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A lever action hypothesis for pendulous hummingbird flowers: experimental evidence from a columbine

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- **Background and Aims** Pendulous flowers (due to a flexible pedicel) are a common, convergent trait of hummingbird-pollinated flowers. However, the role of flexible pedicels remains uncertain despite several functional hypotheses. Here we present and test the 'lever action hypothesis': flexible pedicels allow pendulous flowers to move upwards from all sides, pushing the stigma and anthers against the underside of the feeding hummingbird regardless of which nectary is being visited.
- **Methods** To test whether this lever action increased pollination success, we wired emasculated flowers of serpentine columbine, *Aquilegia eximia*, to prevent levering and compared pollination success of immobilized flowers with emasculated unwired and wire controls.
- **Key Results** Seed set was significantly lower in wire-immobilized flowers than unwired control and wire control flowers. Video analysis of visits to wire-immobilized and unwired flowers demonstrated that birds contacted the stigmas and anthers of immobilized flowers less often than those of flowers with flexible pedicels.
- **Conclusions** We conclude that flexible pedicels permit the levering of reproductive structures onto a hovering bird. Hummingbirds, as uniquely large, hovering pollinators, differ from flies or bees which are too small to cause levering of flowers while hovering. Thus, flexible pedicels may be an adaptation to hummingbird pollination, in particular due to hummingbird size. We further speculate that this mechanism is effective only in radially symmetric flowers; in contrast, zygomorphic hummingbird-pollinated flowers are usually more or less horizontally oriented rather than having pendulous flowers and flexible pedicels.

Key words: Ornithophily, pollination syndrome, floral movement, floral morphology, pendulous flower, floral symmetry, *Aquilegia eximia*, Ranunculaceae, columbine.

INTRODUCTION

Functional examination and experimentation on convergently evolved traits allow tests of ecological and evolutionary pressures and constraints. One area where convergent traits are noticeable is in floral morphology, where specific pollinators or pollinating taxa are associated with particular multitrait floral morphologies. Hummingbird-pollinated plants offer a useful group in which to explore such pressures and constraints. Hummingbirds differ from many insect pollinators in their visual spectrum, large relative size, hovering ability, and sharp and hard bills (Grant and Grant, 1968). As such, they are good candidates for pollinators that may select for distinct floral phenotypes. A suite of floral traits are associated with bird or hummingbird pollination, including flexible pedicels, narrow tubes, thick floral tissues, red flowers, dilute nectar, lack of scent and exserted reproductive structures (Grant and Grant, 1968; Thomson and Wilson, 2008). Although the functions of some traits associated with the hummingbird pollination syndrome, including dilute nectar, narrow tubes and red flowers, have been extensively studied (e.g. several hypotheses for the functional importance of red flowers; Stiles, 1976; Melendez-Ackerman *et al.*, 1997; Bradshaw and Schemske, 2003; Rodríguez-Gironés and Santamaría, 2004), the functions of other traits remain undetermined. One of the most striking of these traits is flexible pedicels, which have repeatedly evolved in hummingbird-pollinated species. Despite several promising hypotheses, we do not have a strong functional understanding of this trait (Sapir and Dudley, 2013). Here we observationally and experimentally evaluate the role of flexible pedicels in a hummingbird-pollinated California wildflower.

