

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24

## Floral Reorientation: The Restoration of Pollination Accuracy after Accidents

W. Scott Armbruster<sup>1,3</sup> & Nathan Muchhala<sup>2</sup>

<sup>1</sup>School of Biological Sciences, University of Portsmouth, Portsmouth PO1 2DY, UK;  
and Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775-7000,  
USA.

ORCID iD: <https://orcid.org/0000-0001-8057-4116>

Twitter: @scottarmbrus

<sup>2</sup>Department of Biology, University of Missouri-St Louis, St Louis, MO 63121-4499, USA.

ORCID iD: <https://orcid.org/0000-0002-4423-5130>

Twitter: @Muchha\_Lab

<sup>3</sup>Author for correspondence: [scott.armbruster@port.ac.uk](mailto:scott.armbruster@port.ac.uk) +44 (0)1983 615361

25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52

## Summary

- Plants sometimes suffer mechanical injury. The non-lethal collapse of a flowering stalk, for example, can greatly reduce plant fitness if it leads to "incorrect" floral orientation and thus reduced visitation or poor pollination. When floral orientation is important for accurate pollination, as has been suggested for bilaterally symmetrical flowers, we predict that such flowers should have developmental and/or behavioural mechanisms for restoring "correct" orientation after accidents.
- We made observations and conducted experiments on 23 native and cultivated flowering-plant species in Australia, South America, North America, and Europe.
- We found that flowers with bilateral symmetry usually have the capacity to reorient after accidents, and that this is manifested through rapid bending and/or rotation of pedicels or sexual organs or slower peduncle bending. Floral reorientation restores pollination accuracy and fit with pollinators. However, experimental floral misorientation in eight species with radially symmetrical flowers showed that, with one exception, they had little capacity to reorient their flowers, in line with expectations that the orientation of radially symmetrical flowers does not substantially affect pollination accuracy.
- Our results suggest that quick corrective reorientation of bilaterally symmetrical flowers is adaptive, highlighting a little-studied aspect of plant-pollinator interactions and plant evolution.

**Key Words:** Adaptive accuracy, floral orientation, flower-pollinator fit, late floral development, plant injuries; pollination, zygomorphic flowers

## Introduction

That “accidents happen” is an aphorism few would argue with. Zoology, as well as medicine, considers the capacity of animals to recover from mechanical injuries as a critical adaptation for mobility, survival, and hence fitness (e.g. Frank *et al.*, 2017; Chang *et al.* 2018). Less attention has been paid to recovery from accidental injury in plants, and virtually no research has addressed response to accidents involving flowers. Yet flowering stalks are often subject to accidental collapse, as when a scape blows down in the wind or coarse litter falls onto a stem, causing irreversible bending without severing the vascular system. Such events often push flowers into inappropriate orientations, even if the flowers are otherwise unharmed.

Embedded in the writings of Sprengel (1793), Darwin (1862), Robertson (1888a,b,c), and, later, Berg (1960) and Stebbins (1974) is the concept that the orientation of flowers relative to the pull of gravity is critical to their proper function and thus an adaptive trait. These characteristics are functionally important because the movement of flying pollinators and their ability to land on flowers is strongly influenced by their orientation relative to the direction of gravitational pull (Robertson, 1888a,b,c; Fenster *et al.*, 2009). Orientation may also be important, particularly for laterally and downwardly oriented flowers as a means to protect nectar from dilution and pollen from damage by rain, UV radiation, or heat (Sprengel, 1793; Huang *et al.*, 2002; Aizen, 2003; Wang *et al.*, 2010; Haverkamp *et al.*, 2019; Lin and Forrest, 2019).

### *Floral orientation affects flower attractiveness and rates of visitation and pollination*

Floral orientation can affect various aspects of pollination. Proper floral orientation can increase visitation rates by pollinators relative to that seen on misoriented flowers (Ushimaru and Hyodo, 2005; Ushimaru *et al.*, 2006; Fulton and Hodges, 1999; Wang *et al.*, 2014a). Floral misorientation may change the composition of the flower-visitor fauna, including increased visitation by poor pollinators and resource thieves (Wang *et al.*, 2014b).

In plants with bilaterally symmetrical (zygomorphic) flowers, misorientation of the flower relative to gravity may also affect flower-pollinator fit by causing pollinators to be misoriented, relative to the flower shape, when they land on the flower. This can reduce access to nectar (depressing attractiveness) and/or lower pollination efficiency because pollen is placed in the wrong location on pollinators relative to the expected site of stigma contact by other flowers in the population. Similarly, the stigmas of misoriented flowers may contact pollinators in the wrong place relative to the expected position of pollen placed by other

87 flowers in the population. The net result is lowering of both male and female components of  
88 reproductive fitness, as has been shown in a few empirical studies (Castellanos *et al.*, 2004;  
89 Ushimaru *et al.*, 2009; Wang *et al.*, 2014a, 2014b).

90 Endress (1994) noted that the plane of symmetry in bilaterally symmetrical flowers is  
91 usually vertical, i.e. in line with the pull of gravity. This may reflect selection generated by  
92 interactions with pollinating animals, which also exhibit bilateral symmetry and  
93 behaviourally orient their planes of symmetry to the vertical, especially in flight. Indeed,  
94 floral orientation interacts functionally, in terms of pollination success, with floral symmetry  
95 (Neal *et al.*, 1998; Fenster *et al.*, 2009, Ushimaru *et al.*, 2005; 2006, 2009; Nikkeshi *et al.*,  
96 2015; Reyes *et al.*, 2016). In a review of floral-symmetry research, Neal *et al.* (1998) came to  
97 two relevant conclusions: (1) bilaterally symmetrical flowers are usually laterally oriented  
98 (face sideways), and (2) floral orientation usually exhibits less within-population variation in  
99 plants with bilaterally symmetrical flowers than in plants with radially symmetrical flowers  
100 (see also Nikkeshi *et al.*, 2015). Both observations are consistent with the operation of  
101 selection for accurate pollination in the evolution of bilaterally symmetric flowers.

102 In this context, it is interesting to think about what kinds of flowers have experienced  
103 the strongest selection for particular orientations. Floral orientation may be a critical factor in  
104 phenotypic and ecological specialization (*sensu* Ollerton *et al.* 2007) of flowers (e.g. Berg,  
105 1960; Fenster *et al.*, 2009). Upwards-facing (vertical) flowers can be approached from many  
106 directions (Fig. 1a; Fenster *et al.*, 2009), and thus might not experience fitness decreases from  
107 small changes in orientation. In contrast, laterally oriented flowers with bilateral symmetry  
108 are approached from consistent directions by pollinators (Fig. 1b,c; Robertson 1888a,b,c;  
109 Fenster *et al.*, 2009); plants with such flowers may incur significantly reduced fecundity  
110 when their flowers vary from the average floral position (“floral misorientation”) because  
111 they attract fewer pollinators or experience misplacement of anther and stigma contacts with  
112 the pollinator, relative to the rest of the population, as noted above.

113

#### 114 *Floral reorientation*

115 If floral orientation is important to the proper functioning of flowers and, hence, plant  
116 reproductive fitness, we predict that plants have the capacity to reorient their flowers if they  
117 become misoriented by some accidental event, such as the bending of a peduncle or stem, at  
118 least in plant species with flowers lasting longer than it takes for reorientation to be  
119 manifested. Rapid, reversible, turgor-mediated reorientation of leaves relative to the sun  
120 (heliotropism) has been well documented and shown to increase photosynthesis

121 (diaheliotropism), and/or reduce transpiration (paraheliotropism; Darwin, 1880; Ehleringer  
122 and Forseth, 1980). Similarly, stems and roots can, through differential growth, reorient  
123 relative to light (phototropism) and gravity (geotropism/gravitropism; Darwin, 1880;  
124 Hangarter, 1997; Raven and Johnson 2002; Christie and Murphy, 2013). Flower and  
125 flowering-shoot reorientation ought to represent natural extensions of such movement  
126 capabilities, yet this phenomenon has been remarkably little-studied. There has been some  
127 work on the movement of individual floral parts, such as petal closure in response to cold or  
128 nightfall (Darwin, 1862, 1880; Bynum and Smith, 2001; Armbruster *et al.*, 2006; Prokop and  
129 Fedor, 2016; Kemp and Ellis, 2019) or the movement of stamens to reduce intersexual  
130 interference (Sprengel, 1793; Martens, 1936; Ren, 2010; Ren and Tang, 2012; Armbruster *et*  
131 *al.*, 2014a). However, the only studies on whole-flower reorientation of which we are aware  
132 are descriptions of floral heliotropism in response to the sun's position (see review in van der  
133 Kooi *et al.*, 2019) and recent work by Yon *et al.* (2017) and Haverkamp *et al.* (2019) on the  
134 daily shift of floral orientation in *Nicotiana attenuata* from upwards by night (promoting  
135 pollination) to downwards by day (keeping interior of flowers cooler). Despite the lack of  
136 literature, however, we expect that, in the absence of constraints, many plants species have  
137 evolved the ability to adjust the orientation of flowers after mishaps knock them out of the  
138 alignment that best promotes pollination ("corrective floral reorientation").

