

# Effects of floral sexual investment and dichogamy on floral longevity

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## Abstract

### Aims

Floral longevity, the duration that a flower remains open and functional, varies greatly among species. Variation in floral longevity has been considered to be optimal strategy for resource allocation under different ecological conditions, mainly determined by the rates of pollination and cost of flower maintenance. However, it is unclear whether an intrinsic factor, floral sexual investment, constrains evolution of floral longevity. The theoretical model also predicts that dichogamy favors long-lived flowers, but empirical studies to test this prediction remain unexplored.

### Methods

To examine the effect of floral sexual investment on floral longevity, we measured flower size together with pollen and ovule production in 37 sympatric flowering plants in a natural community. The duration of the female and male phase in 21 protandrous species and floral longevity of the other 16 adichogamous species were documented in the field.

### Important Findings

Floral longevity varied from 1 day to 15 days, while pollen number per flower varied from 643 to 710 880 and ovule number per

flower from 1 to 426 in the 37 species. Flower size was correlated with pollen production as well as ovule production. Floral longevity was positively related to pollen production but not to ovule production. Consistent with the prediction that dichogamy favors long-lived flowers, we found the floral longevity of protandrous species was significantly longer than that of adichogamous species. In the protandrous species, pollen production per flower was observed to be positively related to male duration, while ovule production was not related to female duration. Our analyses of variation in floral longevity and sexual investment among different species suggest that the floral sexual investment could be an intrinsic factor contributing to the selected floral longevity, particularly the male phase, and that high pollen production could potentially increase pollen removal, i.e. male productive success.

**Keywords:** floral longevity, female phase duration, male phase duration, flower size, floral sexual investment, dichogamy

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## INTRODUCTION

Floral longevity, the duration of time that a flower remains open and functional, varies greatly from a few hours to months among different species (Schoen and Ashman 1995). Early work on floral longevity suggested that multiple factors could potentially affect its variation and evolution, including phenology, elevation, pollinator type, breeding system and floral gender (Primack 1985). From the perspective of a resource allocation strategy, different floral longevity have been shown to be optimal balance between maintenance of existing flowers and the construction of new flowers (Ashman and Schoen 1997; Schoen and Ashman 1995). Long-lived flowers could be favored if the cost of floral maintenance is lower and longer flowering duration provides more opportunities to be disseminate and receive

pollen (Ashman and Schoen 1994, 1996; Schoen and Ashman 1995). Numerous studies have showed that floral longevity of a given species was mainly determined by the fulfillment of male and female fitness (Abdala-Roberts *et al.* 2007; Blair and Wolfe 2007; Castro *et al.* 2008; Clark and Husband 2007; Evanhoe and Galloway 2002; Sato 2002; Stpczyńska 2003).

Considering resource allocation strategy of a species, one cannot ignore the prime cost of the flower. For example, larger flowers of a given species may produce more pollen grains and ovules. To construct such a large new flower would involve a high cost if pollen grains remain in a flower, e.g. under a scarcity of pollinators. Between the two sequentially blooming flowers in *Aquilegia buergeriana*, pollen number of the first open flower was significantly higher and lasted longer than that of the second flower, perhaps as a strategy to maximize male

reproductive success in the first flower (Itagaki and Sakai 2006). An earlier observation suggested that floral longevity was likely related to pollen production per flower (Kerner von Marilaun 1895). On the other hand, in a survey of 110 species from a Costa Rican forest, Stratton (1989) observed that floral longevity was related to both flower size and ovule number per flower. Therefore, it remains unclear whether floral longevity correlates with floral sexual investment. Dichogamy, the temporal separation of male and female phase within a flower, is widespread among the angiosperms. Dichogamy may be selected to reduce sexual interference between pollen removal and receipt (Lloyd and Yates 1982), meanwhile dichogamous flowers may involve longer duration than adichogamous species (Schoen and Ashman 1995). To our knowledge, this prediction has not been tested among species in any community.

To explore whether floral sexual investment constrains evolution of floral longevity, we measured flower size, pollen and ovule production per flower in 37 sympatric flowering species, including 21 protandrous (stigma receptive after anther dehiscence) and 16 adichogamous species. A measurement of floral longevity in these species also allowed us to test the prediction whether dichogamy favors long-lived flowers.

