

## Climatic correlates of temporal demographic variation in the tropical hover wasp *Liostenogaster flavolineata*

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**Abstract** Environmental factors, and particularly climate, play an important role in influencing behaviour in many insects. In social species, climate is known to have a strong influence on social traits, but how this manifests itself in tropical ecosystems is poorly understood. In Peninsular Malaysia, the climate is characterised by relatively consistent annual temperatures with wet/dry cycles, and the tropical hover-wasp *Liostenogaster flavolineata* Cameron is active year-round. Newly emerged females can choose to remain at the natal nest and help, or disperse and found their own nest depending on a balance of ecological and demographic factors. We collated long-term adult and brood census data for populations of *L. flavolineata* in Peninsular Malaysia in three different years to investigate temporal variation in demographics (brood and adult numbers) and how this might be related to climatic factors. Our data indicate that there are multiple, temporally distinct peaks of brood production in this population. The number of newly eclosing females and number of mature brood were positively associated with temperature and negatively associated with the number of rain-days during the observation period.

Furthermore, larger females were produced during the peaks of brood production. We speculate how these patterns may influence the staying or leaving decisions of newly emerged females in a primitively eusocial species such as *L. flavolineata*.

**Keywords** Hover-wasps · Phenology · Seasonality · Tropical · Demography

### Introduction

Ecological factors are key components of the causal mosaics that underlie the evolution and maintenance of social behaviour (Korb and Heinze, 2008; Pen and Weissing, 2000). In social insects, which exhibit the greatest diversity of social forms, social behaviour can exhibit high inter- and intra-specific variation with changes in extrinsic factors (e.g., Cronin, 2001; Field, 2008; Hirata and Higashi, 2008; Molet et al., 2008). Climate, in particular, represents a potent extrinsic element, and climatic variation with latitude, altitude, habitat and over time have been shown to influence social behaviour in a range of insects (Cronin, 2001; Eickwort et al., 1996; Fucini et al., 2009; Hirata and Higashi, 2008; Molet et al., 2008; Richards and Packer, 1995) and other arthropods (Purcell and Aviles, 2007). For example, the Allodapine bee *Exoneura robusta* exhibits a higher proportion of eusocial colonies in subtropical environments relative to temperate environments (Cronin and Schwarz, 1999), while the halictine bee, *Lassioglossum (Evyllaes) baleicum* demonstrates variable proportions of eusocial colonies depending on local temperature (Cronin and Hirata, 2003; Hirata and Higashi, 2008). In such cases social variability stems from the seasonal constraints imposed by temperate environments (O'Donnell, 2001; Yamane, 1996).

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Climatic constraints are likely to be very different in the tropics, where temperature is more consistent and differences between seasons are less extreme. As a result, colony activity can be year-round, which can affect the social development of the colony or population (O'Donnell, 2001; Tsuji and Tsuji, 2005). Nonetheless, while not having harsh winters, most tropical environments are under the influence of wet/dry seasonal variation, and intrinsic (social and demographic) factors continue to influence social structure in tropical species (Gadagkar, 1991). Thus, although activity may be continuous, the opportunities available to individuals emerging at different times are potentially diverse. Given that seasonality is clearly important in temperate species, it is surprising that very few studies have examined the impact of seasonal variation on social behaviour in the tropics (though see Tannure-Nascimento et al., 2005; Torres et al., 2009).

Hover-wasps (Stenogastrinae) inhabit the relatively aseasonal environments of southeast Asian rainforests. The hairy-faced hover wasp, *Liostenogaster flavolineata* Cameron, forms nesting aggregations that may comprise hundreds of nests in sheltered places such as under bridges in Peninsular Malaysia (see Field, (2008) and references therein). Nests are inhabited by up to ten females and brood rearing occurs throughout the year. Sociality is facultative, and newly eclosing females can choose whether to remain as helpers at the nest, or disperse to found or join a nest. Inheritance of the dominant, breeding, position provides the best opportunity for direct fitness benefits, and is determined by an age-based queue (Bridge and Field, 2007). Newly eclosing females must thus balance the decision to stay or leave on a combination of factors including (1) the chance of surviving to inherit dominance, based on expected longevity and anticipated work requirements, (2) the anticipated number of helpers on achieving dominance, (3) the costs of dispersal and nest founding (Field, 2008). All of these criteria are under the influence of extrinsic elements such as available forage, predation pressure, weather and local habitat conditions. However, there has been little or no assessment of the potential importance of seasonal variation in environmental variables on the social behaviour of this species (except see Samuel, 1987).