Considering flexible pedicels as an adaptation to hummingbird pollination has led to a number of interesting hypotheses and elegant experiments, yet the functional role of flexible pedicels in hummingbird pollination remains largely unexplained (Sapir and Dudley, 2013). The flexibility of pedicels and the subsequent pendulous orientation as a common trait of hummingbird-pollinated flowers was first noted by Grant and Grant (1968) who hypothesized that free movement of flowers reduced the chance of ovary damage by hummingbird bills, though they did not test their hypothesis. Some species with flexible pedicels and pendulous flowers, including the columbine we examine here, do not have ovaries in a direct line with (or even close to) the reproductive structures, thus the Grants' hypothesis that free movement reduces the chance of ovary damage by hummingbird bills (Grant and Grant, 1968) is probably inapplicable to these systems. Hurlbert *et al.* (1996) hypothesized that the floral movement allowed by flexible pedicels increased pollinator handling time and thus increased time in contact with reproductive structures. They demonstrated that hummingbirds spent more time at mobile *Impatiens capensis* flowers than experimentally immobilized flowers and that this increased their time in contact with reproductive structures. However, *I. capensis* is rather unique in having a horizontal floral orientation below the flexible pedicel, whereas most flowers with flexible pedicels hang directly vertical with their opening pointing down [assorted species of genera *Aquilegia* (Ranunculaceae), *Ribes* (Grossulariaceae), *Fuchsia* (Onagraceae), *Iochroma*, *Vestia* (Solanaceae), *Cantua* (Polemoniaceae), *Fritillaria* (Liliaceae) and others; LoPresti and Specht, pers. obs., see also Supplementary Data File S1.

Several hypotheses have focused on the downward-pointing orientation (often a consequence of flexible pedicels) and not the flexibility itself. Downward-pointing flowers are not rare, and include many non-hummingbird-pollinated species [e.g. species of *Dodecatheon/Primula* (Primulaceae), *Dicentra* (Papaveraceae), *Erythronium*, *Calocortus* (Liliaceae), *Arctostaphylos* (Ericaceae), *Paeonia* (Paeoniaceae), *Solanum* (Solanaceae), etc.], suggesting that this trait may also have utility in species without hummingbirds as pollinators. Downward-pointing flowers could protect nectar from dilution or pollen from dislodgement during rainfall. However, wiring *Tristerix corymbosus* (Loranthaceae) inflorescences upright provided no support for the hypothesis; inflorescences tethered upright did not have more dilute nectar or greater pollen dislodgement than those naturally or experimentally tethered downwards (Tadey and Aizen, 2001). In contrast, a separate study found significant dilution of nectar in *Besleria sprucei* (Gesneriaceae) if the flower was upward facing (Aizen, 2003). However, the diversity of hummingbird-pollinated species flowering in arid areas throughout the Americas (e.g. California's dry Mediterranean summers), many of which, like *Aquilegia eximia* discussed here, are downward facing strongly suggests that selection from rainfall alone is not a sufficient explanation for this floral morphology.

Finally, because downward-facing pendulous flowers (a consequence of flexible pedicels) are so characteristic of hummingbird pollination, it would be reasonable to predict that hummingbirds prefer this orientation of flowers. In fact, feeding from downward-pointing flowers is energetically costly for hummingbirds; it increases their metabolic rate by approx. 11 % compared with feeding from horizontally oriented flowers (Sapir and Dudley, 2013). Hummingbirds visited artificially positioned horizontal mistletoe flowers preferentially over flowers in their normal downward orientation, as predicted by the increased metabolic cost (Tadey and Aizen, 2003). Fenster *et al.* (2009) found that hummingbirds did not show a preference for any orientation from 45° down to perfectly vertical, although they did not test downward orientation directly. These studies suggest that the selection driving the repeated evolution of flexible pedicels (and thus pendulous downward-pointing flowers) in hummingbird-pollinated plants is not due to hummingbird preferences and probably evolves despite innate hummingbird preferences against it.

Our extensive field observations of serpentine columbine, *A. eximia*, show that when a hummingbird feeds on a columbine spur, the flexible pedicels allow the flower to pivot, causing the exserted reproductive structures to contact the hummingbird's body during feeding. We term this the 'lever action' hypothesis (Fig. 1) and believe that many pendulous hummingbird-pollinated flowers employ this strategy. Nearly all pendulous downward-facing hummingbird flowers are radially symmetric with exserted reproductive structures. This morphology allows access to each nectary or a central pool or ring of nectar, while keeping the orientation of the bird to the flower the same at each visit. The exserted reproductive structures prevent flying to the opposite nectary from the approach direction, instead guiding the pollinator around the circumference of the flower, making each contact with reproductive structures at the same point on the body at each nectary visit, regardless of the initial approach direction or orientation.

