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9 **Context-dependency of resource allocation trade-offs highlights constraints to the evolution**  
10 **of floral longevity in a monocarpic herb**

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32 **Summary**

- 33 • Floral longevity is a critical component of floral display, yet there is a conspicuous  
34 paucity of empirical research on its evolution within species. Evolutionary models of  
35 floral longevity are grounded in resource allocation theory and propose that selection acts  
36 on heritable variation to optimize longevity in light of competing floral construction and  
37 maintenance costs. Key assumptions remain untested within wild species.
- 38 • We measured maximum floral longevity alongside protandry, flower size, flower  
39 number, and flowering rate across families of the monocarpic herb *Sabatia angularis*  
40 grown under high and low resources. We evaluated genetic variation, plasticity, and  
41 correlations between display traits, including fundamental resource-allocation trade-offs  
42 and their interactions with resource availability.
- 43 • All display traits showed significant genetic variation. Resource availability influenced  
44 mean floral longevity and flower number, with genetic variation in these responses.  
45 Importantly, both floral longevity-flower number and flower number-size trade-offs were  
46 significant and stronger under low resources.
- 47 • This study reinforces the application of resource-allocation theory to floral display trait  
48 evolution. Our work highlights the context-dependency of trade-offs and the potential  
49 importance of plasticity in resource allocation, with plants investing in the construction of  
50 new flowers at faster rates when resources are high rather than in the maintenance of  
51 longer-lived flowers.

52  
53 **Keywords:** evolutionary constraints, floral lifespan, floral longevity, genetic correlations,  
54 heritability, plasticity, resource allocation strategy, trade-off

55

## 56 **Introduction**

57           Floral longevity, the length of time that a flower remains open and functional, is a key  
58 trait influencing reproduction because it governs a plant's mating opportunities. Lengthening  
59 floral lifespan can increase plant fitness by providing more time that will ensure sufficient  
60 outcross pollen receipt, increase donor diversity and promote pollen export (Primack, 1985;  
61 Ashman & Schoen, 1994; Rathcke, 2003; Marshall *et al.*, 2010; Eisen *et al.*, 2017). However,  
62 throughout their development and lifespan, flowers demand carbon, nutrient, and water resources  
63 (Nobel, 1977; Bazzaz *et al.*, 1979; Southwick, 1984; Ashman & Schoen, 1997; Galen, 2000).  
64 Consequently, resource allocation theory has been invoked to explain how optimal floral  
65 longevity is shaped by natural selection, with fitness determined by the balance between the rates  
66 of male and female fitness accrual and floral costs (Ashman & Schoen, 1994; Schoen &  
67 Ashman, 1995; Charnov, 1996). Floral longevity varies markedly across species, lasting from a  
68 single day up to weeks (Primack, 1985; Stratton 1989; Ashman & Schoen, 1994; Steinacher &  
69 Wagner, 2010). And, consistent with predictions related to fitness gains, longevity also varies  
70 across species in relation to pollination conditions and to mating system, with those experiencing  
71 high pollen limitation having greater mean floral lifespans (Ashman & Schoen, 1996; Rathcke,  
72 2003); and reduced floral lifespans in selfing compared to outcrossing species (Weber &  
73 Goodwillie, 2013). However, our understanding of the microevolutionary process that lead to  
74 such differences among species is hampered by a lack of empirical data on what generates  
75 variation in floral longevity *within* species and on the trade-offs that may constrain its evolution.

76           Indeed, despite being a critical component of floral display, there is a conspicuous  
77 paucity of investigations of genetic variation in floral longevity that becomes even more patent  
78 when compared to the body of work on genetic variation in other floral traits such as flower size  
79 and number (Ashman & Majetic, 2006; Conner *et al.*, 2014). In fact, current data on the  
80 heritability of floral longevity is derived solely from studies on species of horticultural interest  
81 (Verlinden, 2006). For example, horticultural studies have evaluated postharvest floral longevity,  
82 reporting estimates of narrow sense heritability ranging from 0.0 to 0.77 (Harding *et al.* 1981;  
83 Krahl & Randle, 1999; van der Meulen-Muisers *et al.*, 1999; Schroeder & Stimart, 2001). Fewer  
84 have explored the heritability of intact floral longevity, which would be more directly relevant to  
85 the evolution of floral longevity in wild species. Of those, two demonstrated significant additive  
86 genetic effects underlying variation in intact floral longevity (Krahl & Randle, 1999; Howard *et*

87 *al.*, 2012), while a third showed that postharvest floral longevity is positively correlated to intact  
88 floral longevity in at least one species (Martin & Stimart, 2003). Thus, from this limited  
89 evidence, we know that a response to selection on floral longevity is possible in at least some  
90 horticultural species.

91 Floral longevity should be constrained through trade-offs with other floral display traits if  
92 it evolves as part of a resource allocation strategy. Models of floral longevity explicitly  
93 incorporate and hinge upon a conflict between investments of fixed resources in floral  
94 construction vs. maintenance costs (Ashman & Schoen 1994; Schoen & Ashman, 1995). Yet to  
95 our knowledge this central assumption has not been tested within species. Even studies  
96 evaluating the classic expected trade-off between flower number and flower size have provided  
97 mixed evidence within and across species (e.g., Worley & Barrett, 2000; Worley *et al.*, 2000;  
98 Caruso, 2004; Delph *et al.*, 2004; Ashman & Majetic, 2006; Caruso, 2006; Sargent *et al.*, 2007;  
99 Goodwillie *et al.*, 2010); questioning the validity of assuming that resource allocation trade-offs  
100 drive floral evolution more generally. Still, functional correlations between floral longevity and  
101 other floral traits could constrain the evolution of floral longevity. In particular, floral longevity,  
102 dichogamy, floral display, flowering duration, and flowering rate may be integrated. Dichogamy  
103 sets a minimum longevity to allow for separation of the male and female phase (Schoen &  
104 Ashman, 1995; Ishii & Sakai, 2000); and could drive variation in total floral lifespan, while  
105 longer-lived flowers would contribute to greater floral display and longer flowering duration at  
106 the plant level (Ishii & Sakai, 2001; Harder & Johnson, 2005; Spigler, 2017). Given dichogamy  
107 influences sexual interference and self-fertilization (Lloyd & Yates, 1982; Lloyd & Webb, 1986;  
108 D. Charlesworth & B. Charlesworth, 1987; Bertin & Newman, 1993; Barrett, 2002) and display  
109 size influences the rate of geitonogamy (Klinkhamer & de Jong, 1993; Barrett & Harder, 1996;  
110 Snow *et al.*, 1996), selection on these traits is expected to be strong. Consequently, a response to  
111 selection for increased floral longevity could be hindered if at odds with selection on these other  
112 important traits, particularly in species with strong inbreeding depression.