We collated data from several years' work on a population of *L. flavolineata* in Peninsular Malaysia to examine seasonal trends in demographics and possible links with variation in climate. Our aims are twofold: first to investigate if the pattern of brood rearing varied over the observation period and secondly, to assess whether brood and adult numbers are correlated with climatic cycles. We consider in the Discussion how predictable brood-rearing patterns may influence the decisions of newly emerging females.

## Materials and methods

Colonies of *L. flavolineata* were monitored for varied lengths of time between March and October in 1998, 2002 and 2003, at a total of seven sites located near Fraser's Hill, approximately 50 km north of Kuala Lumpur in Peninsular Malaysia (03°43'N, 101°44'E, 1,280 m). Sites were 200–1,500 m apart, located in culverts beneath a montane road between Raub and The Gap. Each site comprised 20–100 colonies, and 3–4 sites were studied in each year (Table 1). The 'observation period' refers to the time for which census data are available, extending from March to October in most cases. All resident wasps were individually marked and had wing lengths measured, and nests occupants were censused and nests surveyed for newly emerged wasps (unmarked wasps that were coincident with hatching pupae) every 2 days. *L. flavolineata* creates mud nests with an open comb and progressively provisions brood, permitting easy monitoring of adult and brood numbers. Brood present in each nest were surveyed approximately every 10 days for numbers of larvae and closed cells (pupae). Eggs were not counted. Egg to pupal development time is approximately 70 days, while the pupal phase is approximately 33 days (Samuel, 1987). Nests newly established during the course of the study were not included in monitoring, and monitoring was discontinued on nests that were abandoned or failed during the study period.

The ambient temperature of Peninsular Malaysia is relatively consistent throughout the year. There are, however, seasonal fluctuations in precipitation that produce relatively high rainfall in two periods during April and October, which may vary to some degree in timing and magnitude (Samuel, 1987). We obtained monthly average climate data for Fraser's Hill during the study period from the Malaysian Meteorological Service.

In the following analyses, we use data from 3 years of observation (1998, 2002 and 2003). The most comprehensive data are from 2003 (monitored from 26 March to 1 September) and these are used to examine intra-annual patterns of brood development. Three sites were monitored in 2003, and these data are subsequently compared to those for 1998 and 2002 (Table 1) to examine inter-annual variability. All adult and brood census data were grouped into 10-day blocks (day-groups) to facilitate analysis, and the sample sizes (number of colonies) and survey schedule are given in Table 1. For further background on sites and field techniques see (Bridge and Field, 2007; Cronin and Field, 2007; Field et al., 1999).

Statistics were performed with R version 2.10.1 (R Development Core Team, 2008). Generalised estimation equation (GEE) analyses were employed as these can account for non-independent data as occur in time series

**Table 1** Number of colonies sampled for brood census and newly eclosing females

	Colonies by day group												Colonies by site										
	March			April			May			June			July			August			September			October	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Brood																							
1998	-	-	-	-	-	-	-	-	45	-	45	45	45	45	45	45	45	-	-	-	-	6	16
2002	-	-	-	-	-	65	67	92	89	-	88	92	85	83	48	37	46	8	38	62	49	-	19
2003	37	48	88	90	59	53	90	51	82	82	80	79	72	-	33	56	-	-	-	-	-	-	37
New females																							
2002	-	-	-	50	50	74	103	149	149	149	149	149	149	149	103	104	103	103	102	104	75	-	46
2003	-	-	32	89	89	89	89	89	89	89	89	89	89	89	62	-	-	-	-	-	-	-	38

Data are pooled for all sites for each day group, and vary because not all colonies were sampled in each period and some colonies failed toward the end of the study. The total number of colonies surveyed during the entire season at each site and over all sites is also given

and non-normal dependent variables such as count data (Halekoh et al., 2006; Zuur et al., 2009). In GEE analysis, we employed a first order correlation structure (ar1) because autocorrelation between samples was likely to diminish with increasing time difference. Poisson errors were assumed for count data (number of brood or adults), and the waves function (by day-group) was used to account for missing data. The following model was employed: [demographic variable] ~ site + temp + rain-days, with data blocked by colony and ordered by day-group. The number of rain-days per month was chosen instead of rainfall as this is probably a better metric for inferring the affect of inclement weather on foraging behaviour.