The levering action of the movable flower relies on the hummingbird orienting slightly to completely perpendicular to the orientation of the floral tube; this behaviour occurs in the field on nearly every visit and is probably a strategy to minimize the increased energetic cost of feeding on downward-pointing flowers as

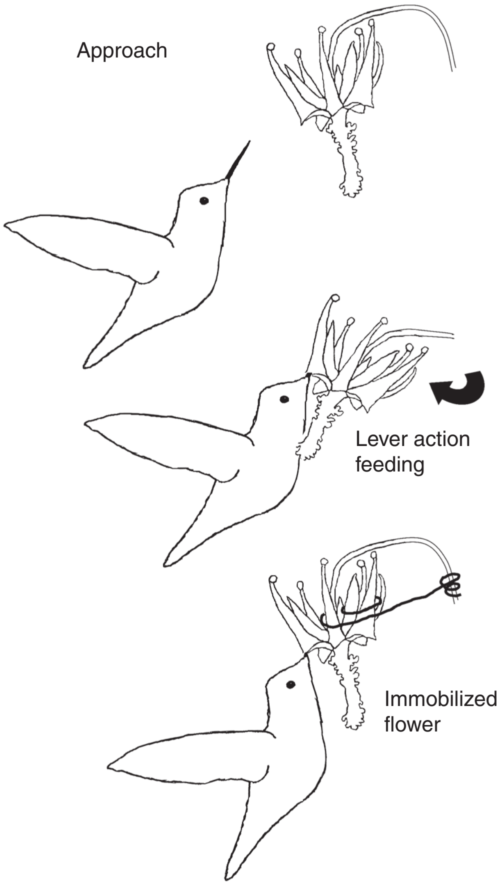

Fig. 1. The lever action hypothesis, as proposed and observed in the field. Top, the hummingbird approaches the pendulous flower. Middle, the bird enters with a slight angle, pulling the flower towards it and levering the reproductive structures into its body. Note that birds approach at a variety of angles (see also Fig. 3), but this is a typical one. Below, an immobilized (or non-flexible) pedicel; angles of the flower and bird are the same as in the upper left. Note that the bird would not be able to get nectar in this situation as the nectary is not in line with the bill, thus necessitating a greater head angle.

described by Sapir and Dudley (2013). This levering action briefly makes a downward-pointing flower into a slightly to completely horizontal one and deposits the pollen on the hummingbird at that time. We speculate that this consistency in contact point helps ensure that pollen is placed in the same spot on the hummingbird at each visit and subsequently deposited precisely onto stigmas. This hypothesis is not mutually exclusive of that of Hurlbert *et al.* (1996) and, indeed, the lever action or general movement of pendulous flowers permitted by flexible pedicels may slow the visit down and lead to a greater time in contact with the reproductive structures. We do not mean to suggest that this describes most flowers relying on hummingbird pollination. Most hummingbird-pollinated flowers are not pendulous or radially symmetrical; such flowers do not have flexible pedicels and rely on hummingbirds approaching them in an upright hovering position to place pollen on the bird effectively [e.g. well known in species *Monarda*, *Salvia* (Lamiaceae), *Penstemon* (Plantaginaceae), *Erythranthe/Mimulus* (Phrymaceae), *Ipomopsis* (Onagraceae), *Centropogon* (Campanulaceae), *Heliconia* [Zingiberales], etc.; LoPresti and Specht, pers. obs.).

In order to test the 'lever action' hypothesis, we tethered flowers in natural populations of columbines, and used a combination of field experiments and video observations to record visitation mechanics and investigate maternal reproductive success. Reduced reproductive success of tethered flowers relative to controls would be consistent with the lever action hypothesis, whereas no difference between the treatments would reject this hypothesis.