113 Because floral longevity can be highly plastic, non-genetic factors likely play a large role  
114 in modulating its evolution. Evidence from a wide variety of taxa including horticultural and  
115 wild species has repeatedly shown how pollination can induce corolla wilting (e.g. Gori, 1983;  
116 Primack, 1985; Webb & Littleton, 1987; van Doorn, 1997; Evanhoe & Galloway, 2002; Castro  
117 *et al.*, 2008, Spigler, 2017). Floral longevity also can be influenced by abiotic conditions such as

118 water availability, altitude, and temperature (e.g., Vesperini & Pacini, 2005; Arroyo *et al.*, 2013;  
119 Jorgenson & Arathi, 2013; Spigler & Kalisz, 2013; Trunschke & Stocklin, 2017). Consideration  
120 of plasticity of floral longevity in response to resource availability may be particularly important  
121 regarding the evolution of floral longevity as a type of resource allocation strategy. For example,  
122 if allocation toward floral maintenance and construction is fixed, one outcome is that plants  
123 respond to increased resource availability by investing proportionately more in each. On average,  
124 plants would have greater floral lifespans and more flowers under high resources than under low  
125 resources, but the trade-off between these traits would remain constant (cf. van Noordwijk & G.  
126 de Jong, 1986). Alternatively, there may be a single allometric trajectory, such that increases in  
127 flower number in response to increased resource availability actually lead to decreases in floral  
128 longevity (cf. Müller *et al.*, 2000; cf. Cheplick, 2005). In this scenario, too, the same trade-off  
129 constrains the evolution of floral longevity regardless of resource availability. Alternatively,  
130 allocation itself can be plastic (e.g., Müller *et al.*, 2000; Tonnabel *et al.*, 2017) or the relative  
131 expression of variation in resource allocation versus resource acquisition may vary with resource  
132 availability (c.f. van Noordwijk & de Jong, 1986). In these cases, the floral longevity-flower  
133 number trade-off itself may vary across resource levels and thus alter the fundamental  
134 parameters governing the evolution of floral longevity. Finally, if there are genotype-by-  
135 environment interactions, heritability of floral longevity can be affected, diverging across  
136 environments or diminished within heterogeneous environments, but plasticity of floral longevity  
137 (or allocation involving longevity) could evolve (reviewed in Scheiner, 1993 and Pigliucci,  
138 2005). Indeed, plasticity of floral longevity may be adaptive, under direct selection or selected  
139 indirectly through its influence on flowering rate and/or duration (Ishii & Sakai, 2001; Harder &  
140 Johnson, 2005; Arroyo *et al.*, 2013; Spigler, 2017).

141 To begin to address the constraints on the evolution of floral longevity in wild species,  
142 we evaluate floral longevity and related floral traits in the wildflower biennial herb *Sabatia*  
143 *angularis* (Gentianaceae) raised under contrasting resource levels. Specifically, we ask: (1) Can  
144 we detect evidence of broad sense genetic variation in floral longevity and other floral traits  
145 (protandry, flower size, flower number, and flowering rate) within a population? (2) To what  
146 degrees are floral longevity and other display traits plastic in response to resource availability  
147 and do they respond according to expectations based on allocation trade-offs? (3) Is there  
148 evidence of genetic-by-environment interactions influencing floral longevity and related traits,

149 suggesting context-dependency of heritability and broad sense genetic variation for plasticity  
150 itself? Finally, (4) do we see evidence of core trade-offs as predicted by resource allocation  
151 theory, and do these trade-offs vary across resource environments?

152

## 153 **Materials and Methods**

### 154 *Study species*

155 *Sabatia angularis* (L.) Pursh (rosepink) is biennial that is distributed throughout eastern  
156 USA and southeastern Canada. Plants are commonly found in open habitats, including prairies,  
157 roadsides, old fields, and serpentine barrens. Plants flower from July through August, producing  
158 tens to hundreds of nectarless, pink flowers. The hermaphroditic flowers are protandrous; the  
159 anthers dehisce upon opening while the stigma lobes remain wrapped around each other. When  
160 entering female phase, the stigma lobes begin to untwist and to expose the receptive stigmatic  
161 surface. The stigma lobes continue to separate from each other while each lobe curls into a spiral  
162 as the flower ages. Receptivity (as measured by peroxidase activity testing under controlled  
163 conditions) peaks ~ 9 days after stigma opening (Spigler, unpublished). However, flowers in  
164 wild populations are typically pollinated by day 4 (Dudash, 1991), and seed set per flower  
165 decreases with floral age, suggesting a cost to increased longevity (Spigler, unpublished).  
166 Pollination is facilitated by generalist pollinators, including leaf-cutter bees (Megachilidae),  
167 sweat bees (Halictidae), andrenid bees (Andrenidae), small carpenter bees (Anthophoridae) and  
168 hoverflies (Syrphidae) (Spigler pers. obs.). The species is self-compatible, and plants are capable  
169 of autonomous self-pollination (Spigler, 2018). Populations range from mixed-mating to highly  
170 outcrossing (Spigler *et al.*, 2010). After pollination, dry, dehiscent fruit capsules mature between  
171 September and November, each containing hundreds to more than a thousand seeds (Dudash,  
172 1991; Spigler & Chang, 2008).