## MATERIALS AND METHODS

### Study site and species

This study was conducted in 2012 at the field station, Shangri-La Alpine Botanical Garden (27°54'5"N, 99°38'17"E, 3300–3350 m above sea level), Yunnan Province, southwest of China. In a 100×200 m meadow, over 200 native species flowered from June to August (see Huang et al. 2015). Thirty-seven sympatric species from 13 families and 29 genera were investigated. These were abundant in the community and phylogenetically diverse, allowing a comparison of floral longevity among montane species that was investigated in other areas (Primack 1985).

### Floral longevity

To measure floral longevity of a single flower from 37 species, for each species we randomly labeled 20 floral buds from 10 to 20 individual plants. We monitored floral morphology twice a day, in the morning (ca. 09:00 am) and at sunset (ca. 19:00 pm), recording when the tepals unfolded, when anthers began to dehisce, when the stigma was exposed or wilted in protandrous species, up until the time when the perianth withered or abscission occurred. Floral longevity was measured as the time from flower unfolding to flower withering (closure, wilting or abscission) (Evanhoe and Galloway 2002; Liu and Huang 2013). In protandrous species, the male phase was the time elapsed from dehiscence of the first anther up until dehiscence of all anthers, or to the opening of the stigmatic lobes (e.g. *Adenophora khasiana*) or exposure of the stigma (e.g. *Aconitum piepunense*, see Itagaki and Sakai 2006). The female phase was the time elapsed from stigmatic lobe opening or stigma exposure up until floral senescence or abscission (e.g. *Salvia przewalskii*).

### Measurement of flower size

To estimate flower size of each species, flower traits of 50 completely opened flowers randomly from 25 to 30 individuals were measured with a digital caliper. Following Hegland and Totland (2005)'s method, flower size of each species was calculated according to the flower shape. Flowers were classified into three main types: for flowers with circular outline (e.g. *Potentilla lancinata*), we calculated the size using the formula  $\pi r^2$ , where  $r$  is one half of the corolla diameter (width). For flowers with tubular structure (e.g. *A. capillaris*) we used the formula  $2\pi rD$ , where  $D$  is corolla tube length, and for the third type (which had both tubular structure and flat corolla) we used the formula  $L \times W + \pi BD$  (e.g. *Pterocephalus hookeri*) or  $\pi r^2 + \pi BD$  (e.g. *Gentiana haynaldii*), where  $L$  and  $W$  are the length and width of the square-shaped flat corolla and  $B$  is the bore diameter of the tubular structure according to its shape. We calculated the sizes of flowers from two leguminous plants using formula  $L \times W + l \times w$ , where  $L$  and  $W$  are the length and width of the banner, and  $l$  and  $w$  are the length and width of the wing (see Table 1 for formulae used for each species).

### Pollen and ovule number

To investigate whether floral sexual investment affects floral longevity, we measured pollen and ovule production per flower in the 37 species. In each species, 20 nearly opening floral buds were randomly collected each from one individual plant and immediately transferred to microcentrifuge tubes containing FAA solution (formalin:acetic acid:alcohol, 5:5:90). Anthers were split and diluted in 1 or 2 ml of ethanol solution, depending on the total number of pollen grains. The pollen suspension was oscillated for ~60 s and five sample drops were immediately placed on a clean slide. Pollen grains were counted under a microscope, while ovules were counted using an anatomical lens.

### Data analysis

To test the relationship between floral longevity and pollen number, ovule number and flower size, we performed regression analyses. All data after log-transformation, the values were normally distributed. One-way analysis of variance was used to test the difference of floral longevity between dichogamous and adichogamous species and the difference of duration between male and female phase in protandrous species. Given that some species had only one ovule, 1 was added to the raw data of ovule number in all species before log-transformation. All statistical analyses were done using SPSS 17.0 (SPSS Inc., Chicago, IL, USA).