MATERIALS AND METHODS

Location and natural history

We conducted field work during the summers of 2016 and 2018 at the University of California-Davis McLaughlin reserve in Lake and Napa Counties, CA, USA. Serpentine columbine, *Aquilegia eximia*, grows in nearly every permanent stream in the area, largely on harsh serpentine soils, flowering between June and October. It has a mixed mating system (LoPresti, 2017); however, individual plants are commonly visited by hummingbirds which carry *A. eximia* pollen and regularly contact anthers and stigmas during visits. Nearly all floral visitors incidentally observed during field work on this species from 2014 to 2018 were hummingbirds. At our field site, we have only seen two hummingbird species visit flowers of *A. eximia* – Anna's (*Calypte anna*) and Rufous (*Selasphorus rufus*) – with the ratio of visitation between these species changing seasonally and year to year. *Calypte anna* were common at the site throughout the study and *S. rufus* moved through seasonally in widely varying numbers. During the summer of 2016, *S. rufus* visits were very rare (<5 % of visits), though in August 2018, they were roughly equally abundant as those of *C. anna* (LoPresti, pers. obs.).

Floral immobility experiment

To determine whether the lever action of a flexible pedicel assisted in pollination success of the flower, we performed a floral immobilization experiment. Flowers were located and identified on their first day of opening (prior to anther dehiscence) or just prior to floral opening, and we used a single flower per plant at any visit, and <10 % of the flowering plants in the population in total was used. *Aquilegia eximia* is self-compatible, and bagged flowers set seed, so all flowers were first gently emasculated by plucking off anthers with fine-tipped forceps. Each was then assigned to one of three treatments (haphazardly, with a fixed order as we came to a flower at the right stage). The first treatment was a control, with no manipulation except emasculation. The second was an immobilization treatment; a thin copper wire was wrapped several times around the pedicel or stem (whichever was at the flower level) then wrapped loosely around two or more nectar spurs in a loose ring (such that the wire was strung horizontally between pedicel/stem and flower; as in Fig. 1). This wire placement kept the flower in place facing downwards, such that the flower did not bend upwards, as it normally would, when visited by a hummingbird. The final treatment was the same as the previous, but the wire was cut between the stem and the flower, allowing free movement of the pedicel; this treatment served as a control in case the presence of wire was either attractive or repellant to hummingbirds or the wire somehow damaged flowers. Fruit were collected from each experimental group just prior to dehiscence (approx. 3–4 weeks), at which point carpels and seeds were counted.

We performed this experiment on approx. 200 flowers in 2016 and approx. 150 flowers in 2018. The realized sample sizes were far lower (64 and 95, respectively); most of the tagged flowers were not recovered in 2016 due to herbivory from an outbreak of *Heliothis phloxiphaga*, the most common herbivore (LoPresti *et al.*, 2015), as well as consumption by brush rabbits (*Sylvilagus bachmani*), and a small pterophorid caterpillar (probably *Amblyptilia pica*). In 2018, we bagged the developing fruit with netting just after the flower senesced, and successfully limited these losses.

Observations of flowers

Although the immobility experiment measured the fertilization success in immobilized and control flowers, it could not give us insight into hummingbird behaviour at these flowers. In 2016, we placed two motion-sensitive game cameras (Bushnell NatureView trail cam) on immobilized and control flowers (no wire controls), moving them approximately every 5 d. We also included videos taken for another study (LoPresti, 2017) on non-immobilized columbine flowers during the same season, so the control group had a larger sample size. Several videos were either too short, too blurry or the ability to assess contact was obscured by the bird or other vegetation; these videos were not included in analyses. Nonetheless, we recorded 111 (80 control, 31 immobilized) scoreable visits. The video data were analysed using Wondershare Filmora (Wondershare, Shenzhen, China) to specifically record whether or not the hummingbird contacted the reproductive structures during each visit.

