Floral reorientation: the restoration of pollination accuracy after accidents

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Summary

- Plants sometimes suffer mechanical injury. The nonlethal 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.

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 (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 (1888) 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 is 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, 1888; 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; Havercamp et al., 2019; Lin & 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 (Fulton & Hodges, 1999; Ushimaru & Hyodo, 2005; Ushimaru et al., 2006; 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 flowers in the population. The net result is lowering of both male and female components of reproductive fitness, as has been shown in a few empirical studies (Castellanos et al., 2004; Ushimaru et al., 2009; Wang et al., 2014a, b).

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

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

**Floral reorientation**

If floral orientation is important to the proper functioning of flowers and, hence, plant reproductive fitness, we predict that plants have the capacity to reorient their flowers if they become misoriented by some accidental event, such as the bending of a peduncle or stem, at least in plant species with flowers lasting longer than it takes for reorientation to be manifested. Rapid, reversible, turgor-mediated reorientation of leaves relative to the sun (heliotropism) has been well documented and shown to increase photosynthesis (diaheliotropism), and/or reduce transpiration (paraheliotropism; Darwin, 1880; Ehleringer & Forseth, 1980). Similarly, stems and roots can, through differential growth, reorient relative to light (phototropism) and gravity (geotropism/gravitropism; Darwin, 1880; Hangarter, 1997; Raven & Johnson, 2002; Christie & Murphy, 2013). Flower and flowering-shoot reorientation ought to represent natural extensions of such movement capabilities, yet this phenomenon has been remarkably little-studied. There has been some work on the movement of individual floral parts, such as petal closure in response to cold or nightfall (Darwin, 1862, 1880; Bynum & Smith, 2001; Armbruster et al., 2006; Prokop & Fedor, 2016; Kemp & Ellis, 2019) or the movement of stamens to reduce intersexual interference (Sprengel, 1793; Martens, 1936; Ren, 2010; Ren & Tang, 2012; Armbruster et al., 2014a). However, the only studies on whole-flower reorientation of which we are aware are descriptions of floral heliotropism in response to the sun’s position (see review in van der Kooi et al., 2019) and recent work by Yon et al. (2017) and Haverkamp et al. (2019) on the daily shift of floral orientation in Nicotiana attenuata from upwards by night (promoting pollination) to downwards by day (keeping the interior of flowers cooler). Despite the lack of...
Adaptive accuracy of pollination

The effect of floral reorientation on plant reproductive success is best understood and quantified in terms of the adaptive accuracy of flowers with respect to pollination (e.g. Poblete Palacios et al., 2019). Adaptive accuracy relates phenotype to fitness by including both trait precision and mean optimality (Armbruster et al., 2004, 2009b; Hansen et al., 2006). As applied to pollination, ‘fundamental’ floral accuracy (sensu Armbruster, 2014) links individual plant phenotypes and the population mean phenotype to inferred fitness. Previous studies of pollination accuracy have tacitly assumed that flowers have a characteristic orientation, and that accuracy is influenced by this orientation due to its effects on the positions of pollen placement on, and retrieval from, animal pollinators (see Armbruster, 2014; Armbruster et al., 2014b). In a typical bilaterally symmetrical flower, the position of the anthers, relative to where the pollinator lands on, or enters, the flower or blossom (cluster of florets acting like a flower), determines where pollen is placed on the pollinator. Similarly, the position of the stigma determines where the stigma contacts the pollinator and picks up pollen. The optimal anther position for an individual flower is that position resulting in pollen being placed on the pollinator at the point where the stigmas of other flowers in the population are expected to contact the pollinator, as estimated by the mean stigma position for the population. Similarly, the optimal position of the stigma of an individual flower is the position that results in its stigmas contacting the pollinator in the site where pollen is expected to be deposited, as determined by the population-mean anther position.

Adaptive inaccuracy, the inverse of accuracy, captures the deviation of an individual or population from the theoretical or empirically estimated optimal phenotype. This is a measure of population-level or individual-level maladaptation, that is the ‘phenotypic load’ (by analogy with genetic load).

\[
\text{Adaptive inaccuracy} = (\text{Trait mean} - \text{Optimum})^2 + \text{VAR}_{\text{trait}} + \text{VAR}_{\text{optimum}},
\]

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

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

Materials and Methods

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 and Aconitum delphinifolium (Ranunculaceae; Alaska), and Stylidium ciliatum (Stylidiaceae; Western Australia). Manipulative experiments on A. delphinifolium and S. 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.