139         The lack of work on reorientation of flowers in response to accidents is a motivation  
140 for empirical observations to assess the potential prevalence and significance this  
141 phenomenon. Here we provide observations on 23 species of plants from multiple sites on  
142 four continents. We emphasize the taxonomic spread and diversity of mechanisms that plants  
143 employ to reorient flowers. Taken together, these observations suggest both multiple origins  
144 of the capacity to reorient flowers and its importance in successful plant reproduction in  
145 changing or unstable environments.

#### 147 *Adaptive accuracy of pollination*

148         The effect of floral reorientation on plant reproductive success is best understood and  
149 quantified in terms of the adaptive accuracy of flowers with respect to pollination (e.g.  
150 Poblete Palacios *et al.*, 2019). Adaptive accuracy relates phenotype to fitness by including  
151 both trait precision and mean optimality (Armbruster *et al.*, 2004, 2009b; Hansen *et al.*,  
152 2006). As applied to pollination, "fundamental" floral accuracy (sensu Armbruster 2014)  
153 links individual plant phenotypes and the population mean phenotype to inferred fitness.  
154 Previous studies of pollination accuracy have tacitly assumed that flowers have a

155 characteristic orientation, and that accuracy is influenced by this orientation due to its effects  
156 on the positions of pollen placement on, and retrieval from, animal pollinators (see  
157 Armbruster, 2014; Armbruster *et al.*, 2014b). In a typical bilaterally symmetrical flower, the  
158 position of the anthers, relative to where the pollinator lands on, or enters, the flower or  
159 blossom (cluster of florets acting like a flower), determines where pollen is placed on the  
160 pollinator. Similarly, the position of the stigma determines where the stigma contacts the  
161 pollinator and picks up pollen. The optimal anther position for an individual flower is that  
162 position resulting in pollen being placed on the pollinator at the point where the stigmas of  
163 other flowers in the population are expected to contact the pollinator, as estimated by the  
164 mean stigma position for the population. Similarly, the optimal position of the stigma of an  
165 individual flower is the position that results in its stigmas contacting the pollinator in the site  
166 where pollen is expected to be deposited, as determined by the population-mean anther  
167 position.

168 Adaptive inaccuracy, the complement of accuracy, captures the deviation of an  
169 individual or population from the theoretical or empirically estimated optimal phenotype.  
170 This is a measure of population-level or individual-level maladaptation, i.e. the “phenotypic  
171 load” (by analogy with genetic load)

$$172$$
$$173 \quad \text{Adaptive Inaccuracy} = (\text{Trait Mean} - \text{Optimum})^2 + \text{VAR}_{\text{trait}} + \text{VAR}_{\text{optimum}} \quad \text{Eq. 1}$$
$$174$$

175 where the optimum for male floral function is the population-mean location of the stigmas,  
176 and the optimum for female function is the population-mean location of anthers (Armbruster  
177 *et al.*, 2004, 2009a, 2009b; Hansen *et al.*, 2006).

178 Following this logic, the adaptive inaccuracy of the male component of pollination  
179 captures the fitness decrement associated with departure of the mean anther position in a  
180 flower, a plant, or a population, from the optimum (difference squared) plus the imprecision  
181 (variance) in anther position. In turn, the adaptive inaccuracy of the female component of  
182 pollination fitness captures the mean deviation of the stigma of a flower, plant, or population,  
183 from the optimal stigma position (difference squared) plus the imprecision (variance) in  
184 stigma positions. These measurements have usually been assessed in linear dimensions of the  
185 flowers, for example by relating the pistil length to the stamen length. However, the  
186 approach can be extended to 2- or 3-dimensional space using Euclidean distances  
187 (Armbruster *et al.*, 2014a).

188

189

190

## Materials and Methods

191

192

193

194

195

196

197

198

199

200

201

202

We observed plant responses to both natural and manipulative experiments that shifted flowers from their normal orientation. We observed the effects of accidents changing floral orientation in *Tricyrtis formosana* (Liliaceae; UK), *Passiflora caerulea* (Passifloraceae; UK), *Delphinium glaucum*, *Aconitum delphinifolium* (Ranunculaceae; Alaska), and *Stylidium ciliatum* (Stylidiaceae; Western Australia). Manipulative experiments on *Aconitum delphinifolium* and *Stylidium ciliatum*, plus an opportunistic sample of 18 additional species (Tables 1, 2) involved misorienting flowers by tethering inflorescences or flowers so that flowers were either 45° (Ecuador) or 90° (elsewhere) off their normal orientation. In one case (*Pelargonium* sp.), we transplanted one plant to achieve the same effect. We then measured floral orientation in each species over the next few days after the manipulation. Experiments in Ecuador were conducted by NM and those in Australia, North America, and Europe by WSA.

203

204

205

206

207

208

209

210

211

212

213

214

215

216

217

218

219

220

221

Where possible, two-dimensional adaptive inaccuracies, scaled to the squared means of flower diameter, were calculated from field measurements or via photographs, measured with ImageJ (Rasband, 1997-2018). We used Equation 1, but omitted the optimum-variance term due to missing information (most species) or, in the case of *Chamerion angustifolium*, in order to make independent estimates of male and female inaccuracies (see Armbruster *et al.*, 2009a, 2014b). The positions of fertile parts were estimated in orthogonal 2-D space, and Euclidian distances from the optimal position were calculated. For most species, the original orientation was assumed to be optimal, and the starting positional imprecisions (variances) were not assessed or incorporated in the inaccuracy calculation (i.e. natural inaccuracy was assumed to be 0%, which corresponds to vertical orientation with no variation). Because adaptive inaccuracy is best represented as the population of Euclidian distances from the optimum, angular data were transformed into 2-dimensional Euclidean distances based on unit circles (radius = 1; Ecuador data), where inaccuracies were scaled to the square of the mean diameter (= 4). For *Chamerion angustifolium* (= *Epilobium angustifolium*, = *Chamaenerion angustifolium*; nomenclature following Elven 2019), stigma positions and anther positions were separately assessed from photos, and their natural (starting) imprecisions and inaccuracies were measured directly. The population mean stamen position (unmanipulated) was treated as the optimum for stigma position, and the population mean stigma position (unmanipulated) was treated as the optimum for stamen position. All

222 distances were measured in proportions of sepal length (SL) and the resulting inaccuracies  
223 were scaled to  $(2*SL)^2$ , a joint measure of flower size and photographic magnification.

224 To assess the adaptive value of floral reorientation, the inaccuracies of the  
225 autonomously reoriented (“corrected”) stigma and/or stamen positions were compared to  
226 inaccuracies of their initial positions immediately after the manipulation. Reorientation  
227 responses are thus also reported as the percent improvement in accuracy afforded by  
228 reorientation relative to the total decrement caused by experimental tethering.