Relationships between time-series variables were explored using cross-correlation analysis in R. This analysis measures the similarity of two time-series as a function of a time-lag applied to one of them (Crawley, 2007). Thus for covariant time series we expect higher correlation coefficients at time 0 and time-lags corresponding to the periodicity of the cycle. Hartigan’s ‘dip’ test of unimodality was applied to all demographic data series (Hartigan and Hartigan, 1985; Hartigan, 1985). While this test does not specify the form of departure from unimodality, bimodality can be inferred post hoc from the existence of two unambiguous peaks in plotted data (Zhang et al., 2003).

**Results**

Patterns of brood development

Analyses of brood-rearing data from multiple sites with GEE indicated that patterns of brood rearing did not differ between sites except in 1998 (Table 2). Data for 2003 were thus pooled across sites for visualisation, and are summa-

**Table 2** Summary of statistics for GEE analyses of demographic variables assuming a first order correlation structure (ar1)

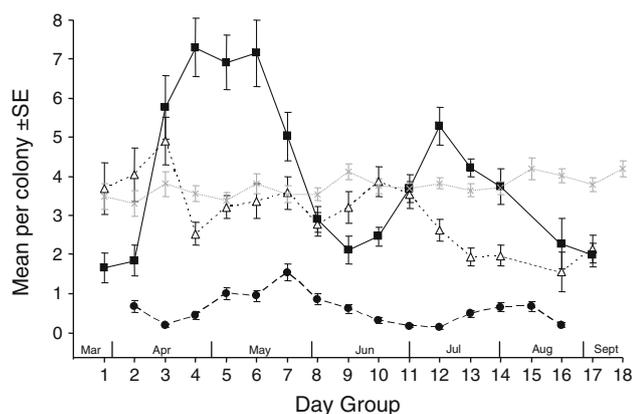
Year	Demographic variable	Wald’s statistic <i>p</i> values		
		Site	Temperature	Rain-days
2003	Larvae	0.318	0.004* (+)	0.506
	Pupae	0.083	0.012* (+)	<0.001* (-)
	New females	0.622	<0.001* (+)	0.006* (-)
	Adult females	0.560	0.101	0.027
2002	Pupae	0.210	<0.001* (+)	<0.001* (-)
	New females	0.012	0.991	<0.001* (-)
1998	Pupae	<0.001*	<0.001* (+)	0.132

*P* values are given for three independent variables tested. Asterisks indicate significance at the 0.05 level after sequential Bonferroni correction. The directionality of relationships is given in parenthesis (sign of Pearson correlations between variables)

rised in Fig. 1. This figure indicates brood-rearing patterns are characterised by two relatively distinct peaks of brood production. Larval numbers are initially high in March and April and again increase in late June, with an overall mean ( $\pm$ standard error) per nest of  $3.00 \pm 0.10$  during the observation period (range 0–19). The mean number of pupae shows a more marked trend, with a large and distinct peak occurring in late April/early May and a second distinct but smaller peak in July (overall mean  $4.28 \pm 0.15$ ; range 0–30). Eclosion of new females follows development of pupae, with distinct peaks in late May and early August (overall mean  $0.59 \pm 0.03$ ; range 0–9). Hartigan's 'dip' test indicated that time-ordered distributions of the number of larvae, pupae and newly eclosing females departed significantly from unimodality ( $p < 0.001$  in all cases), with bimodality strongly suggested for pupae and new females in Fig. 1.

The mean number of adult females per nest was relatively invariant, with only a minor temporary increase in June following the highest eclosing of new females (overall mean  $3.52 \pm 0.05$ ; range 1–9). The variation in mean number of adult females per colony is, however, less than 0.5, despite up to 1.5 new females eclosing per nest in May. Thus, the available data suggest that production of new females does not result in an increase in colony size in existing nests.