Analyses

All statistics were performed and all graphics made in R (R Foundation for Statistical Computing). Mean seeds per carpel was used as the response variable, because flowers naturally vary in carpel number between four and six carpels (with a corresponding number of nectar spurs). This also allowed us to use the data from intact carpels on fruits which had other carpels damaged by caterpillars. The two years were pooled as mean seeds per carpel did not differ between them (two-tailed *t*-test, $P = 0.66$). We used a one-way analysis of variance (ANOVA) to analyse the mean of treatment as a fixed effect; treatments had equal variance, and residuals of the model were roughly normal. χ^2 tests were performed on the video data to examine whether immobilization changed the likelihood of contact with reproductive structures.

RESULTS

The floral immobilization treatment had a >30 % reduction in per carpel seed set compared with each of the control treatments (Fig. 2). These comparisons were highly significant (one-way ANOVA, treatment d.f. = 2, $F = 14.5$, $P < 0.001$; post-hoc comparisons of treatment means: wire–control and wire–wire control: both $P < 0.001$) also see an alternate analysis in Supplementary Data File S2. The two control treatments did not differ, suggesting that the presence of wire did not deter or attract hummingbirds (post-hoc comparison of means, $P = 0.75$).

Analysis of the video data found that overall contact between reproductive structures and hummingbirds was higher in control flowers than in immobilized flowers, with atypical approaches occurring at a high frequency (Table 1). Hummingbirds made visible contact with the reproductive structures of control flowers at a higher rate (85 %) than with those of immobilized flowers (71 %), although this difference was not significant (two-tailed χ^2 test = 2.9, d.f.= 1, $P = 0.09$; but significant one-tailed for this directional hypothesis). Interestingly, more hummingbirds approached the control flowers atypically (i.e. in any manner other than front-first, see Fig. 3; 16 %) than the immobilized flowers (0 %), a significant difference (Fisher's exact test, $P = 0.02$). During these visits, contact only occurred in 38 % of visits, and these atypical visits accounted for almost 67 % of the non-contact visits in the control flowers. When we limited analysis to visits where hummingbirds approached a control flower legitimately, the chances of contacting the reproductive parts was 94 %, a highly significant difference from the immobilized flowers (two-tailed χ^2 test, $P < 0.01$).

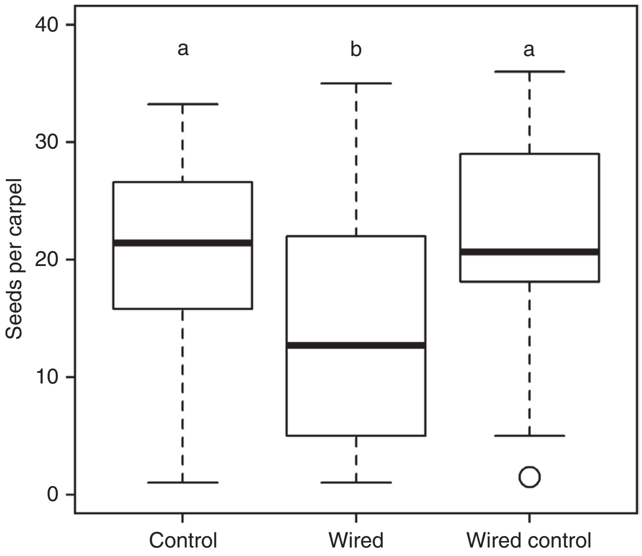

FIG. 2. Combined 2016 and 2018 results of the wiring experiment. Letters indicate significant differences in a Tukey post-hoc test of treatment means.

DISCUSSION

Pendulous, downward-facing, flowers are a classic trait of hummingbird-pollinated flowers, yet strong evidence for their functional role(s) has been lacking. We found strong support for the lever action hypothesis, that flexible pedicels allow the bird to lever the flower up from all sides while hovering to deposit pollen in the same place, increasing pollination success. Of course, other factors besides the lever action also probably affected pollination and reproductive success. Nonetheless, in our experiment, immobilized flowers set far fewer seeds per carpel. This was likely to be due to the lower rates of contact between reproductive structures with hummingbirds during visits (although the duration or force of contact may have also differed). Our results suggest that increased pollination success afforded by levering of flowers may be responsible for the repeated evolution of flexible pedicels and pendulous, downward-facing flowers. Although we do not have data on other pendulous hummingbird-pollinated plants, we expect that the many convergent examples of this morphology use this same mechanism, and we have observed – directly or on video – this lever action occurring in *A. eximia* and *A. formosa* (Ranunculaceae), *Abutilon* sp. (Malvaceae) and *Fuchsia* sp. (Onagraceae), though we do not have pollination success data to go with those observations (see Supplementary data S1).