229 Under the hypothesis that floral reorientation is adaptive because it restores adaptive  
230 accuracy of misoriented flowers, we expected to see reorientation best developed in plants  
231 with bilaterally symmetrical flowers, which generally have more precise pollen placement  
232 and stigma contact with pollinators. To test this idea, we made two planned comparisons of  
233 reorientation after experimental misorientation. Each comparison was between species with  
234 bilaterally symmetrical flowers and species with more-or-less radially symmetrical flowers.  
235 The first comparison involved assessing the proportion of flowers reorienting to within  $30^\circ$  of  
236 the initial orientation after  $90^\circ$  misorientation of flowers of four bilaterally symmetrical  
237 species and three radially symmetrical species (Australia). The species assessed were  
238 *Agapanthus* sp. (bilaterally symmetrical fertile whorls) and three species of *Stylidium* (all  
239 floral whorls bilaterally symmetrical) vs. *Clematis* sp., *Stackhousia* sp., and *Mandevilla* sp.  
240 (all floral whorls essentially radially symmetrical) The second comparison involved  
241 measuring the angular recovery after  $45^\circ$  misorientation of flowers of four bilaterally  
242 symmetrical species and three radially symmetrical species (Ecuador; see Table 1). The  
243 species assessed were *Impatiens* sp., *Burmeistera sodiroana*, *Centropogon nigricans*, and  
244 *Salvia* sp. (all floral whorls bilaterally symmetrical) vs. *Citrus* sp., *Carica papaya* (all floral  
245 whorls radially symmetrical), and *Cavendishia bracteata* (radially symmetrical perianths but  
246 weakly bilaterally symmetrical fertile whorls).

247

248

249

## Results

### *Mechanisms of floral reorientation*

251 The survey species revealed phylogenetically widespread reorientation, at least in  
252 bilaterally symmetrical flowers. Several distinct mechanisms were involved in reorientation  
253 of flowers and restoration of floral accuracy (Tables 2, 3). These mechanisms included  
254 movements of the peduncle (stalk of an inflorescence) or pedicel (stalk of an individual  
255 flower) and varied from species to species. Often two or more mechanisms operated in a

256 single species. We recognized four distinct potential mechanisms of floral reorientation:  
257 peduncle bending, pedicel bending, pedicel rotation, and bending/twisting of sexual organs.

258 *Peduncle bending.* We observed bending of the inflorescence stalk leading to partial  
259 or full restoration of correct floral orientation (with minimal pedicel bending or rotation) in  
260 *Dactylorhiza fuchsii* (Orchidaceae; Fig. 2) and a bilaterally symmetrical *Pelargonium*  
261 species. We also observed restoration of floral orientation by bending of the peduncle tip in  
262 *Stylidium* spp., *Aconitum delphinifolium*, *Delphinium glaucum*, and *Chamerion*  
263 *angustifolium*. In these last four species, peduncle bending occurred as a slow response  
264 associated with new growth, in combination with other, faster reorientation processes.

265 *Pedicel bending and/or rotation.* We observed corrective floral reorientation by  
266 pedicel bending in combination with some rotation in *Aconitum delphinifolium* (Fig. 3),  
267 *Delphinium glaucum*, *Tricyrtis formosana*, *Salvia* sp., *Burmeistera sodiroana*, *Centropogon*  
268 *nigricans*, and *Impatiens* sp. We observed comparatively rapid reorientation of flowers  
269 primarily through rotation of the pedicel (possibly in combination with some bending) in  
270 *Agapanthus* sp., *Stylidium* spp. (Fig. 4), *Diascia* spp., and *Nemesia* sp. (Table 2).

271 *Bending and twisting of fertile parts only.* We observed reorientation of the fertile  
272 parts (but not the perianth) in *Chamerion angustifolium*. This species has protandrous flowers  
273 with a radially symmetrical calyx and a quasi-bisymmetric corolla, but with fertile parts  
274 strongly deflected downwards and thus bilaterally symmetrical. Accurate repositioning (to  
275 the ventral location) of anthers was restored very quickly by filament bending or in some  
276 cases, passive filament drooping, but with high imprecision (stamens with dehisced anthers  
277 did not reorient by drooping or bending). Accurate stigma positioning was restored over  
278 several days by style bending prior to spreading of the stigma lobes, but only in flowers that  
279 were not yet in the female stage at time of manipulation. Female-stage flowers (with  
280 stigmatic lobes already spread) did not reorient styles to restore accurate stigma position.

281

#### 282 *Interactions between reorientation mechanisms*

283 Although we pooled pedicel rotation and pedicel bending as a single mechanisms of  
284 reorientation in the above description, these are actually two distinct mechanisms (Table 3).  
285 However, it is often hard to determine whether one, the other, or both are operating. This is  
286 an area needing further research. When the pedicel is relatively short, it seems that primarily  
287 rotation is occurring. When the pedicel is longer, bending seems to predominate (e.g. Fig. 3;  
288 Table 3). However, ruling out the alternative mechanism is not possible without more  
289 detailed study.

290 We observed bending of the main stem in the transplant experiment with the  
291 *Pelargonium* with bilaterally symmetrical flowers (Tables 1, 2). The direct effect of stem  
292 bending on floral orientation was negative, i.e. moved the floral orientation away from the  
293 optimum. However, this effect was compensated by further bending of the peduncle,  
294 ultimately resulting in the peduncle having undergone sigmoidal bending (Fig. 5). The  
295 bending of the stem led to restoring the original leaf orientation (presumably improving light  
296 capture), as well as restoring the growing axis to vertical. Although we have not observed  
297 any examples of bending of the stem as a mechanism for restoring floral orientation, it  
298 remains a possibility.

299 In *Stylidium* spp., *Aconitum delphinifolium*, and *Delphinium glaucum*, we observed  
300 restoration of floral orientation by pedicel rotation or bending, in combination with a slower  
301 response of the peduncle bending upward. In *Chamerion angustifolium*, slow peduncle  
302 bending occurred in combination with rapid reorientation of stamens and styles. This  
303 combination of reorientation responses is probably common among plants with bilaterally  
304 symmetrical flowers borne in elongated inflorescences, such as spikes.

305

#### 306 *Effect of reorientation on floral adaptive accuracies of bilaterally symmetrical flowers*

307 The corrective reorientation of flowers or fertile parts through rotation or bending led  
308 to dramatic reductions in adaptive inaccuracy (= improved accuracy) in most species (Table  
309 2). In general, species with bilaterally symmetrical fertile whorls exhibited large  
310 improvements in pollination accuracy, with 77.8% to 99.9% recovery of the original accuracy  
311 through corrective reorientation within 10-48 hours after experimental misorientation. In  
312 *Chamerion angustifolia*, restoration of accuracy occurred through corrective reorientation of  
313 fertile parts rather than rotation of entire flowers. This led to recovery of accuracy by up to  
314 89.3% for stamens and 91.7% for stigmas. In contrast, there was very little change in the  
315 pollination accuracy of flowers with bilaterally symmetrical perianths but with radial  
316 symmetry of fertile whorls (androecium and gynoecium), even though they showed whole-  
317 flower reorientation (*Aconitum*, *Delphinium*; Table 2). The advantage of rotation in such  
318 cases is more likely to be related to pollinator attraction and flower handling (i.e. flower-  
319 pollinator fit with respect to reward access), which is not captured by the pollination-  
320 inaccuracy measurement.

321

#### 322 *Planned comparisons of reorientation in bilaterally vs. radially symmetrical flowers*

323 If floral reorientation is simply a consequence of normal plant development and shoot  
324 orientation rather than an adaption related to improving pollination, the extent of floral  
325 reorientation in plants with radially symmetrical flowers should be to be similar to that seen  
326 in plants with bilaterally symmetrical flowers. The alternative hypothesis is that bilaterally  
327 symmetrical flowers show greater reorientation ability, as noted above.

328 In Australia, an average ( $\pm$  SE) of 3.70% ( $\pm$  3.70%; n = 3) of the flowers of species  
329 with radially symmetrical flowers recovered their orientation to within 30° of the original. In  
330 contrast, 95.5% ( $\pm$  1.78%; n= 4) of flowers on species with bilaterally symmetrical flowers  
331 showed recovery of orientation to within 30° of the original orientation (Fig. 6). Note that the  
332 difference was “significant” with a parametric test (independent-samples t-test, not assuming  
333 equal variances, data subjected to angular transformation:  $t = 9.80$ ,  $P = 0.002$ ), and  
334 marginally “significant” with a non-parametric test (Mann-Whitney:  $T = 10$ ,  $P = 0.05$ ).  
335 However, “significance” should not be interpreted strictly because the limited sample  
336 precluded phylogenetic correction (see Felsenstein, 1985; Armbruster, 1992).