173 Spigler (2017) previously evaluated phenotypic variation in floral longevity in *S.*  
174 *angularis*. Corollas live as few as 3 d to up to 20 d, whereas stigmas live for as long as 26 d.  
175 Interestingly, the stigma persists after the corolla has wilted if pollination has not occurred,  
176 whereas if pollination occurs, the stigma wilts prior to the corolla. Both corolla and stigma  
177 longevities were found to be highly plastic in response to pollination and its timing (Spigler,  
178 2017).

179

180 *Experimental design*

181           Plants for this experiment were grown from seed collected from 49 open-pollinated plants  
182 at a southeastern Pennsylvania serpentine grassland population ('UB5', 39°54'810"N,  
183 75°42'711'W). We planted 45 seeds per plant (hereafter, 'family') in flats in Temple  
184 University's Plant Growth Facility using a randomized block design and subjected them to cold  
185 stratification. Approximately three months after germination, we transplanted rosettes into 3-inch  
186 square pots filled with a 3:1 mix of Fafard 3b (Sungro Horticulture, Agawam, MA,  
187 USA):Turface (PROFILE Products LLC, Buffalo Grove, IL, USA). Plants were then vernalized  
188 for 10 weeks in a controlled growth chamber, after which we randomly assigned 5 rosettes per  
189 family to a high resource treatment and another 5 to a low resource treatment. High-resource  
190 treatment plants were transplanted into 5.25-inch square pots, while plants assigned to the low-  
191 resource treatment remained in the 3.25-inch pots. We then placed plants in a randomized  
192 complete block design inside a pollinator-free growth house maintained at 22/15°C with 14-hour  
193 days for the duration of the experiment. All plants were watered every 2-3 days and fertilized  
194 weekly using a combination of epsom salt, 20-20-20, and 15-0-15 fertilizers throughout  
195 flowering, with fertilizer application lasting two additional weeks for the high-resource  
196 treatment. The resource differential between our treatment levels was therefore created by both  
197 extended fertilizer application to the high treatment and the 3.7-fold difference in pot size, which  
198 impacts overall nutrient and water-holding capacity and availability to the plants. Disease  
199 reduced our sample size, and a final total of 279 plants from 38 plant families were included in  
200 the experiment.

201           For all plants we recorded date of first flower, date last flower wilted, and total flower  
202 number. For three flowers per plant, we recorded protandry, and floral longevity and, for three  
203 additional flowers, their size. To measure protandry and floral longevity, we tagged three flower  
204 buds per plant, followed them daily, and for each recorded date of: anthesis, onset of female  
205 phase, stigma wilting, and corolla wilting. These flowers were emasculated to prevent  
206 autonomous self-pollen deposition, which can significantly reduce floral longevity in *S.*  
207 *angularis* (Spigler, 2017). Thus, our floral longevity measurements estimate maximum possible  
208 floral lifespan, also termed potential floral longevity (Steinacher & Wagner, 2010). Although  
209 flowers were emasculated, we estimated protandry as the length of time between flower opening  
210 and the date of onset of female phase, which would represent male-only phase. We measured

211 floral longevity two ways--stigma longevity and corolla longevity--to account for differences in  
212 function, since stigma longevity is considered to serve female fitness, whereas corolla traits often  
213 serve male fitness (e.g. Bell, 1985). Stigma longevity was calculated as the number of days from  
214 anthesis until the stigma wilted, scored when at least the tips of both lobes were brown (Spigler,  
215 2017). Corolla longevity was calculated as the number of days from anthesis until the corolla  
216 wilted, scored when at least three of the five petals began to curl (Spigler, 2017). To estimate  
217 flower size, we measured the length and width (mm) of one random petal for each of three  
218 flowers in female phase. The product of petal length and width (petal area) is highly correlated  
219 with total flower area ( $r_{24}=0.90$ ,  $P<0.0001$ ; Emel *et al.*, 2017). For all flower-level  
220 measurements, we controlled for flower position. Finally, we calculated flowering rate as the  
221 total number of flowers per plant divided by the duration it flowered, where duration is  
222 determined as the time from date first flower opened until the date last flower wilted.

223

#### 224 *Statistical analyses*

225 For all traits, we evaluated the influence of resource environment, family, and family-by-  
226 environment interactions using general linear mixed models (GLMM, proc mixed, SAS<sup>®</sup>  
227 software Version 9.3). Resource level (high or low) was included in the models as a fixed effect.  
228 Family and its interaction with resource level represent random effects. A significant random  
229 genetic (family) by environment interaction could indicate that either there is an imperfect  
230 correlation of genotype (family) means across environments or variances among families in the  
231 two environments are unequal (Conner & Hartl, 2004; Fry, 2004). The former indicates that the  
232 phenotypic rank of families is different between environments and family reaction norms cross,  
233 while the latter has implications for heritability across environments. Furthermore, Fry (2004)  
234 points out that variance component models assume that residual (i.e., non-genetic) variances are  
235 the same between environments, but, if they are different, this too would also have implications  
236 for heritability. Therefore, for each trait we explicitly tested these three hypotheses using  
237 likelihood-ratio tests as described in Fry (2004). For traits measured repeatedly at the individual  
238 plant-level (corolla longevity, stigma longevity, protandry, and flower size), we further included  
239 a random plant effect, though for model simplicity we assumed that among-plant variance was  
240 equal across resource levels.



241 We present point estimates of broad-sense heritability for all measured traits by  
242 environment. Broad-sense heritability ( $H^2$ ) was calculated as  $V_G/V_P$ , where  $V_G$  is the family  
243 (genetic) variance component, and  $V_P$  is the sum of all variance components (family, residual,  
244 and where included, plant identity). We estimated the variance components using the ‘covtest’  
245 option in full models, which allow among-family variance and residual variance to vary across  
246 environments, described above. We note that because  $H^2$  is based on family means from open-  
247 pollinated seed it includes dominance, epistasis and maternal effects in addition to additive  
248 effects. Thus, these estimates may serve as an upper limit to heritability in these traits for the  
249 population and resource environments under study.

