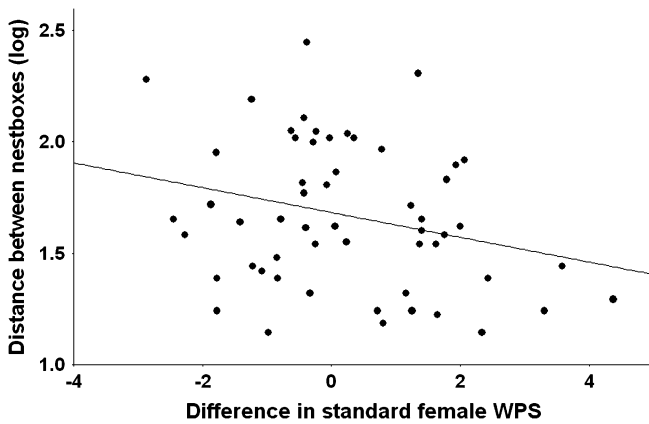


Figure 1
 Relationship between territorial distance and the difference in attractiveness between the mates of the same polygynous male collared flycatcher. Positive differences indicate that the primary female is more ornamented than the secondary female. WPS are standardized for year and binary age.

et al. 1994; Grønstøl et al. 2003), although there are exceptions (Dunn and Hannon 1992; Searcy and Yasukawa 1996). Females may nevertheless decide to enter a polygynous pair-bond, for example, if the better territories of already mated males compensate for the reduction of male parental care (polygyny threshold model; Verner and Willson 1966) or the future attractiveness benefits to young exceed the costs in terms of other fitness components (sexy son hypothesis; Weatherhead and Robertson 1979). However, females may not be free to settle with any potential mate. The risk of good quality breeding opportunities being occupied by other females (Dale et al. 1992) may limit the number of options they can sample (Bensch and Hasselquist 1992; Dale and Slagsvold 1996). Resident females may also behave aggressively toward prospectors (Slagsvold 1993; Sandell 1998). Finally, females may be unaware of the fact that the courting male is already mated (Alatalo et al. 1981; Carlsson 1991; Temrin and Stenius 1994).

These classical theories explaining the costs and benefits of polygynous settlement implicitly assume that the individual quality of females does not differ systematically among mating status categories, which may not be correct (Slagsvold and Lifjeld 1994). For example, it has been suggested that second-

ary females were individuals in bad condition even before mating (Griggio et al. 2003) or old females making their terminal investment in reproduction with the help of the high-quality territories of polygynous males (Forstmeier et al. 2001). There is abundant evidence that ornamental traits in females indicate individual quality and are subject to sexual selection (Amundsen 2000). However, although a recent study suggested that primary females were more attractive than secondary females (Pilastro et al. 2003), the distribution of female ornament expression in long-term data from a polygynous mating system, including monogamous females, has not yet been examined.

The WPS of female collared flycatchers is a partly environmentally determined, age-dependent ornament, and there is observational evidence for a role of this trait at the formation of monogamous pair-bonds (Hegyi et al. 2007). Here, using 6 years of data, we found that when controlling for year, settlement date, and age, there was no difference among the groups of monogamous, primary, and secondary females in WPS. A previous study in our population showed that the lifetime egg production and longevity of females entering a polygynous pair-bond (primary or secondary females) were higher than those of monogamous females, which may reflect different individual quality (Garamszegi, Török, Michl, et al. 2004). Our results show that any such difference in quality between the females of monogamous and polygynous males is not manifested in female WPS. However, when comparing the mates of individual polygynous males, we found that primary females were more ornamented than secondary females and the difference in WPS declined with increasing distance between primary and secondary nest-boxes. Examining the WPS of the 2 females separately, we found that the ornamentation of secondary females increased with territorial distance, whereas there was no such pattern in primary females. The difference in laying date between the 2 nests did not significantly predict the absolute or relative ornamentation of females. When trying to assess the biological significance of these relationships (Nakagawa 2004), the effect size associated with the status × distance interaction in the repeated measures model is small, but the effect of secondary female WPS on territorial distance is close to the medium effect size threshold of 0.3 (Cohen 1988).

There are several potential explanations to these results. For example, the relationship between female WPS and polygyny may reflect a decision by potential secondary females. Large-patched, attractive females may also be more likely to reject a secondary mating status than small-patched females.

Table 3
 Correlates of the territorial distance between the primary and secondary nests of the same polygynous male

	<i>F</i>	df	Variance explained	Effect size (<i>r</i>)	CI lower	CI upper
Year	1.34	5,48	0.122	0.350	0.174	0.504
Female age 1	0.17	1,52	0.003	0.057	-0.132	0.242
Female age 2	0.61	1,52	0.012	0.108	-0.081	0.289
Female WPS 1	0.53	1,52	0.010	0.100	-0.089	0.282
Female WPS 2	4.26*	1,53	0.074	0.273	0.090	0.438
Laying date difference	0.17	1,52	0.003	0.057	-0.132	0.242
Year × WPS 1	0.39	5,42	0.044	0.211	0.024	0.383
Year × WPS 2	1.13	5,43	0.116	0.341	0.164	0.496
Age 1 × WPS 1	0.02	1,50	0.001	0.020	-0.168	0.207
Age 2 × WPS 2	0.29	1,51	0.006	0.075	-0.114	0.259

Repeated measures general linear mixed models with Satterthwaite correction and backward stepwise model selection. The identities of the 2 females as random factors are not shown here (both nonsignificant and removed from the final model). Terms in the final model are shown in bold face. **P* < 0.05; df, degrees of freedom; CI, 95% confidence interval.