337 In Ecuador, the reorientation responses were absent in the two radially symmetrical  
338 species (*Carica papaya* and *Citrus* sp.). *Cavendishia bracteata* displayed an intermediate  
339 level of recovery of 9.4° in 24 hours. This was markedly less than the four fully bilaterally  
340 symmetrical species (Table 2; Fig. 7). The mean corrective reorientation ( $\pm$  SE) was 5.18° ( $\pm$   
341 2.14°; n = 3) in species with radially symmetric perianths, versus 35.2° ( $\pm$  4.09°; n= 4) in  
342 species with bilaterally symmetrical perianths (Fig. 7, independent-samples t-test, not  
343 assuming equal variances:  $t = 6.49$ ,  $P = 0.002$ ). The same phylogenetic caution regarding  
344 “significance” mentioned in the previous paragraph applies to these results as well.

345

#### 346 *Comparison of reorientation in two similar, radially symmetrical flowers*

347 After conducting the above planned comparisons, we added two radially symmetrical,  
348 but phenotypically specialized flowers to this survey. *Passiflora* spp. generally bear one-day  
349 flowers that have a complex arrangement of a corolla platform and corona fringe surrounding  
350 a nectar trough. The fertile parts are borne a consistent distance above the corolla platform so  
351 that nectar-seeking bees of only a certain size will contact the five stamens in the male phase  
352 or the three stigmas (at the same height) in the female phase. *Trycirtis formosana* is a  
353 distinctive lily with flowers almost perfectly convergent on *Passiflora* flowers, except that  
354 the nectar is held in series of 3 pairs of saccate spurs at the base of the sepals, rather than in a  
355 trough (Table 1; Figure 1a). In both cases, we could expect floral function and bee pollination  
356 to work best when flowers face upwards. (Note that there is a radiation of floral orientations

357 in *Passiflora*, with many hummingbird-pollinated and bat pollinated species having laterally  
358 oriented flowers, often with bilaterally oriented fertile whorls, and some bee-pollinated and  
359 some bat-pollinated species having pendent flowers. Here we are referring only to classic  
360 bee-pollinated species like *P. caerulea* and *P. foetida* with normally upward-facing flowers.)

361 Although the flowers and pollination of these two species are uncannily similar, the  
362 difference in the variation in their floral orientation could not have been greater. *Passiflora*  
363 *caerulea* had a large proportion of its flowers apparently misoriented and showed no ability  
364 to correctively reorient them (Table 2). In contrast, *Tricyrtis formosana* had almost all of its  
365 flowers facing perfectly upwards, and, when stems collapse from the vertical, flowers quickly  
366 reorient (usually within a day) by pedicel bending (Table 2). This contrast may be related to  
367 one or both of two factors: *Passiflora* is a lax vine with short-lived (usually 1-day) flowers,  
368 and *Tricyrtis* is a rhizomatous herb with usually erect ramets and long-lived flowers (4+  
369 days).

370

371

## Discussion

372 Floral orientation is critical for accurate pollen placement and retrieval, especially in  
373 bilaterally symmetrical (= zygomorphic, = monosymmetric) flowers. But mechanical  
374 accidents happen on occasion, such as misorientation of stems and scapes due to wind,  
375 herbivore damage, or coarse litter falling from above. Even if a plant survives, fitness costs  
376 can be large if pollinators fail to visit misoriented flowers or if pollen is now placed on  
377 pollinators (or stigmas contact them) in the “wrong” place relative to the location of stigma  
378 (and anther) contact by the rest of the population (i.e. if flowers experience reduced  
379 pollination accuracy). Because the fitness cost of floral misorientation is potentially so great,  
380 we expected to find plants to have evolved mechanisms to reorient flowers and thus restore  
381 pollination accuracy and pollinator fit after accidents. We found that most species with  
382 bilaterally symmetric flowers exhibited one or a combination of distinct mechanisms of  
383 corrective floral reorientation (Table 3).

384

385 Experimental misorientation of flowers by 90° of rotation reduced the theoretical  
386 pollination accuracy of bilaterally symmetrical flowers by up to about 50% of the maximal  
387 decrement (= 180° of rotation). Natural corrective reorientation of these flowers or flower  
388 parts returned pollination accuracy to within about 5% of the starting maximum (Table 2, Fig.  
389 6). Similar results were observed with experimental floral misorientation by 45° of rotation:  
390 the theoretical pollination accuracy of bilaterally symmetrical flowers was reduced by about  
15% of the maximum possible decrement. Natural corrective reorientation of these flowers

391 returned pollination accuracy to within a few percent of the starting maximum (Table 2, Fig.  
392 7). Thus, our survey suggests that most plants with bilaterally symmetrical flowers have the  
393 capacity to reorient their flowers, returning pollination accuracy to within a few percent of  
394 the original value within a day or two.

395 It is interesting that two species with bilaterally symmetrical perianths but radially  
396 symmetrical fertile parts, *Aconitum* and *Delphinium*, also showed dramatic corrective  
397 reorientation. For these species, we estimated that pollination accuracy would be unaffected  
398 by misorientation, because the stamens and stigmas are centrally located and their orientation  
399 would not affect sites of pollen placement or stigma contact. However, reorientation may be  
400 adaptive because attractiveness depends on pollinators handling the flowers and reaching the  
401 nectar efficiently. The nectar spur being in the “wrong” place in misoriented flowers may  
402 reduce attractiveness (because of reduced nectar accessibility) and visitation rates. Hence  
403 attraction, not pollination efficiency, is likely a key factor in some species (i.e. those with  
404 radially symmetrical fertile whorls but bilaterally symmetrical perianths).

405 In contrast, species with bilaterally symmetrical fertile whorls but with radially or  
406 sub-radially symmetrical perianths (e.g. *Chamerion*, *Agapanthus*, and, to a lesser extent,  
407 *Cavendishia*) do experience some improvement in pollination accuracy with corrective  
408 reorientation of flowers or fertile floral parts. Visitation rates are presumably unaffected by  
409 rotation of the corolla, however. Indeed, *Chamerion* has not evolved the capacity to  
410 correctively reorient the perianth --only the fertile parts move correctively, whereas  
411 *Agapanthus* rotates the entire flower.

412 Not all radially symmetrical flowers are unable to reorient. Notably, *Tricyrtis*  
413 *formosana* showed a strong and rapid response to misorientation, usually restoring upwards  
414 orientation of the misoriented flowers within a day. However, *Passiflora caerulea*, with  
415 similarly complex flowers pollinated in a similar fashion, did not reorient its flowers. The  
416 difference may be explained by the *Tricyrtis* having multi-day flowers and the *Passiflora* 1-  
417 or 2-day flowers. Reorientation in species with short-lived flowers may not happen fast  
418 enough to affect pollination fitness significantly. Indeed, all the species we examined in this  
419 study that had the ability to reorient flowers correctively had flowers lasting several days or  
420 longer.

421 We suggest that corrective reorientation of flowers after accidents is an  
422 underappreciated plant behaviour worthy of greater scrutiny. It would be valuable to next  
423 assess experimentally the extent to which reorientation increases pollinator visitation and/or  
424 pollen transfer relative to flowers that remain misoriented. Further research may reveal other

425 morphological and developmental feature of flowers and inflorescences to be heretofore  
426 unappreciated adaptations for floral reorientation after mechanical accidents. For example,  
427 the evolution of elongated pedicels could be favoured because they promote the capacity for  
428 rapid floral reorientation (see Figs. 1b, 2). Future research on floral function and pollination  
429 should explore such possibilities, as well as extend the sampling of reorientation capabilities  
430 across a broader range of flowering plant species.

431

432

### Acknowledgements

433

434

435

436

437

438

### Author Contributions

439

440

441

442

### References

443

444

445

446

447

448

449

450

451

452

453

454

455

456

457

WSA acknowledges grant support from the Royal Society of London and from the British Council. WSA thanks Juliet Wege for help in identifying plants and Marjory Caw for hospitality during stays in Parkerville, WA. NM acknowledges the National Geographic Society for grant support and Daniela Proaño for assistance in the field.

Both authors conceived of the initial hypotheses and conducted fieldwork. WSA wrote the first draft, and both authors contributed revisions.