250 We predicted that there will be trade-offs among floral traits, specifically between flower  
251 number and floral longevity and between flower number and flower size, and that these trade-  
252 offs are likely to be stronger under low compared to high resource levels. To evaluate these  
253 hypotheses, we included total flower number and an interaction between total flower number and  
254 treatment as covariates in the models of corolla longevity, stigma longevity, and flower size  
255 described above. When the interaction was significant, we evaluated the slope and significance  
256 of the relationship between the dependent variable and flower number within treatment levels  
257 (proc plm). We note that inclusion of covariates that are themselves influenced by the  
258 experimental treatment are strongly cautioned against, because adjusted treatment means will be  
259 artificial, corresponding to conditions that may not be biologically possible. To avoid this  
260 problem, we first removed the treatment effect from total flower number and included the  
261 residuals as a covariate instead. This approach sets mean flower number within each treatment to  
262 zero; consequently, least squares means calculated for each dependent variable from the GLMM  
263 do not adjust for differences in mean flower number between treatments.

264 Finally, we present phenotypic (individual-level) and broad-sense genetic (family-level)  
265 correlations between the following traits within each resource level: corolla longevity, stigma  
266 longevity, protandry (duration of male-only phase), flower size, flower number, and flowering  
267 rate. We first calculated mean value per individual for those traits measured more than one time  
268 per plant. We evaluated phenotypic correlations using Pearson correlation coefficient (proc corr).  
269 For family-level correlations, we used Pearson correlation coefficients based on family-level  
270 means per trait and evaluated significance based on an FDR of 0.05 within each resource level.  
271 According to resource allocation theory, we predicted trade-offs among flower number, flower

272 size and flower longevity. Based on previous results (Spigler, 2017), we also expected a negative  
273 correlation between floral longevity and flowering rate.

274

## 275 **Results**

276 We detect significant genetic variation (family effect), and thus heritability, for floral  
277 longevity (Table 1, Fig. **1a,b**). Potential corolla lifespan averaged across all families and  
278 resource levels is 12.2 ( $\pm 0.16$  SE) days, but family means range from 9.5 ( $\pm 0.98$  SE) to 15.9  
279 ( $\pm 1.19$  SE) days. Potential stigma longevity per family, averaged across resource levels, ranges  
280 from 11.3 ( $\pm 0.53$  SE) days to 17.3 ( $\pm 1.00$  SE) days, with an average of 14.4 ( $\pm 0.18$  SE) days  
281 across all families. We similarly detect significant genetic variation for all other traits: protandry,  
282 flower size, flower number, and flowering rate (Table 1, Fig. **1c-f**).

283 Resource availability, however, also impacts floral longevity and several other floral  
284 display traits. Mean corolla longevity is slightly but significantly reduced under high relative to  
285 low resource availability by 0.7 days, representing a 5.6% decline (Table 1, Fig. **1b**), in contrast  
286 to predictions. This reduction is accompanied by a tendency for diminished protandry under high  
287 resources as well, but resource availability has no impact on stigma longevity (Table 1, Fig.  
288 **2a,c**). Flower number and flowering rate are highly plastic in response to resource availability.  
289 Under high resource availability, flower number per plant is approximately 4.5 times greater and  
290 plants flower at 4x the rate compared to low resource availability (Fig. **1e,f**). Flower size is not  
291 significantly influenced by resource level on average (Fig. **1d**), though the interaction between  
292 resource level and flower number is significant (Table 1).

293 Genotype-by-environment ( $G \times E$ ) interactions were evident for floral longevity, in terms  
294 of corolla longevity, and all other display traits, but not stigma longevity (Table 1, Fig. 1). Tests  
295 of the underlying basis for the significant  $G \times E$  effect on corolla longevity revealed that it was  
296 attributable to an imperfect cross-environment genetic correlation, i.e. family rank was altered by  
297 resource level (Table 1). Genetic variance and residual, non-genetic components of variance for  
298 corolla longevity, however, did not differ significantly between resource treatments (Table 1).  
299 Residual variance increased under high resources compared to low for all remaining traits  
300 (protandry, flower size, flowering rate, and flower number), but this was matched by an increase  
301 in genetic variance under high resources for flowering rate and total flower number as well. For

302 flower number, families also varied enough in their response to the resource treatment that the  
303 cross-environment genetic correlation was significantly less than 1.

304 Heritability estimates (Table 2) are similar across environments for stigma and corolla  
305 longevity, flower size and flower number. However, they are twice as great for protandry and  
306 half as great for flowering rate under low resources. Notably, broad-sense heritability estimates  
307 for corolla longevity are more than double that of stigma longevity within each resource level  
308 and are comparable to those for flower number.

309 Consistent with theoretical predictions, there are significant trade-offs between floral  
310 display traits (Fig. 2). The general linear mixed model results indicate that flower number has a  
311 significant negative effect on both corolla and stigma longevity, on average, across both  
312 resource levels (Table 1). For both longevity measures, the interaction between flower number  
313 and resource level is also significant. Further analysis reveals that the interactions are due to  
314 significant trade-offs under low but not high resources for corolla ( $t = -3.78$ ,  $P = 0.0002$  vs.  $t =$   
315  $0.62$ ,  $P = 0.54$ , respectively) and stigma longevity ( $t = -2.36$ ,  $P = 0.02$  vs.  $t = 0.25$ ,  $P = 0.80$ ,  
316 respectively) (Fig. 2a). Similarly, we show a highly significant, negative main effect of flower  
317 number on flower size and a significant flower number by resource treatment interaction (Table  
318 1). In this case, the trade-off is significant at both low ( $t = -3.2$ ,  $P = 0.002$ ) and high ( $t = -3.64$ ,  $P$   
319  $= 0.0003$ ) resource levels, but is 3.5 times as steep under low resources (slope  $-0.32$  vs.  $-0.09$ ,  
320 respectively) (Fig. 2b).