Flexible pedicels, leading to pendulous downward-facing flowers, have evolved repeatedly despite the increased energetic cost of feeding from flowers in this orientation and hummingbird preference against this morphology (e.g. Tadey and Aizen, 2001; Sapir and Dudley, 2013), suggesting that the benefit of this outweighs the cost. Indeed, the increased energy expenditure associated with feeding vertically from downward-pointing flowers may help ensure the levering action, and pollination transfer, is completed in each feeding bout. The bird, while feeding somewhat horizontally despite a mostly vertical approach, probably reduces energy expenditure (Figs 1 and 3A, B) and ensures that the levering action occurs. An additional pollen transfer benefit is consistent location of pollen placement, regardless of which nectary is fed upon. Another benefit may be the exclusion of other, probably less effective, pollinators. Very few insects visit *A. eximia* flowers (although the smaller flowered, also pendulous, *A. formosa* hosts many insect floral visitors: Zemenick *et al.*, 2018). Bees and hawkmoths may have a strong aversion to downward-facing flowers (Hodges *et al.*, 2003; Ushimaru and Hyodo 2005; Makino and

TABLE 1. *Percentage of visits with successful contact with reproductive structures in videos, by treatment and approach type*

		Treatment	
		Control	Immobilized
Approach	Typical	94 % (63/67)	71 % (22/31)
	Atypical	38 % (5/13)	

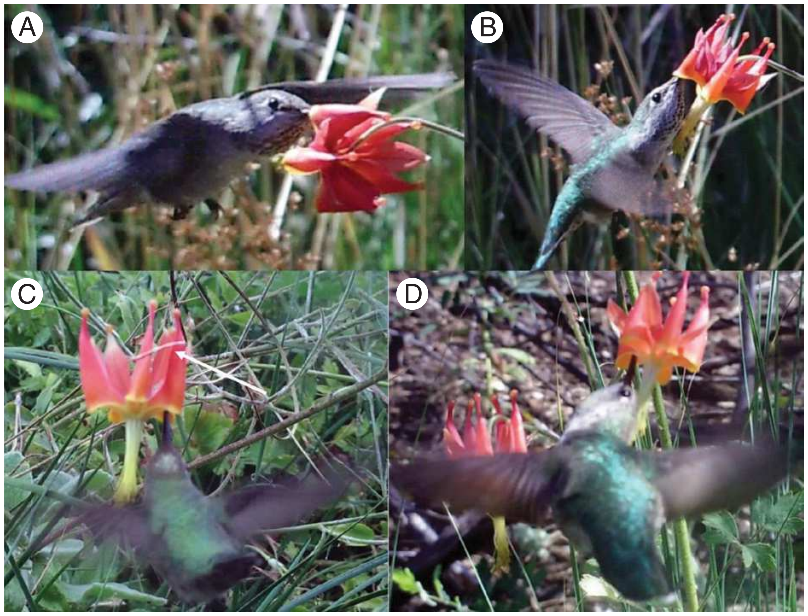

Fig. 3. Stills from videos showing: (A) a very pronounced levering of the flower, with the hummingbird in an almost horizontal feeding position and contact between the bird and the reproductive structures; (B) a more typical contact position; (C) an immobilized flower where the hummingbird is not making contact with the reproductive structures (the whitish pollen on its forehead is from *Stachys albens*), wire indicated with a white arrow; and (D) an atypical approach, where the bird is rotated with respect to the flower and not making contact with reproductive structures.