## RESULTS

The measured floral traits varied greatly among sympatric species (Table 1). Flower size spanned several orders of magnitude, from <6 mm<sup>2</sup> in *Pimpinella diversifolia* to around 1400 mm<sup>2</sup> in *Delphinium yuanum* (1399.52). Mean number of

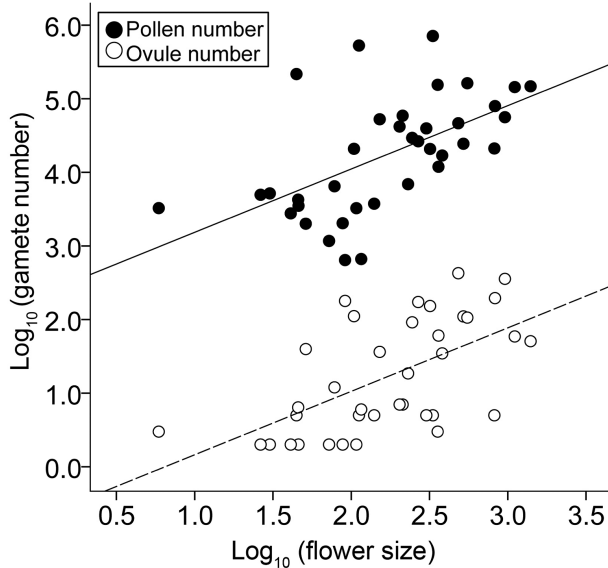
**Table 1:** flower size (mm<sup>2</sup>), pollen number, ovule number and phase duration (days) for each species

Species	Flower formula	Flower size	Pollen number	Ovule number	Male phase	Female phase	Floral longevity
<i>Aconitum piepunense</i>	$L \times W + \pi BD$	1107.83	143 865	58	4.83	3.83	8.67
<i>Adenophora capillaris</i>	$2\pi rD$	318.95	20795	152	2.00	3.96	5.96
<i>A. jasionifolia</i>	$2\pi rD$	1755.86	79 395	194	2.26	2.29	4.55
<i>A. khasiana</i>	$2\pi rD$	1488.44	56 097	356	1.25	2.80	4.05
<i>Allium cyathophorum</i>	$2\pi rD$	213.16	58 795	6	5.52	9.33	14.90
<i>A. wallichii</i>	$\pi r^2$	203.74	41 851	6	2.58	5.92	8.50
<i>Aster oreophilus</i>	$2\pi rD$	30.19	5177	1	1.10	3.45	4.55
<i>A. vestitus</i>	$2\pi rD$	26.38	4961	1	1.40	2.40	3.80
<i>Cyananthus delavayi</i>	$\pi r^2 + \pi BD$	381.46	16 949	34	2.55	2.82	5.36
<i>Delphinium yuanum</i>	$L \times W + \pi BD$	1399.52	147 429	50	7.14	4.07	12.93
<i>Dipsacus asperoides</i>	$L \times W + \pi BD$	88.20	2037	1	1.32	2.89	4.16
<i>Gentiana haynaldii</i>	$\pi r^2 + \pi BD$	483.28	46 435	426	4.11	3.22	7.33
<i>Halenia elliptica</i>	$2\pi rD$	230.94	6908	18	1.50	3.10	4.60
<i>Pimpinella diversifolia</i>	$\pi r^2$	5.90	3270	2	3.88	4.38	8.25
<i>Polygonum runcinatum</i>	$2\pi rD$	77.32	1169	1	1.45	4.64	6.09
<i>Pterocephalus hookeri</i>	$L \times W + \pi BD$	107.85	3262	1	1.10	4.90	6.00
<i>Silene asclepiadea</i>	$\pi r^2 + \pi BD$	245.35	29 398	91	3.35	3.00	6.35
<i>S. chungtienensis</i>	$\pi r^2 + \pi BD$	268.11	26 427	172	2.89	6.53	9.26
<i>S. gracilicaulis</i>	$\pi r^2 + \pi BD$	361.09	11 896	60	2.00	4.65	6.65
<i>S. yunnanensis</i>	$\pi r^2 + \pi BD$	521.01	24 472	109	3.28	4.00	7.28
<i>Swertia punicea</i>	$\pi r^2$	104.14	20 888	110	1.04	1.63	2.67
<i>Cynoglossum amabile</i>	$\pi r^2 + \pi BD$	112.10	527 320	4			5.19
<i>Epilobium wallichianum</i>	$\pi r^2$	91.34	643	178			2.50
<i>Euphrasia regelii</i>	$2\pi rD$	51.25	2005	39			3.43
<i>Geranium sibiricum</i>	$2\pi rD$	115.88	665	5			1.00
<i>Ixeridium biparum</i>	$2\pi rD$	46.07	3518	1			1.00
<i>Lotus corniculatus</i>	$L \times W + l \times w$	152.09	52 601	35			7.25
<i>Microula sikkimensis</i>	$\pi r^2 + \pi BD$	44.71	216 420	4			3.60
<i>Onosma confertum</i>	$2\pi rD$	332.15	710 880	4			2.84
<i>Phlomis tatsienensis</i>	$2\pi rD$	171.21	39 540	4			5.94
<i>Picris hieracioides</i>	$2\pi rD$	41.11	2770	1			5.50
<i>Potentilla lancinata</i>	$\pi r^2$	551.74	162 480	105			4.72
<i>Prunella vulgaris</i>	$2\pi rD$	140.22	3753	4			2.10
<i>Salvia przewalskii</i>	$2\pi rD$	3986.35	21 116	4			2.24
<i>Spenceria ramalana</i>	$\pi r^2$	356.77	154 615	2			4.67
<i>Stellaria yunnanensis</i>	$\pi r^2$	78.22	6471	11			2.17
<i>Trifolium repens</i>	$L \times W + l \times w$	45.84	4256	5			3.55