It is also worth noting the discrepancy between numbers of pupae and numbers of eclosing adults (overall means of 4.28 vs. 0.59), which can be explained as follows: females were scored as 'newly eclosed' when the census of an unmarked female coincided with disappearance (assumed to reflect hatching) of a pupa. Although it is not possible to more accurately track the eclosion of adults without constant monitoring of all nests, the approach used does not



**Fig. 1** Mean ( $\pm$ standard error) number of larvae (*open triangles, dotted line*), pupae (*closed squares, solid line*), newly eclosing females (*closed circles, dashed line*) and adult females (*crosses, dotted grey line*) per colony during 2003. Data are summarised into 10-day group throughout the observation period and pooled over all sites. The number of colonies for each sample is given in Table 1

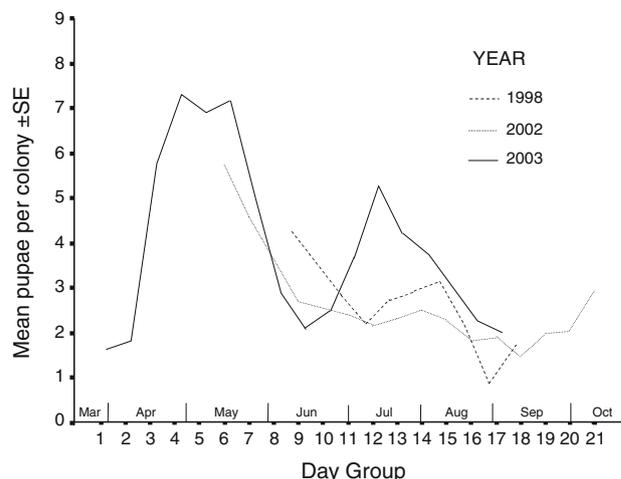
permit us to account for pupae that were destroyed or failed, adults that left the colony or died just after eclosing, and males. We never observed pupae being destroyed during many hours of observation but, as males usually leave the nest soon after reaching adulthood (Field, 2008), it was not possible to accurately quantify the number of males eclosing (see also Field et al., 1999). It is also impossible to distinguish between dispersal and early mortality. The difference between numbers of pupae and numbers of new adults thus comprises all these cryptic data. Nonetheless, it remains clear that many of the newly eclosed females that were recorded did not remain at the natal nest, as evidenced by the difference between numbers of newly eclosing females and adult females per nest.

#### Variation between years

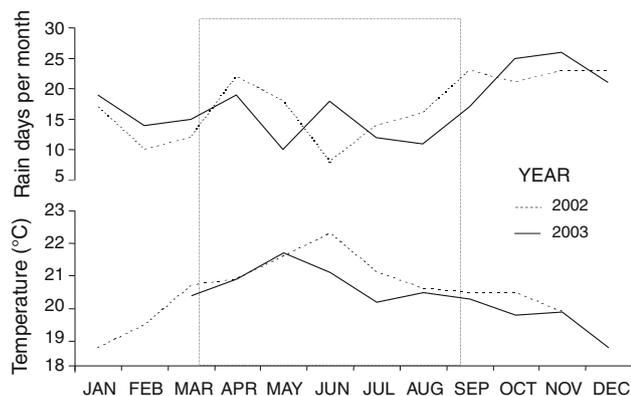
The number of pupae per nest provided the most distinct trend with respect to patterns of brood development and hence is used to compare data between years in Fig. 2. Data from all years indicate a similar pattern of two peaks of brood production, though the data for 1998 are incomplete and the data for 2002 lack strong evidence of a second brood. These data suggest that the overall pattern of brood rearing did not differ between years, though the magnitude and timing of trends may vary.

#### Effect of climate

Climate data for 2003 and 2002 are summarised in Fig. 3 and suggest that the observation period occurs during the peak of annual temperatures, and between wetter periods in April and October. In 2003, rain-day data exhibit two peaks in April and June, whereas there is only a single peak in 2002. Analyses with GEE indicated significant



**Fig. 2** Mean number of pupae per colony throughout the observation period for all sites in 1998, 2002 and 2003



**Fig. 3** Climate variables in 2002 and 2003. Climate data given are mean rain-days per month (*top*) and mean ambient temperature (*bottom*) for 2002 (*dashed line*) and 2003 (*solid line*) for Fraser's Hill, Pahang, Malaysia. The *box* indicates the approximate extent of phenology data presented in Fig. 1