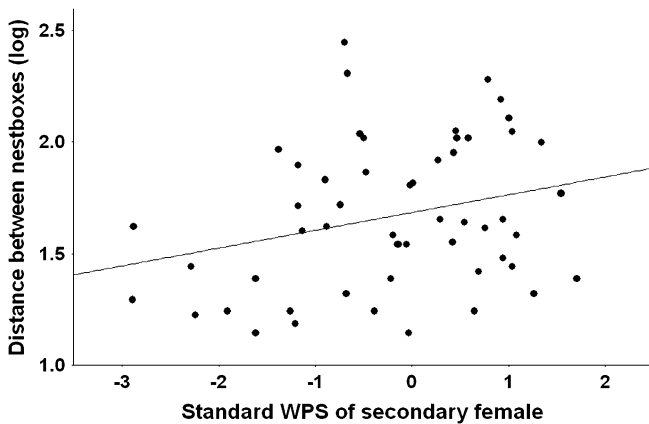


Figure 2

Relationship of the distance between the primary and secondary territories of the same polygynous male collared flycatcher with the ornamentation of the secondary female. WPS are standardized for year and binary age.

If it is easier for prospectors to detect the already mated status of courting males when the primary nest is close by (Slagsvold and Drevon 1999; Slagsvold et al. 1999), the potential of large-patched females to exercise their choice may decrease with territorial distance. However, late-arriving females, the most likely candidates for a secondary position, are under a strong time pressure because of seasonally declining environmental quality (Garamszegi, Török J, Tóth, et al. 2004) and the need to finish breeding and the summer molt before migration to the wintering quarters (Hemborg and Merilä 1998). Thus, these females are unlikely to show a strong choice among potential breeding opportunities. Therefore, female competition is more likely to explain the context-dependent difference in WPS between primary and secondary females.

In flycatchers, it is generally the most ornamented males that become polygynous (Gustafsson et al. 1995; our unpublished data). The heritability of attractiveness may more than compensate primary females for the small disadvantage suffered in terms of current breeding success (Huk and Winkel 2006, but see Gustafsson and Qvarnström 2006). If so, we expect females to compete for the most favorable primary breeding positions, with a potential advantage to elaborately ornamented females (Slagsvold and Lifjeld 1994; Grønseth et al. 2003). However, our results suggest that the difference in ornamentation is driven by the secondary female. This pattern could be explained if highly ornamented secondary females were aggressive and destroyed the nearby breeding attempt of the primary female (Hansson et al. 1997). In this case, only less ornamented females would be found in a nearby secondary position. However, there is no indication of infanticide in our population (Hegyí G, Rosivall B, Szöllös, E, Hargitai R, Török J, personal observation). Another explanation to the pattern in secondary female ornamentation may be the aggression of the resident female. Resident female collared flycatchers are highly aggressive toward intruding females, especially early in the breeding season (Král et al. 1996). A study in our population has shown that the aggression of resident territorial males increased with the WPS of the intruder (Garamszegi et al. 2006). If WPS is a similar trigger of intrasexual aggression in females, we may expect that large-patched females can settle as secondary only beyond a certain distance from the primary nest.

Irrespective of whether our results are explained by intra- or intersexual selection, they strongly suggest a role for a quality-indicating female ornament in a facultatively polygynous mat-

ing system. This has important implications for studies of the adaptive value of polygyny to females. For example, the first variable on which decisions between adaptive and nonadaptive models of polygyny are based is reproductive success (Slagsvold and Lifjeld 1994; Bensch 1996). Female ornamentation often predicts parental quality (Linville et al. 1998; Massaro et al. 2003; Mänd et al. 2005), so its covariation with mating status may obscure or exaggerate the effect of polygyny on reproductive success (also see Forstmeier et al. 2001). More importantly, however, sexual ornamentation generally shows genetic correlation between the sexes (e.g., Price 1996; Roulin and Dijkstra 2003). A potentially major benefit of polygyny to females is offspring attractiveness (sexy sons, Weatherhead and Robertson 1979). Evidence for sexy son effects is very equivocal in birds. For example, sexy son benefits have been detected in both primary and secondary broods of starlings (Gwinner and Schwabl 2005) and in primary but not secondary broods of pied flycatchers (Huk and Winkel 2006). However, no sexy son benefits could be found in a Swedish population of collared flycatchers (Gustafsson and Qvarnström 2006). This inconsistency among studies may partly be due to systematic differences in genetically determined attractiveness among the groups of primary, secondary, and monogamous females. We therefore conclude that to better understand the costs and benefits of mating status and the selection pressures shaping female signals, it is an urgent task to incorporate polygyny in research programs on female sexual ornamentation (Amundsen 2000; Grønseth et al. 2003; Komdeur et al. 2005). In our specific population, experimental studies are needed to determine the role of WPS in female–male and female–female interactions. With more years of observational data, it will also be possible to evaluate the fitness consequences of polygyny to females of different WPS, or, in other words, the importance of the selection pressure that polygyny exerts on female ornamentation.

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