Flower formulas for calculations of area of flower size:  $\pi r^2$  ( $r$  = corolla radius) for flowers with circular outline,  $2\pi rD$  ( $r$  = tube radius,  $D$  = tube depth) for flowers with tubular structure,  $L \times W + \pi BD$  ( $L$  = flat length,  $W$  = flat width of square-shaped part;  $B$  = bore diameter,  $D$  = depth of tubular part) or  $\pi r^2 + \pi BD$  ( $r$  = radius of circular part;  $B$  = bore diameter,  $D$  = depth of tubular part) for the third type which had both tubular structure and flat corolla and  $L \times W + l \times w$  ( $L$  = length,  $W$  = width of banner;  $l$  = length,  $w$  = width of wing) for the two leguminous plants.

pollen grains per flower was  $71\,906 \pm 23\,839$  (mean  $\pm$  standard error), ranging from 643 in *Epilobium wallichianum* to 710 880 in *Onosma confertum*; while mean number of ovules was  $61 \pm 16$  ranging from 1 to 426. Overall mean floral longevity of 37 species was  $5.39 \pm 0.49$  days. While floral longevity was only 1 day in two species (*Geranium sibiricum* and *Ixeridium biparum*), it could be up to an average of 15 days in *Allium cyathophorum*.

Both pollen ( $r = 0.515$ ,  $F_{1,35} = 12.66$ ,  $P = 0.001$ ) and ovule number ( $r = 0.502$ ,  $F_{1,35} = 11.78$ ,  $P = 0.002$ ) were positively correlated with flower size (Fig. 1), indicating that larger flowers generally associated with more gametes, i.e. higher investment of sexual resources. Among 21 dichogamous species, male phase duration ( $r = 0.504$ ,  $F_{1,19} = 6.49$ ,  $P = 0.002$ ) and floral longevity ( $r = 0.353$ ,  $F_{1,35} = 5.00$ ,  $P = 0.032$ ) were positively correlated with the flower size but female phase duration was

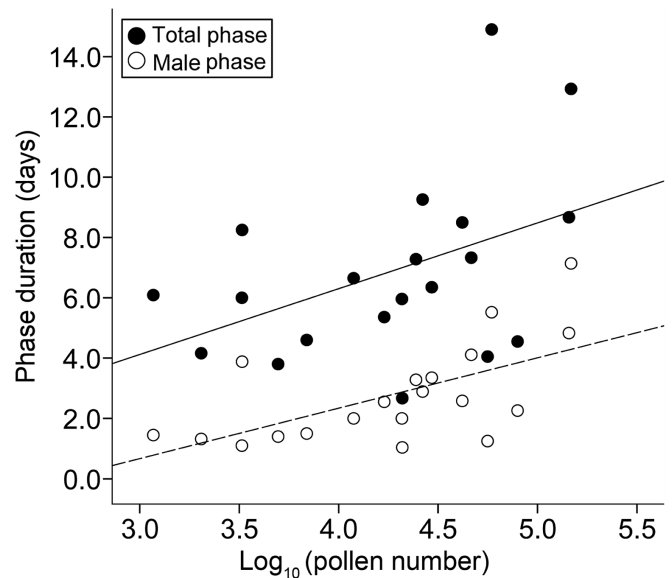


**Figure 1:** bivariate plot showing the relationship between flower size and pollen (closed circles, solid line) and ovule (open circles, dashed lines) number in 37 sympatric species.