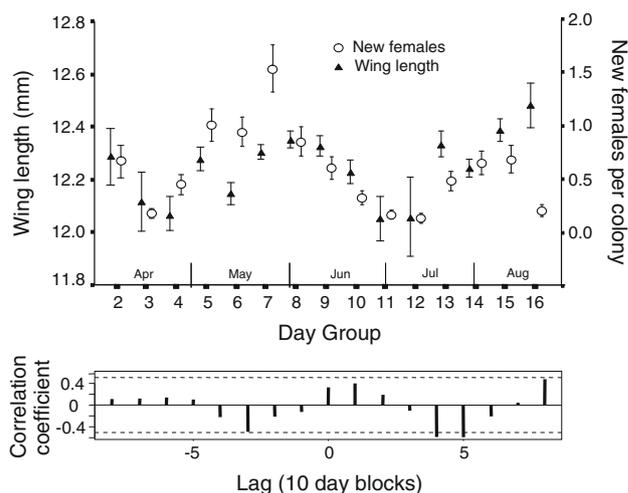
relationships between climate and brood data in the majority of tests for 2003 (Table 2). Specifically, numbers of pupae and new females, which exhibit the clearest trends, were positively associated with temperature and negatively associated with the number of rain-days. In contrast, there is no relationship between climate data and the number of adult females. Brood data are also associated with climate variables in 2002 and 1998, though data vary between sites in 1998 and show no association between temperature and new females in 2002.

#### Timing of eclosion and female size

The size (as indicated by wing-length) of newly eclosing females varied over the observation period, and this variation is summarised relative to the number of females eclosing per colony in Fig. 4 for 2003. Figure 4 suggests a strong relationship between timing of adult eclosion and wing length, with the largest females produced at the time when most females are eclosing. This relationship was explored with a cross-correlation analysis, the result of which presented in Fig. 4, and suggests a relationship between the two variables at a period of 4 units (40 days). Put another way, whereas wing-length of females did not differ between first and second emergence peaks of new females (day-groups 5–9 and 13–16, respectively), it was significantly greater during these peaks than at other times (Kruskal–Wallis  $\chi^2_2 = 20.15$ ,  $p < 0.001$ ).

## Discussion

Colony activity can occur year-round in tropical social insects, which can influence the social development of the colony or population relative to temperate-zone species



**Fig. 4** Variation in wing-length and number of eclosing females ( $\pm$ standard error) throughout the observation period in 2003. Also shown is the result of a cross-correlation function analysis for the two variables, indicating a relationship with a 40 day lag period. *Dashed lines* indicate 95% confidence limits

(O'Donnell, 2001; Tsuji and Tsuji, 2005). Studies of inter- and intra-specific behavioural variation in insects have, however, suffered a temperate bias to date. *L. flavolineata* inhabits the relatively aseasonal environments of Peninsular Malaysia. While brood rearing occurs throughout the year at the sites studied (Field, 2008), there can be variation during the year in group size, brood numbers and the frequency of nest founding (Field, 2008; Samuel, 1987; Shreeves and Field, 2002). This can lead to very different opportunities for individuals eclosing at different times, and has the potential to influence the expression of social behaviour.

The data presented here indicate that during the period for which nests were observed, colonies exhibit two distinct periods of increased brood output, the first in late May and the second in August. These peaks occur during the warmest part of the year and between two wetter periods. The relationship between demographic and climatic variables within years suggests that this inter-annual variation could at least in part be environmentally driven. Our data do not cover the entire annual cycle, but a previous study of this species includes the period outside that covered by our observations: Samuel, (1987) monitored colonies from 1978 to 1984 at a lower-altitude site approximately 60 km south of the present study. Samuel, (1987) reported that, as with our study, maximum numbers of brood varied seasonally. Combined with our data, this suggests that brood production in *L. flavolineata* waxes and wanes through several annual cycles, and that these are consistent between years. Hence, there would appear to be a predictable seasonal pattern of variation in colony demography.