321 Phenotypic (individual-level) and genotypic (broad-sense, family-level) correlations  
322 between traits are presented in Table 2. As seen from the general linear mixed model results,  
323 there are significant, negative phenotypic correlations between total flower number and both  
324 metrics of floral longevity in the low—but not high—resource treatment and significant negative  
325 correlations between flower number and size in both environments. We also find significant  
326 negative phenotypic correlations between flowering rate and both metrics of floral longevity  
327 under both environments; plants with short-lived flowers flower more rapidly. Positive  
328 phenotypic correlations are also evident between pairs of traits under both resource levels:  
329 stigma and corolla longevity, corolla longevity and flower size, and flower number and  
330 flowering rate. Correlations between stigma and corolla longevity and between flower number  
331 and flowering rate are strong in both environments ( $r > 0.70$ ). Protandry is not correlated with  
332 either measure of floral longevity nor any of the other floral traits.

333 We detect significance of some of these correlations at the family-level despite limited  
334 power at this level. In both resource treatments, stigma and corolla longevity are again strongly  
335 correlated, as are flower number and flowering rate and flower size and flower number, though  
336 the flower size-number trade-offs does not remain significant after correction for multiple tests.  
337 The negative relationship between corolla longevity and flowering rate is also seen at the family-  
338 level, even under high resource levels, though it does not retain statistical significance under high  
339 resource availability after correction for multiple tests.

340

### 341 **Discussion**

342 Our study validates the use of resource allocation theory (Charnov, 1982; Lloyd, 1988) to  
343 model the evolution of floral longevity and floral display traits more broadly (Schoen & Dubuc,  
344 1990; D. Charlesworth & Morgan, 1991; Brunet, 1992; Ashman & Schoen, 1994; Schoen &  
345 Ashman, 1995). Models of floral longevity hinge upon the trade-off between allocation of  
346 limited resources to either floral maintenance or construction of new flowers constraining  
347 potential longevity (Ashman & Schoen, 1994; Schoen & Ashman, 1995). We show a negative  
348 relationship between floral longevity and flower number in *S. angularis*, supporting this central  
349 hypothesis. Indeed, even in a nectarless plant such as *S. angularis*, construction of floral tissue  
350 can comprise a considerable amount of a plant's carbon budget, while maintenance can exact a  
351 toll via transpiration and respiration (Nobel, 1977; Ashman & Baker, 1992; Ashman & Schoen,  
352 1994, 1996; Galen *et al.*, 1999; Galen, 2000; Teixido & Valladares, 2014a). In addition, our  
353 finding of a significant flower number-size trade-off supports another critical assumption that  
354 further partitioning of allocation to construction constrains plants to make either many small or  
355 few large flowers (reviewed in Worley & Barrett, 2000; Caruso, 2004). Both trade-offs in our  
356 study were evident at phenotypic and genotypic levels, although our power to detect significance  
357 of moderate to low genetic correlations was limited. While ours is the only study to directly  
358 evaluate the trade-off between floral longevity and flower number, a number of studies have  
359 evaluated the trade-off between flower size and number, with mixed support (reviewed in  
360 Worley & Barrett, 2000; Caruso, 2006; Caruso *et al.*, 2012). The magnitudes of the trade-offs in  
361 *S. angularis* as measured by correlations are moderate, though in or near the range of that found  
362 in other studies (e.g. Worley & Barrett, 2001; Caruso, 2004), and could constrain the evolution

363 of floral display traits in *S. angularis*. For example, Caruso (2004) found a moderate flower size-  
364 number trade-off restricted a response to selection on floral display in *Lobelia siphilitica*.

365 By employing high and low resource treatments, our results highlight the context-  
366 dependency of resource-allocation trade-offs and the potential importance of plasticity in  
367 resource allocation. Theoretically, resource availability should not alter allocation trade-offs if  
368 allocation is canalized (van Noordwijk & G. de Jong, 1986). Rather, plants would invest  
369 proportionately more in each trait under high compared to low resource availability. However,  
370 we found that floral longevity *decreased* on average under high resources compared to low,  
371 while total flower number per plant increased on average by 360% and flower size was not  
372 affected. This result is more in line with expectations if plants followed a single allometric  
373 relationship across resource environments (e.g. Müller *et al.*, 2000), wherein plants at high  
374 resources are larger and make more flowers but at the expense of further decreases in floral  
375 longevity. Yet, the trait responses in *S. angularis* are clearly disproportionate, and both the floral  
376 longevity-flower number trade-off and the flower size-number trade-off are steeper under low  
377 compared to high resource levels, based on estimates of the slopes of these relationships tested at  
378 the phenotypic level. Allocation is difficult to evaluate (Goldman & Wilson, 1986; Charlesworth  
379 & Morgan, 1991; Cheplick, 2005), but we note that the difference in the floral longevity-flower  
380 number trade-off under low vs. high resources remains significantly different even when  
381 evaluated on a log-log scale and when plant height is included as another covariate related to  
382 plant size (data not shown). Other studies investigating aspects of reproductive allocation have  
383 similarly found trade-offs to either be present only or stronger under reduced resources (e.g.,  
384 Lubbers & Lechowicz, 1989; Delph, 1990; Ashman & Schoen, 1997). One possible explanation  
385 for this finding in our study is that the high resource treatment provided greater opportunity for  
386 the expression of variation in resource acquisition. Trade-offs can be masked where variation in  
387 resource acquisition exceeds that for allocation (van Noordwijk & de Jong, 1986), and we found  
388 15.5 times greater total variation in flower number under high compared to low resources. This  
389 hypothesis has been proposed to explain equivocal support for trade-offs among floral display  
390 traits more generally (Worley & Barrett, 2000; Caruso *et al.*, 2012). Alternatively, differential  
391 plasticity of floral longevity, flower number, and flower size in response to resource availability  
392 could reflect a shift in allocation strategy, altering trade-offs across resource levels. If we  
393 consider the ratio of floral longevity to flower number per plant as a composite metric of

394 allocation, acknowledging the associated biological and statistical limitations (Jasienski &  
395 Bazzaz, 1999; Cheplick, 2005), we see this ratio decline for all families under high resources,  
396 with families converging on disproportionately greater investment in flower number under high  
397 resources (Supporting Information Fig. S1). Although our experiment was conducted in a  
398 controlled environment, we expect these trade-offs to be relevant and even stronger in wild *S.*  
399 *angularis* populations, where resource limitation is more severe than our low resource treatment.