not ( $r = 0.129$ ,  $F_{1,19} = 0.32$ ,  $P = 0.577$ ). Pollen production per flower in dichogamous species was positively correlated with duration of male phase ( $r = 0.629$ ,  $F_{1,19} = 12.43$ ,  $P = 0.002$ ) and floral longevity ( $r = 0.345$ ,  $F_{1,35} = 4.72$ ,  $P = 0.037$ ; Fig. 2), but not with female phase duration ( $r = 0.108$ ,  $F_{1,19} = 0.23$ ,  $P = 0.641$ ). By contrast, ovule number was not significantly correlated with male ( $r = 0.301$ ,  $F_{1,19} = 1.89$ ,  $P = 0.186$ ), female phase duration ( $r = 0.217$ ,  $F_{1,19} = 0.94$ ,  $P = 0.345$ ) or floral longevity ( $r = 0.189$ ,  $F_{1,35} = 1.30$ ,  $P = 0.263$ ; Fig. 3). These results suggested that floral longevity was affected by investment in male rather than female function. In support of the prediction of a theoretical model that dichogamy should select for long-lived flowers, we observed that floral longevity of protandrous species ( $6.75 \pm 0.65$  days) lasted significantly longer ( $F_{1,35} = 13.922$ ,  $P = 0.001$ ) than that of adichogamous species ( $3.60 \pm 0.45$  days). Within 21 protandrous species, female phase ( $3.99 \pm 0.37$  days) was significantly longer ( $F_{1,40} = 6.298$ ,  $P = 0.016$ ) than male phase duration ( $2.69 \pm 0.36$  days).

## DISCUSSION

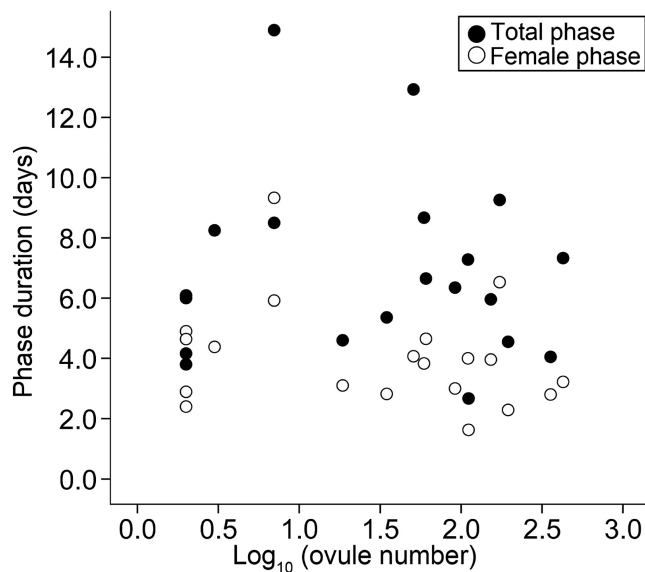
Our investigation has shown that flower size is associated with floral sexual investment, as large flowers likely producing more pollen and ovules. Floral longevity was found to be positively related to pollen number per flower but not to ovule number. This result is consistent with previous observation by Kerner von Marilaun (1895) that floral longevity was associated with pollen production; but partly different from Stratton's survey (1989) that large flowers had longer lifespan and floral longevity was related to ovule production. As predicted by Schoen and Ashman (1995), we observed that



**Figure 2:** bivariate plot showing the relationship between floral longevity (closed circles, solid line) and male (open circles, dashed lines) phase duration and pollen production per flower in 21 protandrous species.

dichogamous flowers lasted longer than adichogamous flowers. Particularly, we found that male duration as well as floral longevity was positively related to pollen number, but female duration as well as floral longevity was not related to ovule number in dichogamous species. These results suggested that floral longevity could be influenced by male investment of flowers.