**Aizen MA. 2003.** Down-facing flowers, hummingbirds and rain. *Taxon* **52**: 675–80.

**Armbruster WS. 1992.** Phylogeny and the evolution of plant-animal interactions. *BioScience* **42**: 12-20.

**Armbruster WS. 2014.** Floral specialization and angiosperm diversity: phenotypic divergence, fitness trade-offs and realized pollination accuracy. *AoB Plants*. **6**: plu003.

**Armbruster WS, Corbet SA, Vey AJM, Liu SJ, Huang SQ. 2014a.** In the right place at the right time: *Parnassia* resolves the herkogamy dilemma by accurate repositioning of stamens and stigmas. *Annals of Botany* **113**: 97-103.

**Armbruster WS, Edwards ME, Debevec EM. 1994.** Character displacement generates assemblage structure of Western Australian triggerplants (*Stylidium*). *Ecology* **75**: 315-329.

**Armbruster WS, Hansen TF, Pélabon C, Bolstad GH. 2009a.** Macroevolutionary patterns of pollination accuracy: A comparison of three genera. *New Phytologist* **183**: 600-617.

- 458 **Armbruster WS, Hansen TF, Pélabon C, Pérez-Barrales R, Maad J. 2009b.** The adaptive  
459 accuracy of flowers: measurement and microevolutionary patterns. *Annals of Botany*  
460 **103**: 1529-1545.
- 461 **Armbruster WS, Pélabon C, Hansen T, Mulder CPH. 2004.** Floral integration and  
462 modularity: distinguishing complex adaptations from genetic constraints. Pp. 23-49  
463 in, M. Pigliucci and K. A. Preston (eds.), *Phenotypic Integration. Studying the*  
464 *Ecology and Evolution of Complex Phenotypes*, Oxford University Press, Oxford,  
465 UK.
- 466 **Armbruster WS, Pérez-Barrales R, Arroyo J, Edwards ME, Vargas P. 2006.** Three-  
467 dimensional reciprocity of floral morphs in wild flax (*Linum suffruticosum*): A new  
468 twist on heterostyly. *New Phytologist* **171**: 581–590.
- 469 **Armbruster WS, Shi X-Q, Huang S-Q. 2014b.** Do specialised flowers promote  
470 reproductive isolation? Realised pollination accuracy of three sympatric *Pedicularis*  
471 species. *Annals of Botany* **113**: 331-340.
- 472 **Berg RL. 1960.** The ecological significance of correlation pleiades. *Evolution* **14**: 171–180.
- 473 **Bynum MR, Smith WK. 2001.** Floral movements in response to thunderstorms improve  
474 reproductive effort in the alpine species *Gentiana algida* (Gentianaceae). *American*  
475 *Journal of Botany* **88**: 1088–95.
- 476 **Castellanos MC, Wilson P, Thomson JD. 2004.** ‘Anti-bee’ and ‘pro-bird’ changes during  
477 the evolution of hummingbird pollination in *Penstemon* flowers. *Journal of*  
478 *Evolutionary Biology* **17**:876–885.
- 479 **Chang YH, Housley SN, Hart KS, Nardelli P, Nichols RT, Maas H, Cope TC. 2018.**  
480 Progressive adaptation of whole-limb kinematics after peripheral nerve injury.  
481 *Biology Open* **7**: UNSP bio028852 (DOI: 10.1242/bio.028852).
- 482 **Christie, J.M., and Murphy, A.S. (2013).** Shoot phototropism in higher plants: New light  
483 through old concepts. *American Journal of Botany* **100**: 35-46
- 484 **Darwin CR. 1862.** *On the various contrivances by which British and foreign orchids are*  
485 *fertilised by insects*. Murray, London.
- 486 **Darwin, CR. 1880.** *The power of movement in plants*. London: John Murray.
- 487 **Ehleringer J, Forseth I. 1980.** Solar tracking by plants. *Science* **210**: 1094-1098.
- 488 **Elven R (ed.). 2019.** *Annotated Checklist of the Panarctic Flora (PAF). Vascular Plants.*  
489 (www. <http://panarcticflora.org/>).

490 **Endress PK. 1994.** *Diversity and evolutionary biology of tropical flowers*. Cambridge  
491 University Press, Cambridge, UK (511 pp).

492 **Felsenstein J. 1985.** Phylogenies and the comparative method. *American Naturalist* **126**: 1-  
493 25.

494 **Fenster CB, Armbruster WS, Dudash MR. 2009.** Specialization of flowers: Is floral  
495 orientation an overlooked first step? *New Phytologist* **183**: 502-506.

496 **Frank ET, Schmitt T, Hovestadt T, Mitesser O, Stiegler J, Linsenmair KE. 2017.** Saving  
497 the injured: Rescue behavior in the termite-hunting ant *Megaponera analis*. *Science*  
498 *Advances* **3**: e1602187 (DOI: 10.1126/sciadv.1602187).

499 **Fulton M, Hodges SA. 1999.** Floral isolation between *Aquilegia formosa* and *Aquilegia*  
500 *pubescens*. *Proceedings of the Royal Society B-Biological Sciences* **266**: 2247-2252.

501 **Hansen TF, Carter, AJR, Pelabon C. 2006.** On adaptive accuracy and precision in natural  
502 populations *American Naturalist* **168**: 168-181.

503 **Hangarter RP 1997.** Gravity, light, and plant form. *Plant, Cell & Environment* **20**: 796–800.

504 **Haverkamp A, Li X, Hansson BS, Baldwin IT, Knaden M, Yon F. 2019.** Flower  
505 movement balances pollinator needs and pollen protection. *Ecology* **100**: UNSP  
506 e02553.

507 **Huang SQ, Takahashi Y, Dafni A. 2002.** Why does the flower stalk of *Pulsatilla cernua*  
508 (Ranunculaceae) bend during anthesis? *American Journal of Botany* **89**: 1599–603.

509 **Kemp JE, Ellis AG. 2019.** Cryptic petal coloration decreases floral apparency and herbivory  
510 in nocturnally closing daisies. *Functional Ecology* **33**: 2130–2141.

511 **Lin SY, Forrest JRK. 2019.** The function of floral orientation in bluebells: interactions with  
512 pollinators and rain in two species of *Mertensia* (Boraginaceae). *Journal of Plant*  
513 *Ecology* **12**: 113-123.

514 **Martens P. 1936.** Pollination et biologie florale chez *Parnassia palustris*. *Bulletin de la*  
515 *Société Royale Botanique Belgique* **68**: 183–221.

516 **Neal PR, Dafni A, Giurfa M. 1998.** Floral symmetry and its role in plant-pollinator systems:  
517 terminology, distribution, and hypotheses. *Annual Review of Ecology & Systematics*  
518 **29**: 345-373.

519 **Nikkeshi A, Kurimoto D, Ushimaru A. 2015.** Low flower-size variation in bilaterally  
520 symmetrical flowers: Support for the pollination precision hypothesis. *American*  
521 *Journal of Botany* **102**: 2032-2040.

522 **Ollerton J, Killick A, Lamborn E, Watts S, Whiston M. 2007.** Multiple meanings and  
523 modes: on the many ways to be a generalist flower. *Taxon* **56**: 717– 728.