400       Whether or not the patterns related to plasticity of floral longevity and resource allocation  
401 shown here are adaptive of course remains to be tested, but is still constructive to consider in  
402 light of existing theory for the evolution of floral longevity. In general, because greater longevity  
403 may translate into more opportunities for outcrossing (Bingham & Orthner, 1998; Torres-Díaz *et*  
404 *al.*, 2011), plastic increases in longevity under more favorable abiotic conditions, as seen in other  
405 species (Arathi *et al.*, 2002; Arroyo *et al.*, 2013; Jorgensen & Arathi, 2013), could be interpreted  
406 as adaptive, so long as the resulting increase in overall display does not lead to high levels of  
407 geitonogamy (Harder & Barrett, 1995; Ishii & Sakai, 2000). In contrast, we found decreased  
408 floral longevity under high resources. Yet, when viewed instead as part of an overall allocation  
409 strategy, limits to the fitness benefits of increased longevity even under increased resources  
410 become clear. Ashman and Schoen (1994) suggested that floral lifespan is governed by a tipping  
411 point, beyond which it becomes more advantageous to construct a new flower rather than  
412 maintain an existing one. We hypothesize that resource availability could shift the tipping point.  
413 Low resource levels impose a strict limit to flower number. Because maintenance costs are a  
414 fraction of construction costs (Ashman & Schoen, 1994), fitness under low resource conditions  
415 might be optimized through greater longevity at the expense of flower number. Alternative  
416 strategies along the axis of the trade-off between flower number and flower size might still be  
417 maintained if pollination conditions are variable among years, as has been found in *S. angularis*  
418 populations (Spigler, 2018). However, the high efficiency strategy of investment in maintenance  
419 where resources are insufficient to support new growth would no longer present a selective  
420 advantage when resources are high (c.f. Bloom *et al.*, 1985). Consequently, plastic increases in  
421 floral longevity in proportion to increases in flower number—even if physiologically possible—  
422 are unlikely optimal. Indeed, although ovule number per flower in *S. angularis* is large, it is  
423 finite. Beyond some point, fitness returns per flower will diminish. In contrast, because *S.*  
424 *angularis* is monocarpic and flowering is indeterminate, fitness gains should rise sharply with

425 continued allocation to the construction of new flowers provided resources are available, even if  
426 each flower is slightly shorter lived. Importantly, *S. angularis* plants under high resource levels  
427 produced the nearly 5x as many flowers more rapidly compared to low resources, which could be  
428 key given selection on flowering duration in wild populations (Emel *et al.*, 2017) against a  
429 backdrop of continuous resource depletion across the reproductive season (Spigler, 2018).

430 Finally, in addition to the expected resource-based trade-offs, we explored heritabilities  
431 and phenotypic and genotypic correlations among floral display traits. We detected significant  
432 genetic variation for all display traits in *S. angularis*, showing for the first time heritability of  
433 floral longevity in a wild species. The point estimates of heritability were relatively low  
434 compared to mean estimates for corolla traits and flower number in other wild species (Ashman  
435 & Majetic, 2006), especially considering that broad-sense estimates may be inflated due to non-  
436 additive genetic and maternal effects (Falconer, 1981). Nevertheless, heritability for corolla  
437 longevity was among the highest examined in the current study, comparable in magnitude to that  
438 for flower number and greater than that for flower size. Despite heritable variation in protandry  
439 and a tendency for it to respond similarly to resource availability as corolla longevity, protandry  
440 was not correlated with either metric of floral longevity. Instead, increased floral longevity in *S.*  
441 *angularis* scales with female phase duration, as might be expected in species with high ovule  
442 numbers per flower (Stratton, 1989). Routley and Husband (2003) selected on protandry in the  
443 herbaceous perennial *Chamerion angustifolium* and similarly found that it was independent of  
444 total longevity. Other display traits, however, were significantly correlated with floral longevity  
445 in *S. angularis*. Primack (1985) hypothesized that flower size and floral longevity would be  
446 positively correlated across species if increased longevity maximizes gains from investment in  
447 larger, more expensive flowers, a pattern seen across species (Stratton, 1989; Zhang *et al.*, 2017).  
448 On the other hand, reduced longevity could curtail the resource drain of large flowers, leading to  
449 a negative relationship (Teixido & Valladares, 2014b). The significant positive correlations  
450 between flower size and longevity in both environments in our study supports the former  
451 hypothesis. We also saw that plants and families with shorter floral longevity flowered more  
452 rapidly. This relationship is intuitive since shorter longevity, in addition to more rapid anthesis  
453 rates, should condense the duration of floral display (Harder & Johnson, 2005). Although most  
454 correlations we report in this study are weak to moderate, several are in line with the magnitude

455 of floral trait and floral-inflorescence trait correlations seen across species, particularly for  
456 radially symmetric flowers (Ashman & Majetic, 2006; Conner *et al.*, 2014).

457

#### 458 *Conclusions*

459 We provide critical support for viewing the evolution of floral longevity as a resource  
460 allocation strategy. We illustrate how resource availability can fundamentally alter the  
461 parameters determining optimal longevity and suggest future models incorporate plasticity in  
462 response to resource availability in determining the tipping point at which investment in  
463 maintenance of flowers should be transferred to the construction of new flowers. We further  
464 reveal broad-sense genetic variation in potential floral longevity and its plasticity. The plastic  
465 response seen in *S. angularis* could be adaptive, with plants above a certain resource threshold  
466 investing in the production of more flowers more quickly, even if shorter lived, rather than in  
467 longer-lived flowers. Experiments evaluating the fitness implications of these responses in the  
468 field are needed, especially considering that pollination can trigger floral senescence long before  
469 potential floral longevity is realized. Such studies can help understand how microevolutionary  
470 processes lead to differentiation in floral longevity and its plasticity among populations (Giblin,  
471 2005; Trunschke & Stöcklin, 2017).

472

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477

#### 478 **Author Contribution**

479 RBS conceived of and designed the study. AJW performed the research and data collection. RBS  
480 performed statistical analyses. AJW and RBS interpreted the data and wrote the manuscript.