Given that predictable seasonal demographic patterns exist, we can speculate about how they might influence the options for emerging females in *L. flavolineata*. It is worth first outlining some life-history particulars of this species: whereas most independently founding (non-swarming) wasps, including tropical species, have a determinate colony cycle, with recurring phases of founding, growth, and decline (Gadagkar, 1991; Ito and Kasuya, 2005; West-Eberhard, 1969), hover-wasp colonies do not decline and are thus potentially immortal (Field, 2008). Hence, whereas strong time constraints operate on individuals in temperate societies, with late emerging females more constrained than earlier emerging females (because of seasonal limitations), in *L. flavolineata* this is not the case. Thus, while opportunities for dispersal are likely to vary seasonally, there is no absolute time limit on the option to disperse. Secondly, *L. flavolineata* has a strict age-based queue to inherit the dominant, egg-laying position (Bridge and Field, 2007). This has the effect of removing (or at least minimising) the influence of physiological constraints such as size on the probability of inheritance. Indeed, there is no evidence that size is correlated with dominance in *L. flavolineata* (Field et al., 1999; Sumner et al., 2002). Finally, relatedness in *L. flavolineata* does not vary with inheritance rank (Bridge and Field, 2007), and thus cannot form a basis for behavioural decisions. Intra-colony relatedness is anyway moderately high, and generally in the range 0.4–0.5 (Field, 2008). While insurance-based advantages (Field, 2008; Field et al., 2000) to helping are probably important in *L. flavolineata*, they are unlikely to vary seasonally because group size was almost constant during monitoring (thus brood are not threatened with starvation).

These factors aside, there is still scope for predictable seasonal variation in the number of adults eclosing, colony size, brood numbers, and female size, to lead to different opportunities for eclosing females depending on timing of emergence. The benefits of joining an inheritance queue will depend on the chance of surviving until inheritance (i.e., the length of the queue) and the anticipated colony size (i.e., work force) at inheritance (Shreeves and Field, 2002). Information on queue length is presumably immediately available to newly emerging females. All else being equal, there may be a maximum queue length beyond which joining becomes unprofitable (e.g., Kokko and Johnstone, 1999; Shreeves and Field, 2002), which may explain the lack of fluctuation in colony size beyond the mean of around 3.5 females per nest. Nonetheless, if females are able to predict seasonal trends in colony growth, this may favour helping when colony size is predicted to increase toward the time of inheritance, even when queues are longer (Shreeves and Field, 2002).

The alternative to helping, dispersal, is also presumably under seasonal influence, though quantifying this is more

problematic. It is impossible to accurately quantify dispersal because of the difficulty in distinguishing between dispersal and mortality. This is further complicated because lower ranked wasps, which are presumably more likely to disperse, also spend more time off the nest foraging, which increases the likelihood they will be missed during a census of nest occupants (Field et al., 1999). Our data indicate that numbers of eclosing females fluctuated seasonally and that this did not lead to corresponding increases in colony size. If we assume that mortality of nest residents is more or less consistent year-round, this implies that dispersal maxima occur when adult eclosion rates are highest. Interestingly, it is at this time that the largest females also eclose. Because *L. flavolineata* relies on a gerontocracy for inheritance, there is no size advantage for wasps joining the inheritance queue. This begs the question of why larger wasps are reared in seasonal pulses, when resources could presumably be allocated toward producing more, smaller wasps instead. Nests are almost never at carrying capacity (i.e., all available nest cells are rarely occupied with brood) and thus space for rearing more brood is not likely to be a constraint (Field et al., 1998; Cronin and Field, pers. obs). One possibility is that larger wasps represent a dispersing morph (e.g., as in mole-rats O’Riain et al., 1996), though assessment of this possibility suffers from the same difficulties as for quantifying dispersal per se.

Dispersal is, however, only one alternative. Indeed, the available data suggest that only a minority of leavers start their own nests, adopt vacant nests or join other nests (Field, 2008), while others become nest-less ‘floaters’ and remain on the fringes of nesting aggregations. Newly emerged females that join nests as low ranking helpers probably suffer very high mortality because of high foraging rates, and thus floating and awaiting a more attractive vacancy may be a viable alternative in an environment where there is no truncation of life-spans associated with severe winter weather. Floaters also ‘test’ resident wasps, and can join established colonies by usurping high ranks (Cronin and Field, 2007). It is possible that size provides some advantage in usurpation and dispersal that is not applicable to joiners.

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