Thomson, 2012; Wang *et al.*, 2014; Salas-Arcos *et al*., 2019) or may be less able to access nectar from them (Haverkamp *et al.*, 2019). Haverkamp *et al.* (2019) further suggested that there is a 'maximum downward orientation' of a flower on which a hawkmoth could feed, and found a marked reduction in nectar removal in flowers experimentally manipulated to 45° below horizontal. In deterring many floral visitors, downward orientation probably complements other traits, such as narrow tubes and dilute nectar (Castellanos *et al.*, 2004; Thomson and Wilson, 2008; Salas-Arcos *et al*., 2019), which also deter non-hummingbird floral visitors.

We believe that the lever action hypothesis for pendulous flowers only works in radially symmetric flowers, as anther contact occurs in the same location on the bird regardless of the approach direction. A similar argument has been made by Ushimari and Hydoro (2005) and Fenster *et al.* (2009); though neither tested downward-facing pendent flowers. We know of no pendulous downward-facing zygomorphic flowers. However, Castellanos *et al.* (2004) artificially manipulated a bee-pollinated zygomorphic *Penstemon* species to be pendulous. Informatively, they found that this manipulation reduced the success of hummingbirds at contacting the reproductive structures. Compared with controls, hummingbirds deposited less pollen on and missed contact with stigmas more often in the artificially pendulous *Penstemon* flowers. They noted that hummingbirds often 'approach from an angle that dodges reproductive organs'; which, in a zygomorphic flower, is a large proportion of the possible directions.

Although radially symmetric flowers are difficult to approach in an ineffective way (i.e. not with the chest of the bird facing the centre of the flower; see Fig. 3), such approaches to the flower occurred in an unexpectedly high percentage (16 %) of video-recorded visits to the control flowers. The significance of this behaviour is unknown but may have interesting ramifications. It is tempting to conclude that it is unimportant; after all, the untethered flowers had a higher contact rate than immobilized flowers even with the low contact rate (33 %) of these atypical visits. However, it is worth considering this behaviour because an atypical approach is only possible on vertically upright or downward-pointing flowers. The analogous hovering behaviour for a horizontally oriented flower would be flying upside down or sideways, which is unlikely or rare; though perching birds may orient their bodies vertically and visit a flower below them, such that their head is inverted or perpendicular relative to that flower (E. LoPresti., pers. obs.). Preventing such behaviour may select for flowers held far out from stems, as is the case in columbines and in pendulous flowers held well below long stems (i.e. *Ribes speciosum*; pictured in Grant and Grant, 1968). During years of observation of hummingbirds on columbine, we have noticed perched birds feeding, but the hummingbirds were always perched on adjacent columbines or other vegetation, never the same individual plant (LoPresti, pers. obs.).

Anecdotally, we know that wholly flexible pedicels are probably less effective than the actual columbine pedicels, which bend easily but still offer some resistance. An attempt to construct artificial columbine flowers hanging on a fishing line demonstrated that they rock and twist easily, in contrast to actual flowers which flex, but do not twist greatly at the same time (LoPresti, Goidell and Karban; pers. obs). However, even if they did twist readily, or even slightly, the keeled spurs of columbine probably prevent this motion from affecting the location of pollen deposition substantially. We further hypothesize that these keels are especially important in centring reproductive structures during pollination in wind, which moves columbine flowers quite substantially.

Flexible pedicels as a component of the hummingbird pollination syndrome

Very few terms philosophically divide the community of pollination biologists quite like the phrase 'pollination syndrome'. For decades, this predictive classification has been embraced in floristic and comparative work (e.g. excellent studies of *Penstemon*: Thomson *et al.*, 2000; Castellanos *et al.*, 2004). Others, often field ecologists, have sought to restrict or discard its usage because of the complexities of pollination, the increasing recognition that many flowers are generalized or rely on multiple pollinator guilds and because many 'pollinators' visit flowers that they may not actually pollinate (Waser *et al.*, 1995, 2018; Ollerton *et al.*, 2009, 2015). Recent work which purported to demonstrate the applicability and utility of these concepts at a broad scale (Rosas-Guerrero *et al.*, 2014; Johnson and Wester, 2017) has been questioned (Ollerton *et al.*, 2015). We do not believe that our results will settle this debate, though we feel that these results should inform future work on the hummingbird pollination syndrome.