481



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- 695

696 **Figure Legends**

697

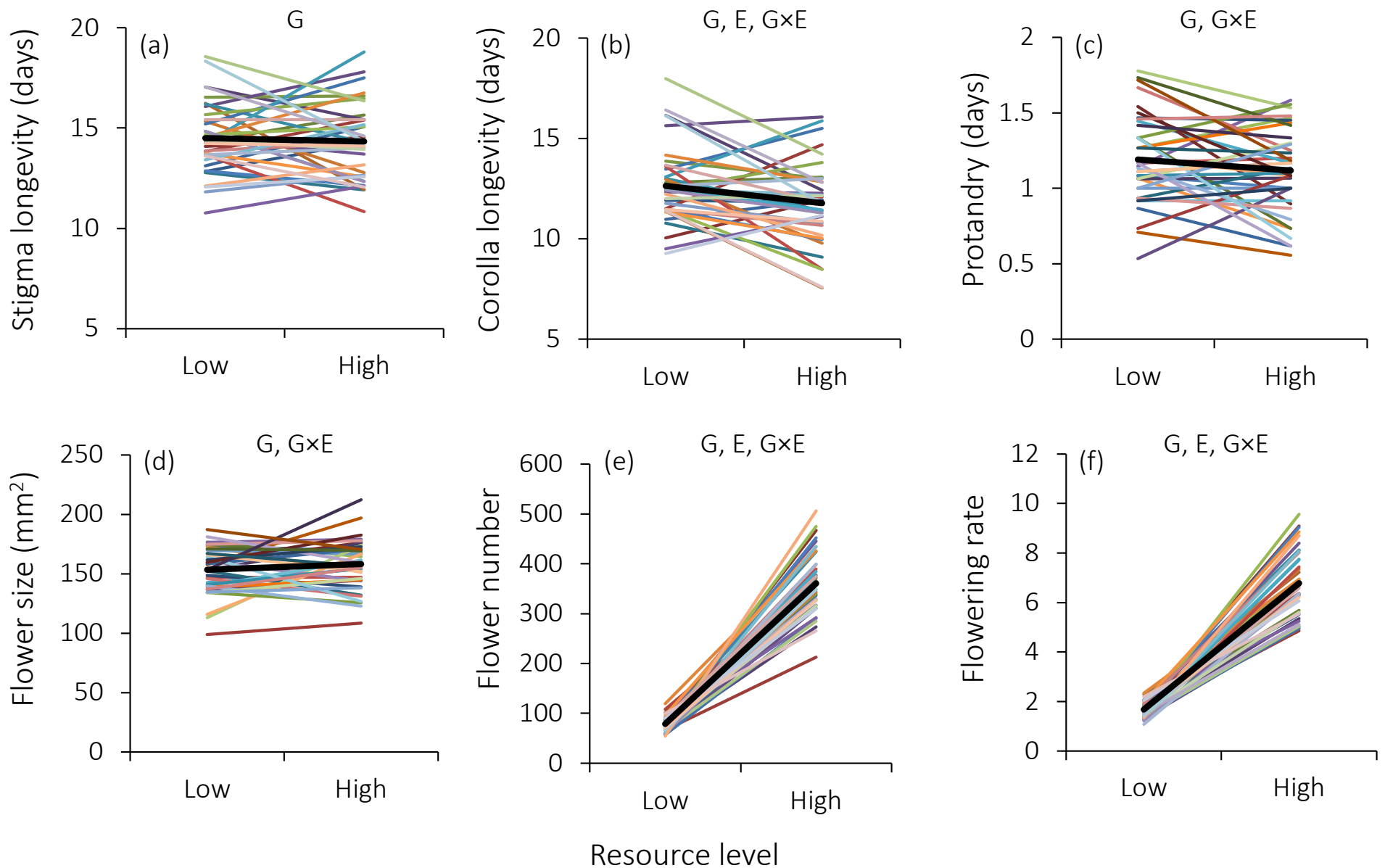
698 **Figure 1.** Reaction norms illustrating response of floral longevity and related floral traits to  
699 resource availability in *S. angularis*. Each colored line represents the mean for a given family;  
700 the thicker, black line indicates the mean response across families. The letters G, E, or G×E  
701 indicate whether there are significant genotype (family), environment (resource level), or  
702 genotype-by-environment interaction effects influencing each trait, respectively, as indicated in  
703 Table 1.

704

705 **Figure 2.** Scatterplots of the relationship between (a) corolla longevity and flower number and  
706 (b) flower size and flower number under low (open circles) and high (closed circles) resource  
707 levels. Data points represent individuals. Solid regression lines indicate a significant relationship.

708

709 **Supporting Information Figure 1.** Reaction norms illustrating convergence on allocation to  
710 construction of new flowers vs. maintenance under high resources in *S. angularis*. The ratio of  
711 floral longevity (days until corolla wilting) to flower number per plant was used as a possible  
712 composite metric of allocation. Each colored line represents the mean reaction norm for a given  
713 family; the thicker, black line indicates the mean response across families.



**Figure 1.** Reaction norms illustrating response of floral longevity and related floral traits to resource availability in *S. angularis*. Each colored line represents the mean for a given family; the thicker, black line indicates the mean response across families. The letters G, E, or G×E indicate whether there are significant genotype (family), environment (resource level), or genotype-by-environment interaction effects influencing each trait, respectively, as indicated in Table 1.