Where possible, 2-D 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 Eqn 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-D Euclidean distances based on unit circles (radius = 1; Ecuador data), where inaccuracies were scaled to the square of the mean diameter (= 4). For C. angustifolium (= Epilobium angustifolium, = Chamaenerion angustifolium; nomenclature following Elven, 2019), stigma positions and anther positions were separately assessed from photographs, 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 distances were measured in proportions of sepal length (SL) and the resulting inaccuracies were scaled to \((2 \times \text{SL})^2\), a joint measure of flower size and photographic magnification.

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

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

### Results

#### Mechanisms of floral reorientation

The survey species revealed phylogenetically widespread reorientation, at least in bilaterally symmetrical flowers. Several distinct
Table 2 Summary of floral responses to ‘natural’ and manipulative experiments misorienting flowers.

<table>
<thead>
<tr>
<th>Family: species</th>
<th>Misorientation ‘treatment’</th>
<th>Symmetry</th>
<th>Response</th>
<th>Change in mean²-scaled pollination inaccuracy* (% restoration towards original accuracy)</th>
<th>Effect</th>
<th>Time taken for response or duration of observation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amaryllidaceae: Agapanthus sp.</td>
<td>Manipulation</td>
<td>Radial perianth, bilateral androecium &amp; gynoecium</td>
<td>Pedicel rotation</td>
<td>–</td>
<td>Accurate orientation usually restored</td>
<td>2–3 d</td>
</tr>
<tr>
<td>Balsaminaceae: Impatiens sp.</td>
<td>Manipulation</td>
<td>Radial</td>
<td>Pedicel rotation</td>
<td>0% change</td>
<td>No change in accuracy or pollinator foraging</td>
<td>10–30° rotation d⁻¹</td>
</tr>
<tr>
<td>Campanulaceae: Burmeistera sodiroana</td>
<td>Manipulation</td>
<td>Bilateral</td>
<td>Pedicel rotation</td>
<td>14.6% → 2.87% (80.3%)</td>
<td>Accurate orientation mostly restored</td>
<td>1 d</td>
</tr>
<tr>
<td>Campanulaceae: Centropogon nigricans</td>
<td>Manipulation</td>
<td>Bilateral</td>
<td>Pedicel rotation</td>
<td>14.6% → 0.03% (99.8%)</td>
<td>Accurate orientation fully restored</td>
<td>2 d (was bud when misoriented)</td>
</tr>
<tr>
<td>Caricaceae: Carica papaya</td>
<td>Manipulation</td>
<td>Radial</td>
<td>No rotation</td>
<td>0% change</td>
<td>No change in accuracy or pollinator foraging</td>
<td>2 d (was bud when misoriented)</td>
</tr>
<tr>
<td>Celastraceae: Stackhousia huegelii</td>
<td>Manipulation</td>
<td>Radial</td>
<td>No rotation</td>
<td>0% change</td>
<td>No change in accuracy or pollinator foraging</td>
<td>3 d</td>
</tr>
<tr>
<td>Ericaceae: Cavendishia bracteata</td>
<td>Manipulation</td>
<td>Radial perianth, bilateral androecium</td>
<td>Pedicel rotation</td>
<td>14.6% → 10.0% (31.5%)</td>
<td>Small improvement in stamen accuracy</td>
<td>1–2 d</td>
</tr>
<tr>
<td>Geraniaceae: Pelargonium sp.</td>
<td>Manipulation</td>
<td>Bilateral</td>
<td>Peduncle bending</td>
<td>–</td>
<td>Accurate orientation fully restored</td>
<td>1–2 d</td>
</tr>
<tr>
<td>Lamiaceae: Salvia sp.</td>
<td>Manipulation</td>
<td>Bilateral</td>
<td>Pedicel rotation</td>
<td>14.6% → 0.24% (98.4%)</td>
<td>Accurate orientation fully restored</td>
<td>1 d</td>
</tr>
<tr>
<td>Liliaceae: Tricytis formosana</td>
<td>Manipulation</td>
<td>Radial</td>
<td>Pedicel bending</td>
<td>–</td>
<td>Upwards orientation restored</td>
<td>1–2 d</td>
</tr>
<tr>
<td>Onagraceae: Chamerion angustifolium</td>
<td>Manipulation</td>
<td>Calyx radial, corolla quasi-bisymmetric, androecium &amp; gynoecium bilateral</td>
<td>Stamen and style bending (no pedicel rotation); (+ bending of peduncle tip)</td>
<td>Anthers: 31.7% → 3.40% (89.3%) Stigmas: 26.3% → 2.18% (91.7%)</td>
<td>Accurate anther and stigma positions mostly restored</td>
<td>Reorientation of fertile parts: 1–2 d</td>
</tr>
<tr>
<td>Orchidaceae: Dactylorhiza fuchsii</td>
<td>Manipulation</td>
<td>Bilateral</td>
<td>Peduncle bending</td>
<td>73.6% → 7.83% (89.4%)</td>
<td>Accurate orientation restored in young flowers</td>
<td>1–2.5 d</td>
</tr>
<tr>
<td>Passifloraceae: Passiflora caerulea</td>
<td>Natural ‘experiment’</td>
<td>Radial</td>
<td>No movement</td>
<td>–</td>
<td>No detectable upwards reorientation</td>
<td>No reorientation in 1–2 d lifetime of flower</td>
</tr>
<tr>
<td>Ranunculaceae: Aconitum delphinifolium</td>
<td>Natural ‘experiment’</td>
<td>Bilateral</td>
<td>Pedicel bending</td>
<td>0% change</td>
<td>Optimal orientation for foraging bumble bees fully restored</td>
<td>1 d</td>
</tr>
<tr>
<td>Ranunculaceae: Delphinium glaucum</td>
<td>Natural ‘experiment’</td>
<td>Perianth bilateral, fertile whors radial</td>
<td>Pedicel bending</td>
<td>0% change</td>
<td>Optimal orientation for foraging bumble bees fully restored</td>
<td>3 d of observation</td>
</tr>
<tr>
<td>Ranunculaceae: Clematis aff. pubescens</td>
<td>Manipulation</td>
<td>Radial</td>
<td>No rotation</td>
<td>0% change</td>
<td>No change in accuracy or pollinator foraging</td>
<td>2 d of observation</td>
</tr>
</tbody>
</table>
We observed bending of the inflorescence rotation and bending/twisting of sexual organs. We recognised four distinct potential mechanisms of floral reorientation: peduncle bending, pedicel bending, pedicel rotation and bending/twisting of sexual organs.