- 524 **Poblete Palacios, JA, Soterias F, Cocucci AA. 2019.** Mechanical fit between flower and  
525 pollinators in relation to realized precision and accuracy in the hummingbird-  
526 pollinated *Dolichandra cynanchoides*. *Biological Journal of the Linnean Society* **126**:  
527 655–665.
- 528 **Prokop P, Fedor P. 2016.** Why do flowers close at night? Experiments with the lesser  
529 celandine *Ficaria verna* Huds. (Ranunculaceae). *Biological Journal of the Linnean*  
530 *Society* **118**: 698-702.
- 531 **Rasband, W.S. 1997-2018.** ImageJ. U. S. National Institutes of Health, Bethesda, Maryland,  
532 USA, <https://imagej.nih.gov/ij/>.
- 533 **Raven PH, Johnson GB. 2002.** *Biology, 6<sup>th</sup> edition*. McGraw-Hill, New York.
- 534 **Ren M-X. 2010.** Stamen movements in hermaphroditic flowers: diversity and adaptive  
535 significance. *Chinese Journal of Plant Ecology* **34**: 867–875.
- 536 **Ren M-X, Tang J-Y. 2012.** Up and down: stamen movements in *Ruta graveolens* (Rutaceae)  
537 enhance both outcrossing and delayed selfing. *Annals of Botany* **110**: 1017–1025.
- 538 **Reyes E, Sauquet H, Nadot S. 2016.** Perianth symmetry changed at least 199 times in  
539 angiosperm evolution. *Taxon* **65**: 945-964.
- 540 **Robertson C. 1888a,b,c.** Zygomorphy and its causes. I–III. *Botanical Gazette* **13**: 146–151,  
541 203–208, 224–230.
- 542 **Sprengel CK. 1793.** *Das Entdeckte Geheimnis der Natur im Bau und in der Befruchtung der*  
543 *Blumen*. Facsimile reprint 1972, J. Cramer, Lower Saxony, Germany: Lehre.
- 544 **Stebbins GL. 1951.** Natural selection and differentiation of angiosperm families. *Evolution*  
545 **5**: 299-324.
- 546 **Stebbins, GL. 1974.** *Flowering plants. Evolution above the species level*. Harvard University  
547 Press, Cambridge, MA, USA.
- 548 **Ushimaru A, Dohzono I, Takami Y, Hyodo F. 2009.** Flower orientation enhances pollen  
549 transfer in bilaterally symmetrical flowers. *Oecologia* **160**: 667-674.
- 550 **Ushimaru A, Hyodo F. 2005.** Why do bilaterally symmetrical flowers orient vertically?  
551 Flower orientation influences pollinator landing behaviour. *Evolutionary Ecology*  
552 *Research* **7**: 151-160.
- 553 **Ushimaru A, Kawase D, Imamura A. 2006.** Flowers adaptively face down-slope in 10  
554 forest-floor herbs. *Functional Ecology* **20**: 585-591.
- 555 **van der Kooi CJ, Kevan PG, Koski MH. 2019.** The thermal ecology of flowers. *Annals of*  
556 *Botany* **124**: 343-353.

- 557 **Wang H, Tie S, Yu D, Guo Y-H, Yang C-F. 2014a.** Change of floral orientation within an  
558 inflorescence affects pollinator behavior and pollination efficiency in a bee-pollinated  
559 plant, *Corydalis shearerii*. *PLoS ONE* **9**: e95381.
- 560 **Wang H, Xiao C-L, Gituru RW, Xiong Z, Yu D, Guo Y-H, Yang C-F. 2014b.** Change of  
561 floral orientation affects pollinator diversity and their relative importance in an alpine  
562 plant with generalized pollination system, *Geranium refractum* (Geraniaceae). *Plant*  
563 *Ecology* **215**: 1211-1219.
- 564 **Wang Y, Meng LL, Yang YP, Duan YW. 2010.** Change in floral orientation in *Anisodus*  
565 *luridus* (Solanaceae) protects pollen grains and facilitates development of fertilized  
566 ovules. *American Journal of Botany* **97**: 1618-1624.
- 567 **Yon F, Kessler D, Joo Y, Llorca LC, Kim SG, Baldwin IT. 2017.** Fitness consequences of  
568 altering floral circadian oscillations for *Nicotiana attenuata*. *Journal of Integrative*  
569 *Plant Biology* **59**: 180-189.
- 570

571

## Tables

572

573 Table 1. Plant species used in manipulative experiments of floral misorientation.

Family	Species	Native (N) vs. Cultivated (C)	Sample size (plants)	Samples size (flowers)	Location
Amaryllidaceae	<i>Agapanthus</i> sp.	C	2	24	Pittwater, New South Wales, Australia
Apocynaceae	<i>Mandevilla</i> sp.	C	2	9	Pittwater, New South Wales, Australia
Balsaminaceae	<i>Impatiens</i> sp.	C	4	4	Siempre Verde Cloud Forest Reserve, Pichincha, Ecuador
Campanulaceae	<i>Burmeistera sodiroana</i> Zahlbr.	N	1	1	Siempre Verde Cloud Forest Reserve, Pichincha, Ecuador
Campanulaceae	<i>Centropogon nigricans</i> Zahlbr.	N	1	1	Siempre Verde Cloud Forest Reserve, Pichincha, Ecuador
Caricaceae	<i>Carica papaya</i> L.	C	4	4	Siempre Verde Cloud Forest Reserve, Pichincha, Ecuador
Celastraceae	<i>Stackhousia huegelii</i> Endl.	N	1	6	Mundaring Shire, Western Australia
Ericaceae	<i>Cavendishia bracteata</i> (Ruiz & Pav. ex J.St.-Hil.) Hoerold	N	5	5	Siempre Verde Cloud Forest Reserve, Pichincha, Ecuador
Geraniaceae	<i>Pelargonium</i> sp.	C	1	20	San Luis Range, California
Lamiaceae	<i>Salvia</i> sp.	N	5	5	Siempre Verde Cloud Forest Reserve, Pichincha, Ecuador
Liliaceae	<i>Tricyrtis formosana</i> Baker	C	3 (ramets)	7	Binstead, Isle of Wight, England
Onagraceae	<i>Chamerion angustifolium</i> (L.) Holub.	N	4	19	Goldstream Valley, Alaska, USA
Orchidaceae	<i>Dactylorhiza fuchsii</i> (Druce) Soó	N	3	21	Binstead, Isle of Wight, England
Passifloraceae	<i>Passiflora caerulea</i> L.	C	2	30	Binstead, Isle of Wight, England

Ranunculaceae	<i>Aconitum delphinifolium</i> DC.	N	4	25	Goldstream Valley, Alaska, USA
Ranunculaceae	<i>Clematis pubescens</i> Huegel ex Endl.	N	1	12	Mundaring Shire, Western Australia
Ranunculaceae	<i>Delphinium glaucum</i> S. Wats.	N	3	60	Goldstream Valley, Alaska, USA
Rutaceae	<i>Citrus</i> sp.	C	5	5	Siempre Verde Cloud Forest Reserve, Pichincha, Ecuador
Scrophulariaceae	<i>Diascia</i> spp.	C	5	15	Binstead, Isle of Wight, England
Scrophulariaceae	<i>Nemesia</i> sp.	C	4	13	Binstead, Isle of Wight, England
Stylidiaceae	<i>Stylidium ciliatum</i> Lindl.	N	6	30	Mundaring Shire, Western Australia
Stylidiaceae	<i>Stylidium hispidum</i> Lindl.	N	1	5	Mundaring Shire, Western Australia
Stylidiaceae	<i>Stylidium amoenum</i> R.Br.	N	3	11	Mundaring Shire, Western Australia

575  
 576 Table 2. Summary of floral responses to “natural” and manipulative experiments misorienting flowers  
 577

Family: Species	Misorientation “treatment”	Symmetry	Response	Change in mean <sup>2</sup> -scaled pollination inaccuracy* (% restoration towards original accuracy)	Effect	Time taken for response or duration of observation
Amaryllidaceae: <i>Agapanthus</i> sp.	manipulation	radial perianth, bilateral androecium & gynoecium	pedicel rotation	--	accurate orientation usually restored	2-3 days
Apocynaceae: <i>Mandevilla</i> sp.	manipulation	radial	pedicel rotation	0% change	no change in accuracy or pollinator foraging	10- 30° per day
Balsaminaceae: <i>Impatiens</i> sp.	manipulation	bilateral	pedicel rotation	14.6% → 2.87% (80.3%)	accurate orientation mostly restored	1 day
Campanulaceae: <i>Burmeistera sodiroana</i>	manipulation	bilateral	pedicel rotation	14.6% → 0.03% (99.8%)	accurate orientation fully restored	2 days (was bud when misorientated)
Campanulaceae: <i>Centropogon nigricans</i>	manipulation	bilateral	pedicel rotation	14.6% → 1.94% (86.7%)	accurate orientation fully restored	2 days (was bud when misorientated)
Caricaceae: <i>Carica papaya</i>	manipulation	radial	no rotation	0% change	no change in accuracy or pollinator foraging	2 days
Celastraceae: <i>Stackhousia huegelii</i>	manipulation	radial	no rotation	0% change	no change in accuracy or pollinator foraging	3 days
Ericaceae: <i>Cavendishia bracteata</i>	manipulation	radial perianth, bilateral androecium	pedicel rotation	14.6% → 10.0% (31.5%)	small improvement in stamen accuracy	1 - 2 days
Geraniaceae: <i>Pelargonium</i> sp.	manipulation	bilateral	peduncle bending	--	accurate orientation fully restored	1-2 days
Lamiaceae: <i>Salvia</i> sp.	manipulation	bilateral	pedicel rotation	14.6% → 0.24% (98.4%)	accurate orientation fully restored	1 day
Liliaceae: <i>Tricyrtis formosana</i>	natural “experiment”	radial	pedicel bending	--	upwards orientation restored	1-2 days