As we detailed above, not all hummingbird-pollinated flowers have flexible pedicels with pendulous, downward-facing flowers. The flowers with this pollination syndrome seem to take more than one convergent form; here we hypothesize that these forms correlate with floral symmetry and are constrained by how hummingbirds interact with the flower. We are not the first to note the existence of multiple discrete floral morphologies of hummingbird-pollinated flowers; some hedging has been done on this issue to fit it neatly into a single pollination syndrome (e.g. hummingbird pollination features 'inclined-flowers or flexible pedicels'; Thomson *et al.* 2000). We believe our hypothesized distinction of 'lever-able' pendulous radially symmetric flowers from more or less horizontal zygomorphic flowers makes clearer the possible evolution of these discrete forms. Many hummingbird-pollinated flowers are neither pendulous nor radially symmetric; these do not have wholly flexible pedicels and rely on hummingbirds approaching them from an upright position to effectively place pollen in a particular location on the bird (Fenster *et al.*, 2009). The lever action hypothesis is thus posited only for the pendulous case (which we hypothesize are more likely to be radially symmetrical). We believe that symmetry is the fundamental split between the two types of flowers, and ongoing comparative work aims to test this broader hypothesis. If our hypothesis of multiple hummingbird flower forms is borne out in later investigations, we expect that the 'hummingbird syndrome' might occupy two distinct regions of trait space.

We also believe that the functional uniqueness of hummingbirds as a large, hovering pollinator calls into question the ornithophilous syndrome at large. If hummingbirds perched on columbines, the described lever action would not work, as the bird would not be approaching each nectary from the outside (unless the perches surround the whole flower, unattached to it, allowing levering from all directions). Hummingbird floral approach and hovering feeding strategy are quite distinct from those of perching birds (e.g. sunbirds or warblers) or from walking birds (e.g. seedsnipe; Sersic and Cocucci, 1996), in much the same way that bees interact with flowers differently from butterflies, wasps or flies. For this reason, it seems likely that the ornithophilous syndrome includes too much functional pollinator variation to be broadly useful. Ollerton *et al.* (2009) analysed pollination syndromes of plants in six locations of the world, determined actual pollinators and looked at success rate. Their analysis – like many treatments of pollination syndromes – treated all birds as equal. Whether this is partially responsible for the low predictive power of the bird pollination syndrome (14.9 % correct predictions), these fundamental differences between different birds and possible effects on floral evolution deserve to be carefully considered. However, we would like to note that in the absence of strong tests, we do not reject the pollination syndrome framework. Instead, we suggest that future work on pollination syndrome should treat different groups of avian pollinators (hovering, perching and walking) as distinct, as well as recognize the constraints which floral symmetry – often an ancestral trait – imposes on floral form and position within a complex morphospace.

Conclusions

Using a hummingbird-pollinated California wildflower, we find strong observational and experimental evidence for the lever action hypothesis, the idea that flexible pedicels increase pollination success by allowing pendulous downward-facing flowers to lever into a more horizontal feeding position. This study makes two contributions. First, the pendulous radially symmetric hummingbird flowers may be 'levered' by feeding hummingbirds, resulting in more effective pollination than a fixed downward-facing morphology. Secondly, this mechanism, dictated by radial symmetry, may have different parameters for selection and constraint on form and function from those described for other hummingbird-pollinated flowers.

The experiments detailed here can be easily and quickly repeated in the field with other plants. We hope that similar tests are performed and the results published; examples of flowers of similar morphologies not benefitting from the lever mechanism would be especially important to our evolutionary understanding of hummingbird pollination.

SUPPLEMENTARY DATA

Supplementary data are available online at https://academic.oup.com/aob and consist of the following. File S1: Other flowers with apparent lever action motion. File S2: Another analytical way to the same answer.

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