Peduncle bending We observed bending of the inflorescence stalk leading to partial or full restoration of correct floral orientation (with minimal pedicel bending or rotation) in Dactylorhiza fuchsi (Orchidaceae; Fig. 2) and a bilaterally symmetrical Pelargonium species. We also observed restoration of floral orientation by bending of the peduncle tip in Stylidium spp., A. delphinifolium, D. glaucum and C. angustifolium. In these last four species, peduncle bending occurred as a slow response associated with new growth, in combination with other, faster reorientation processes.

Pedicel bending and/or rotation We observed corrective floral reorientation by pedicel bending in combination with some rotation in A. delphinifolium (Fig. 3), D. glaucum, T. formosana, Salvia sp., B. sodiroana, C. nigricans and Impatiens sp. We observed comparatively rapid reorientation of flowers primarily through rotation of the pedicel (possibly in combination with some bending) in Agapanthus sp., Stylidium spp. (Fig. 4), Diascia spp. and Nemesia sp. (Table 2).

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

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

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

In *Stylidium* spp., *A. delphinifolium* and *D. glaucum*, we observed restoration of floral orientation by pedicel rotation or bending, in combination with a slower response of the peduncle bending upward. In *C. angustifolium*, slow peduncle bending occurred in combination with rapid reorientation of stamens and

### Table 3 A classification of reorientation responses.

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

Fig. 2 *Dactylorhiza fuchsii* tethered on 13.06.2019, 13:00 GMT. (a) 13.06.2019, 13:15 GMT. (b) 14.06.2019, 10:15 GMT. (c) 15.06.2019, 09:28 GMT.
styles. This combination of reorientation responses is probably common among plants with bilaterally symmetrical flowers borne in elongated inflorescences, such as spikes.