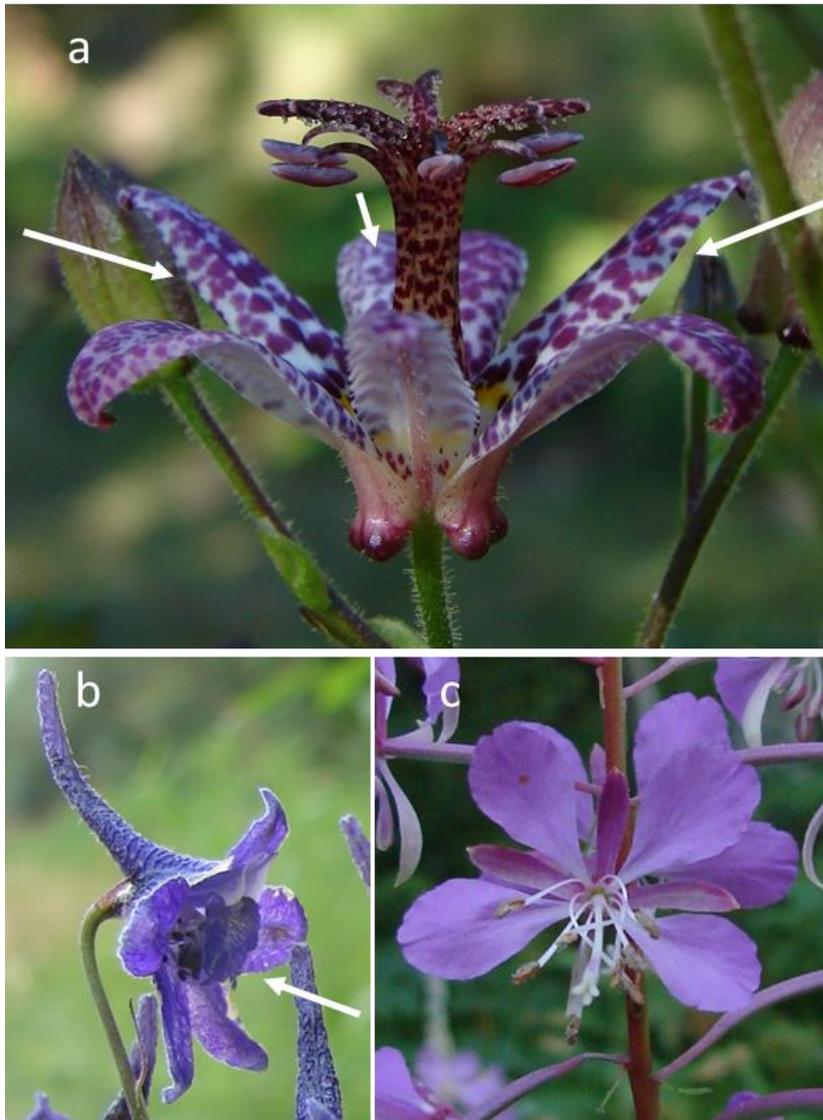
Onagraceae: <i>Chamerion angustifolium</i>	manipulation	calyx radial, corolla quasi-bisymmetric, androecium & gynoecium bilateral	Stamen and style bending (no pedicel rotation); (+bending of peduncle tip)	anthers: 31.7% → 3.40% (89.3%) stigmas: 26.3% → 2.18% (91.7%)	accurate anther and stigma positions mostly restored	reorientation of fertile parts: 1-2 days  bending of peduncle tip: 2-4 days
Orchidaceae: <i>Dactylorhiza fuchsii</i>	manipulation	bilateral	peduncle bending	73.6% → 7.83% (89.4%)	accurate orientation restored in young flowers	1-2.5 days
Passifloraceae: <i>Passiflora caerulea</i>	natural "experiment"	radial	no movement	--	no detectable upwards reorientation	no reorientation in 1-2 day lifetime of flower
Ranunculaceae: <i>Aconitum delphinifolium</i>	natural "experiment"	bilateral	pedicel bending	0% change	optimal orientation for foraging bumble bees fully restored	?
<i>Aconitum delphinifolium</i>	manipulation	perianth bilateral, fertile whorls radial	pedicel bending	0% change	optimal orientation for foraging bumble bees fully restored	1 day
Ranunculaceae: <i>Delphinium glaucum</i>	natural "experiment"	perianth bilateral, fertile whorls radial	pedicel bending	0% change	optimal orientation for foraging bumble bees fully restored	?
<i>Ranunculaceae: Clematis aff. pubescens</i>	manipulation	radial	no rotation	0% change	no change in accuracy or pollinator foraging	3 days of observation
Rutaceae: <i>Citrus sp.</i>	manipulation	radial	no rotation	0% change	no change in accuracy or pollinator foraging	2 days of observation
Scrophulariaceae: <i>Diascia sp.</i>	manipulation	bilateral	bending and twisting of pedicel	--	accurate reorientation usually partial, often stopping at about 30° from original position	2-3 days
Scrophulariaceae: <i>Nemesia sp.</i>	manipulation	bilateral	bending and twisting of pedicel	180° treatment: 100% → 0.07% (99.9%) 90° treatment: 50% → 11.1% (77.8%)	accurate reorientation in all but old flowers (1 excluded in each experiment)	15-34 hours  10 hours

Stylidiaceae: <i>Stylidium ciliatum</i>	manipulation and "natural" experiment	bilateral	pedicel rotation, (+ bending peduncle tip)	50.0% → 2.33% (95.3%)	accurate reorientation in all but old flowers	pedicle rotation: 1-2 days; peduncle bending: 3-4 days
<i>Stylidium hispidum</i>	manipulation	bilateral	pedicel rotation, (+ bending peduncle tip)	50.0% → 2.44% (95.1%)	accurate reorientation in all but old flowers	pedicle rotation: 1-2 days; peduncle bending: 3-4 days
<i>Stylidium. amoenum</i>	manipulation	bilateral	pedicel rotation, (+ bending peduncle tip)	50.0% → 7.12% (85.8%)	accurate reorientation in all but old flowers	pedicle rotation: 1-2 days; peduncle bending: 3-4 days

578

579 \*First number is starting inaccuracy after experimental misorientation, second number is finishing inaccuracy after corrective reorientation

Type of response	Description	Example taxa
1. Peduncle bending, (with minimal pedicel bending or rotation)	Base or tip of peduncle bends towards vertical leading to restoration of accuracy of all flowers or young flowers, respectively	-Only peduncle bends: <i>Dactylorhiza fuchsii</i> (Orchidaceae) <i>Pelargonium</i> sp. (species with bilaterally symmetrical flowers) (Geraniaceae) -Peduncle bends in combination with other mechanisms: <i>Chamerion angustifolium</i> (Onagraceae) <i>Aconitum delphinifolium</i> , <i>Delphinium glaucum</i> (Ranunculaceae) <i>Stylidium</i> spp. (Stylidiaceae)
2. Pedicel bending (with some rotation)	Bending of long pedicel restoring “correct” floral orientation	<i>Tricyrtis formosana</i> (Liliaceae), <i>Aconitum delphinifolium</i> (Ranunculaceae) <i>Delphinium glaucum</i> (Ranunculaceae) <i>Diascia</i> spp. (Scrophulariaceae)
3. Pedicel rotation (possibly with some bending)	Twisting of short pedicel rotating flower to the “correct” orientation	<i>Stylidium</i> spp. (Stylidiaceae); <i>Impatiens</i> sp. (Balsaminaceae), <i>Burmeistera sodiroana</i> <i>Centropogon nigricans</i> (Campanulaceae), <i>Salvia</i> sp. (Lamiaceae)
4. Bending (and twisting?) of fertile parts only	Bending of filaments and styles restore “correct” position of anthers and stigmas, respectively	<i>Chamerion angustifolium</i> (Onagraceae)
5. None	No significant change in orientation or change in orientation does not affect pollination accuracy	<i>Carica papaya</i> (Caricaceae) <i>Citrus</i> sp. (Rutaceae) <i>Clematis</i> sp. (Ranunculaceae) <i>Mandevilla</i> sp. (Apocynaceae) <i>Stackhousia</i> sp. (Stackhousiaceae)