The overall mean floral longevity of 5.4 days in the alpine area is consistent with the global pattern in which floral longevity of montane species were 4.2–7.8 days (Primack 1985). The mean value of floral longevity of 110 species (2.7 days) in a Costa Rican cloud forest was longer than in tropical lowland species (1 day) (Stratton 1989), suggesting that floral longevity is related to pollinator abundance and activity (Ashman and Schoen 1994). Stratton (1989) divided ovule number from 40 species into three categories (1–5, 5–50, >50 ovules) and calculated mean floral longevity of the three categories (1.60, 1.98, 3.40 days, respectively), and found that species with over 50 ovules tended to have longer flower lifespan than species with few ovules. He also noted that female phase lasted longer than male phase in eight dichogamous species, as we observed here. Therefore, Stratton (1989) proposed that the evolution of floral longevity in those species resulted from maximization of female reproduction. Some studies showed that flower longevity was greatly shortened under artificial pollination, i.e. pollination-induced flower senescence, supporting the hypothesis that floral longevity is influenced primarily by female reproductive success (Blair and Wolfe 2007; Proctor and Harder 1995). However, recent studies showed that there was a minimum longevity for male functions even when female function was completed with enough pollination (Evanhoe and Galloway 2002; Ishii and



**Figure 3:** bivariate plot showing lack of relationship between floral longevity (closed circles, solid line) and female (open circles, dashed lines) phase duration and ovule production per flower in 21 protandrous species.

Sakai 2000; Zhang and Li 2009). For example, flower senescence in a spring herb *Erythronium japonicum* in Japan could be deduced by pollen deposition on the stigma, but the flowers lasted around 13 days and did not abscise during that period (Ishii and Sakai 2000). An experimental pollination showed that floral longevity in *Brassica napus* was governed by pollen removal in which flower senescence was hastened when pollen was removed from the anthers rather than pollen deposition (Bell and Cresswell 1998).

A single pollinator visit to an adichogamous flower may deposit pollen on the stigmas and remove pollen from the anthers, beneficial to both female and male function. Floral longevity of a given species would be determined by the balance of the rates of pollen removal and receipt and costs of floral maintenance (Ashman and Schoen 1994). Dichogamy may be selected for avoiding sexual interference between pollen removal and receipt (Lloyd and Webb 1986). In dichogamous species, however, pollen removal and receipt involve at least two pollinator visits. The rates of pollen removal and receipt would be just a half of adichogamous species, other things being equal. Our comparison of 21 protandrous and 16 adichogamous species from the same community indicated that the former have evolved longer flower lifespan (averaging 3 days longer) than the latter, providing the first empirical evidence in support of the theoretical model of Schoen and Ashman (1995).

Within the six-flowered inflorescence of an alpine ladybell *A. jasionifolia* (Campanulaceae), Liu and Huang (2013) found that temporal decline in floral longevity within the plant was associated with floral sexual investment (both pollen and ovule number, see also Cao *et al.* 2015) in sequentially blooming flowers. In this protandrous species, the decline of floral

longevity was due to a decrease of female phase duration in later flowers rather than male phase duration that did not vary significantly among flowers. In protandrous herb *A. buergeriana* var. *oxysepala*, each plant has 2–3 racemes, and each raceme bears 1–2 flowers. Itagaki and Sakai (2006) found that pollen production was greater in the first produced (distal) flower than in the second produced (basal) flower. Correspondingly the male phase of the first flower lasted longer, and this may provide more opportunities for pollen to be removed.

Bateman's principle (Bateman 1948) has been widely used for understanding sex allocation in flowering plants, implying that male reproductive success is typically limited by access to mates while female reproductive success is limited by resources. In fact, pollen removal from anthers usually requires numerous visits by pollinators but pollen deposition on stigmas usually requires only a few visits. To maximize male reproductive success, plants may evolve gradual pollen presentation strategies that limit the amount of pollen removed from the flower by one pollinator visit (Thomson 2006). Therefore, longer lived flowers would be favored if species have higher pollen production. We observed that floral longevity correlated with pollen production but not ovule production per flower among the 37 sympatric species studied. Particularly, we found male phase duration was positively correlated with pollen production, but female phase duration was not related to ovule production in protandrous species. Such a differential pattern of floral sexual investment and floral longevity has not been illustrated before, awaiting additional studies to further explore the evolution of floral longevity.

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