Effect of reorientation on floral adaptive accuracies of bilaterally symmetrical flowers

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

Planned comparisons of reorientation in bilaterally vs radially symmetrical flowers

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

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

In Ecuador, the reorientation responses were absent in the two radially symmetrical species (C. papaya and Citrus sp.). Cavendishia bracteata displayed an intermediate level of recovery of 9.4° in 24 h. This was markedly less than the four fully bilaterally symmetrical species (Table 2; Fig. 7). The mean corrective reorientation (± SE) was 5.18° (± 2.14°; \(n = 3\)) in species with radially symmetrical perianths, vs 35.2° (± 4.09°; \(n = 4\)) in species with bilaterally symmetrical perianths (Fig. 7, independent-samples \(t\)-test, not assuming equal variances: \(t = 6.49, P = 0.002\)). The same phylogenetic caution regarding ‘significance’ mentioned in the previous paragraph applies to these results as well.

Comparison of reorientation in two similar, radially symmetrical flowers

After conducting the above planned comparisons, we added two radially symmetrical, but phenotypically specialised flowers to this survey. Passiflora spp. generally bear 1-d flowers that have a complex arrangement of a corolla platform and corona fringe surrounding a nectar trough. The fertile parts are borne a consistent distance above the corolla platform so that nectar-seeking bees of only a certain size will contact the five stamens in the male phase or the three stigmas (at the same height) in the female phase. Trycyrtis formosana is a distinctive lily with flowers almost perfectly convergent on Passiflora flowers, except that the nectar is held in a series of three pairs of saccate spurs at the base of the sepal, rather than in a trough (Table 1; Fig. 1a). In both cases, we could expect

![](image1)

**Fig. 4** Floral reorientation in Stylidium ciliatum. (a) Normal orientation. (b) Floral reorientation 2 d after floral scape was tethered to the horizontal.

![](image2)

**Fig. 5** Pelargonium sp. with bilaterally symmetrical flowers. Peduncle bending over 5 d leading to restoration and maintenance of correct floral orientation. Day 0 (not shown); transplanted so main shoot and inflorescence are horizontal (i.e. 90° off original orientation); both flowers and leaves are misoriented. (a) Days 1–2: peduncle bends 90°, restoring ‘correct’ orientation of weakly bilaterally symmetrical flowers; leaves still ‘misoriented’. (b) Day 5: stem has reoriented 90°; leaves are now back to the original horizontal positions (presumably maximising photosynthesis); meanwhile the peduncle has bent another 180° in compensation, so the peduncle is now sigmoidal. (c) Close-up of peduncle showing sigmoidal bending and flowers in correct orientation.
floral function and bee pollination to work best when flowers face upwards. (Note that there is a radiation of floral orientations in *Passiflora*, with many hummingbird-pollinated and bat-pollinated species having laterally oriented flowers, often with bilaterally oriented fertile whorls, and some bee-pollinated and some bat-pollinated species having pendent flowers. Here we are referring only to classic bee-pollinated species such as *Passiflora caerulea* and *Passiflora foetida* with normally upward-facing flowers.)

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

**Discussion**

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

Experimental misorientation of flowers by 90° of rotation reduced the theoretical pollination accuracy of bilaterally symmetrical flowers by up to c. 50% of the maximal decrement (= 180° of rotation). Natural corrective reorientation of these flowers or flower parts returned pollination accuracy to within c. 5% of the starting maximum (Table 2; Fig. 6). Similar results were observed with experimental floral misorientation by 45° of rotation: the theoretical pollination accuracy of bilaterally symmetrical flowers was reduced by c. 15% of the maximum possible decrement. Natural corrective reorientation of these flowers returned pollination accuracy to within a few per cent of the starting maximum (Table 2; Fig. 7). Thus, our survey suggests that most plants with bilaterally symmetrical flowers have the capacity to reorient their flowers, returning pollination accuracy to within a few per cent of the original value within a day or two.

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

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

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

We suggest that corrective reorientation of flowers after accidents is an underappreciated plant behaviour worthy of greater scrutiny. It would be valuable to next assess experimentally the extent to which reorientation increases pollinator visitation and/or pollen transfer relative to flowers that remain misoriented. Further research may reveal that other morphological and developmental features of flowers and inflorescences are unappreciated adaptations for floral reorientation after mechanical accidents. For example, the evolution of elongated pedicels could be favoured because they promote the capacity for rapid floral reorientation (see Figs 1b, 2). Future research on floral function and pollination should explore such possibilities, as well as extend the sampling of reorientation capabilities across a broader range of flowering plant species.

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**Author contributions**

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

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