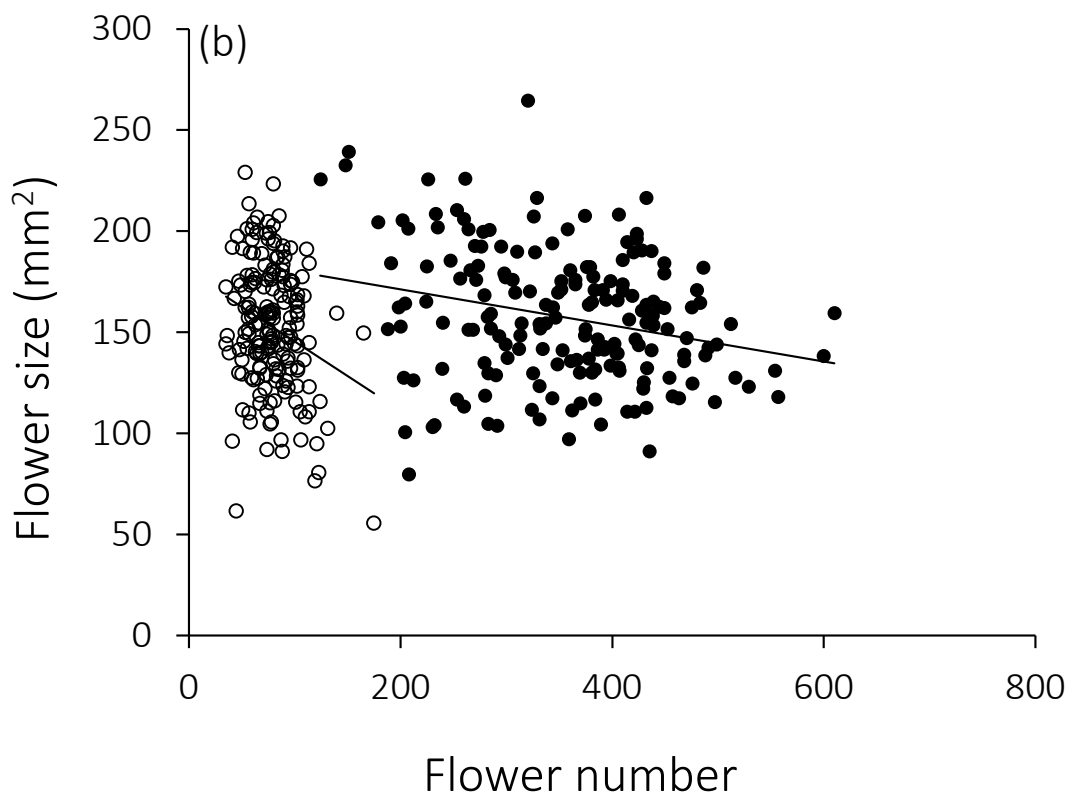
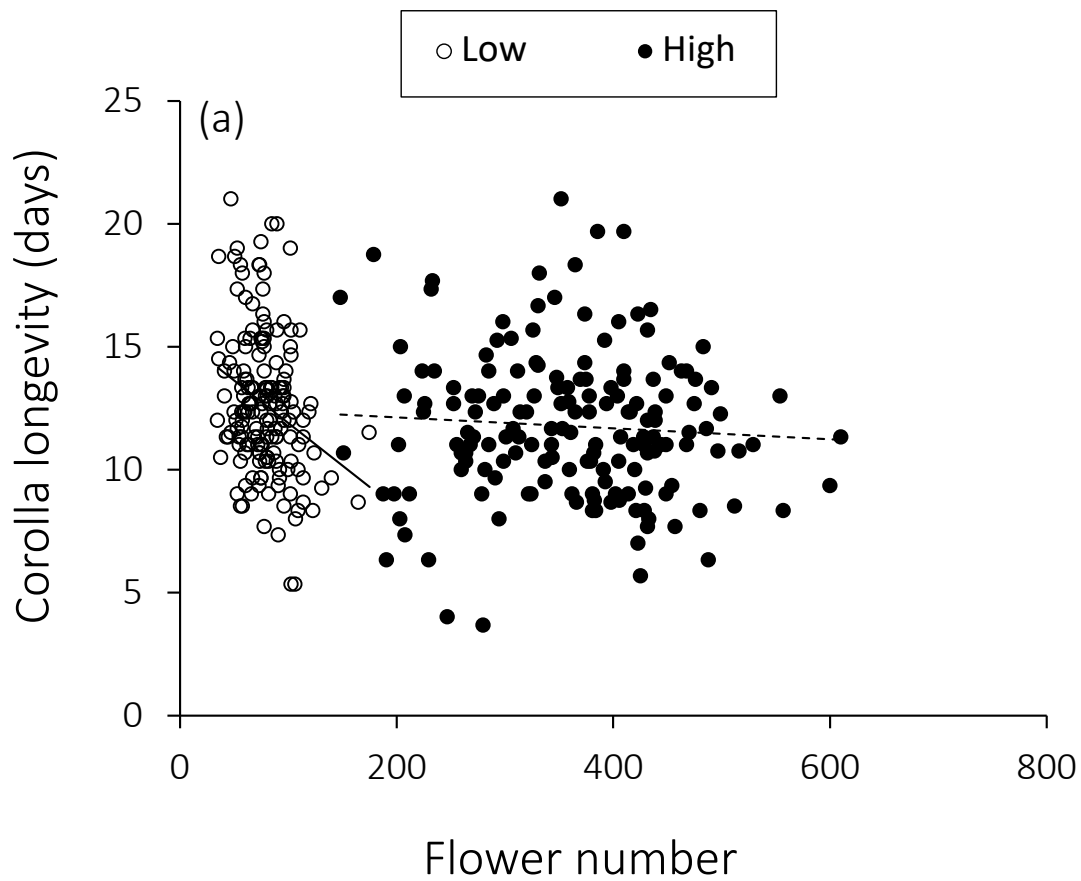


Figure 2. Scatterplots of the relationship between (a) corolla longevity and flower number and (b) flower size and flower number under low (open circles) and high (closed circles) resource levels. Data points represent individuals. Solid regression lines indicate a significant relationship.



***New Phytologist* Supporting Information**

**Article title:** Context-dependency of resource allocation trade-offs highlights constraints to the evolution of floral longevity in a monocarpic herb

**Authors:** Rachel B. Spigler and Alyssa J. Woodard

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The following Supporting Information is available for this article:

**Fig. S1** Reaction norms illustrating convergence on allocation to construction of new flowers vs. maintenance under high resources in *S. angularis*.

**Figure S1.** Reaction norms illustrating convergence on allocation to construction of new flowers vs. maintenance under high resources *S. angularis*. The ratio of floral longevity (days until corolla wilting) to flower number per plant was used as a potential composite metric of allocation. Each colored line represents the mean reaction norm for a given family; the thicker, black line indicates the mean response across families.