587 Fig. 1. Examples of floral orientation and symmetry. (a) *Tricyrtis formosana*, (Liliaceae), a  
 588 species with upwards-facing flowers with radial symmetry; note that pollinators can approach  
 589 and land on the flower from any direction (arrows). (b) *Delphinium glaucum* (Ranunculaceae),  
 590 a species with laterally oriented flowers with bilaterally symmetrical calyces and corollas, but  
 591 with essentially radially symmetrical androecia and gynoecia at the centre. Note that the  
 592 bumble-bee pollinator can approach the flower and insert its proboscis from only one  
 593 direction (arrow). (c) *Chamerion angustifolium* (Onagraceae), a species with laterally  
 594 oriented flowers with radially symmetrical calyces and quasi-bisymmetric corollas; the  
 595 pendent androecia and gynoecia are bilaterally symmetrical or asymmetric (i.e. one or no line  
 596 of reflective symmetry).



599

600 Fig. 2. *Dactylorhiza fuchsii* tethered on 13.06.2019, 1300 GMT. (a) 13.06.2019, 1315 GMT.

601 (b) 14.06.2019, 1015 GMT. (c) 15.06.2019, 0928 GMT.

602

603



604

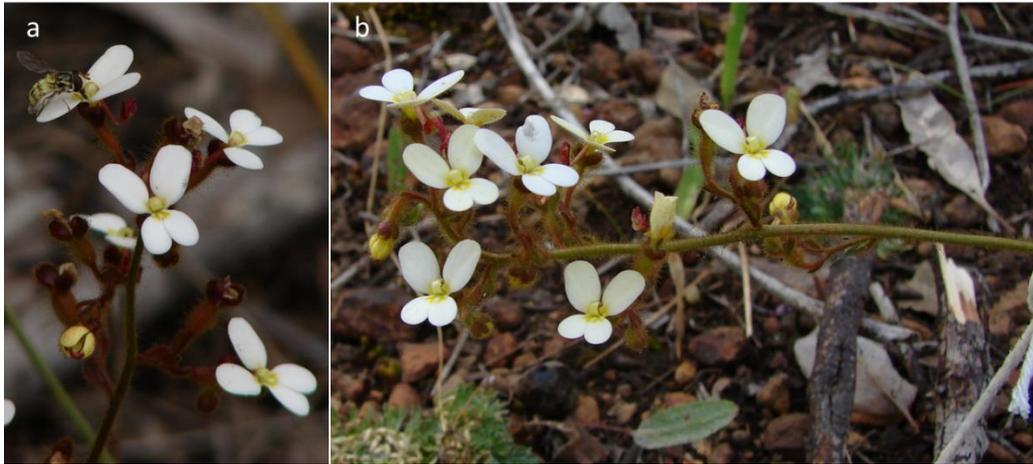
605 Fig. 3. *Aconitum delphinifolium* tethered on 10.07.2019, 1850 Alaska Summer Time. (a)

606 10.07.2019, 0853 Alaska Summer Time. (b) 10.07.2019, 1706 Alaska Summer Time. (c)

607 11.07.2019, 0909 Alaska Summer Time.

608

609



610

611 Fig. 4. Floral reorientation in *Styliidium ciliatum*. (a) Normal orientation. (b) Floral  
 612 reorientation two days after floral scape was tethered to the horizontal.

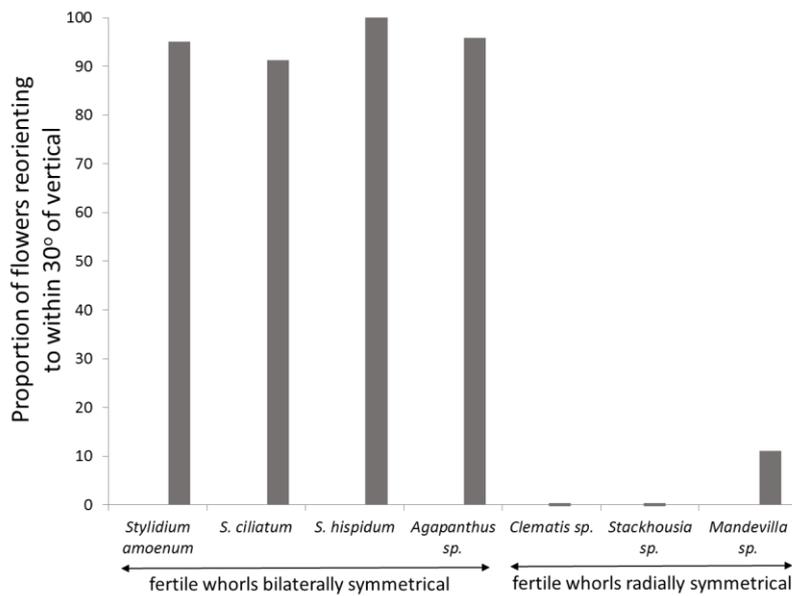
613



614

615 Fig. 5. *Pelargonium* sp. with bilaterally symmetrical flowers. Peduncle bending over 5 days  
 616 leading to restoration and maintenance of correct floral orientation. Day 0 (not shown):  
 617 Transplanted so main shoot and inflorescence is horizontal, i.e.  $90^\circ$  off original orientation;  
 618 both flowers and leaves are misoriented. (a) Days 1-2: Peduncle bends  $90^\circ$ , restoring  
 619 “correct” orientation of weakly bilaterally symmetrical flowers; leaves still “misoriented”.  
 620 (b) Day 5: Stem has reoriented  $90^\circ$ ; leaves are now back to the original horizontal positions  
 621 (presumably maximizing photosynthesis); meanwhile the peduncle has bent another  $180^\circ$  in  
 622 compensation, so peduncle is now sigmoidal. (c) Close-up of peduncle showing sigmoidal  
 623 bending and flowers in correct orientation.

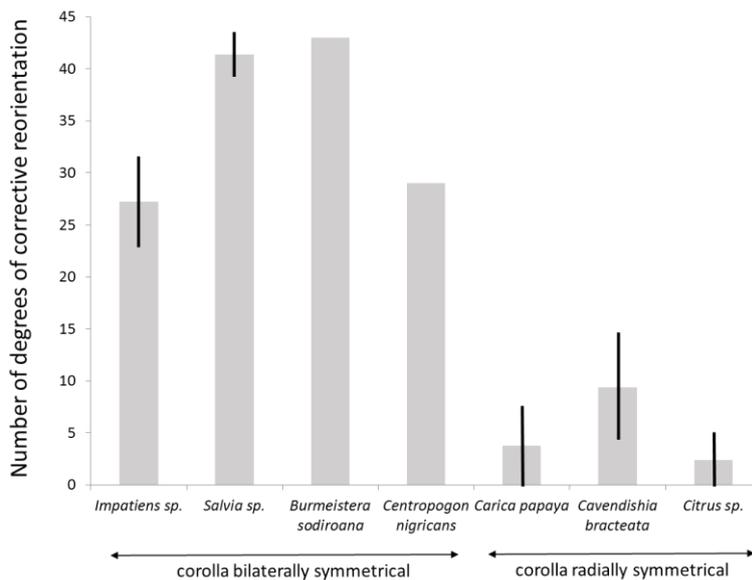
624



625

626 Fig. 6. Planned comparison of reorientation of bilaterally and radially symmetrical flowers in  
627 Australia. Percent of flowers returning to within 30° of original orientation 1-3 days after  
628 tethering to -90° (= vertical → horizontal).

629



630

631 Fig. 7. Planned comparison of reorientation of bilaterally and radially symmetrical flowers in  
632 Ecuador. Mean number of degrees of return towards vertical 24 hrs (48 hours for *Burmeistera*  
633 and *Centropogon*) after tethering to -45°. Bars are +/- 1 standard deviation. *Burmeistera* and  
634 *Centropogon* are missing SD bars because only one flower was successfully tracked for each  
635 species.