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Are superior ovaries damaged by the bills of flower-visiting birds and does this preclude adaptation to bird pollinators?

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A biological trait may promote adaptation to particular pollinators, and this may be a major factor governing the variation of pollination systems among angiosperm taxa. For instance, one long-standing hypothesis is that compared with superior ovaries, inferior ovaries of angiosperm flowers may be protected from damage by visiting bird bills and, therefore, inferior ovaries may be associated more frequently with bird pollination. To test this hypothesis, we explored the pollination ecology of two *Cerasus* spp. (Rosaceae) with superior ovaries and investigated the potential damage to superior ovaries by bird bills, because such damage must be predicted by the hypothesis. To test whether there is a general relationship between ovary position and bird pollination, we examined published community-level studies involving bird pollination. *Cerasus cerasoides* is more inclined to bird pollination than *C. conradinae* in floral syndrome and pollination experiments, whereas damage to the ovaries or decline in fruit set after bird visitation was not detected in either species. The birds extended their tongues longer than the ovaries, demonstrating why the predicted damage was absent. Bird pollination was not less frequent in plants with superior ovaries in reviewed studies. Our findings did not support the prediction that superior ovaries are damaged by flower-visiting birds and overall the frequency of bird pollination varies with ovary position. These results highlight the complexity in predicting how floral traits affect plant adaptation to pollinators.

ADDITIONAL KEYWORDS: bird pollination – *Cerasus* – floral syndrome – floral trait – inferior ovary – *Prunus* – *Zosterops palpebrosa*.

INTRODUCTION

Convergent and divergent floral evolution in relation to adaptation to pollinators has contributed enormously to floral diversity in angiosperms (van der Niet & Johnson, 2012; Schiestl & Johnson, 2013). A remarkable aspect of floral evolution and diversity is that pollination systems involving different functional groups of pollinators do not show an even taxonomic distribution, but instead are concentrated in specific angiosperm lineages. For instance, bird pollination seems to be common in Gesneriaceae, Loranthaceae and Zingiberales, whereas moth pollination tends to occur in Rubiaceae and Apocynaceae (Proctor, Yeo & Lack, 1996; Cronk & Ojeda, 2008; Willmer, 2011;

Macgregor *et al.*, 2015). To interpret why specific pollination systems are closely related to different angiosperm lineages, one might expect some floral trait of plants to pave the way for repeated evolution and/or evolutionary persistence of the pollination system in those lineages (Stebbins, 1989; Wilson, 2006; Armbruster, Lee & Baldwind, 2009). In bird-pollinated taxa, an inferior ovary is such a trait. The idea of an evolutionary link between bird pollination and inferior ovaries can be traced back to Grant (1950), who hypothesized that inferior ovaries and their ovules are protected from damage by rigid bird bills and therefore bird pollination tends to occur in plants with inferior ovaries. In contrast, superior ovaries might be vulnerable to bird bills and therefore preclude adaptation to bird pollinators. In support of Grant's hypothesis (Grant, 1950), several studies

have considered inferior ovaries as a trait associated with the bird pollination syndrome (Primack, Duke & Tomlinson, 1981; Proctor, Yeo & Lack, 1996; Luteyn, 1989; Turner, 2001; Willmer, 2011; Fang, Chen & Huang, 2012). However, to our knowledge the protective role of the inferior position of ovaries has never been empirically tested possibly because it is impossible to change inferior ovaries into superior ones without damage.

Although the inferior ovary hypothesis seems reasonable, there are two reasons to suspect the protective role of the inferior position of ovaries. First, bird pollination has evolved independently many times and flourished in many angiosperm lineages that do not have inferior ovaries or other protective morphologies proposed by Grant (1950) (e.g. *Penstemon* Schmidel and Neotropical *Ruellia* L. and *Salvia* L.) (Wilson, 2006; Tripp & Manos, 2008; Wester & Claßen-Bockhoff, 2011). Second, hummingbirds feeding on sugar solutions in artificial containers can extend a considerable length of the tongue beyond the tip of the bill (Grant, 1992; Kim *et al.*, 2012), implying that when a bird is visiting the flower the bill does not necessarily contact the ovary usually located in the base. In addition, the original arguments for this hypothesis by Grant (1950) may not be valid in the context of later studies. For example, he argued that Amaryllidaceae and Iridaceae have inferior ovaries and both families are pollinated largely by birds, whereas Liliaceae have superior ovaries and are pollinated largely by insects (Goldblatt & Manning, 2006; Kwembeya *et al.*, 2007; Johnson, 2010). However, at least in sub-Saharan Africa where the three families are all well represented, only 76 of 988 species of Iridaceae for which information on pollination ecology is available are pollinated by birds, and many of Amaryllidaceae, including some red-flowered species, may be insect-pollinated in this region (Goldblatt & Manning, 2006; Kwembeya *et al.*, 2007; Johnson, 2010). In contrast, *Aloe* L. (Asphodelaceae, but assigned to Liliaceae in Grant's time; Grant, 1950) alone has *c.* 350 species in sub-Saharan Africa, most of which are partially or wholly pollinated by birds (Cousins & Witkowski, 2012).

In this study we tested Grant's hypothesis (here we call it the inferior ovary protection hypothesis). Given that we could not manipulate plants with inferior ovaries to expose ovaries in any non-destructive way, we choose two species of *Cerasus* Mill. (Rosaceae; = *Prunus* L. *p.p.*) as experimental species, which have superior ovaries, to test the hypothesis from the perspective of damage to superior ovaries rather than protection of inferior ovaries. On the other hand, unless superior ovaries are damaged by bird bills, inferior ovaries cannot be regarded as a trait that can avoid bird bill-mediated damage and therefore promote adaptation to bird pollinators.

Ovaries in *Cerasus* do not possess any other protective morphologies against birds that Grant (1950) proposed, so damage to ovaries are supposed to occur according to the inferior ovary protection hypothesis. The two *Cerasus* spp. display different floral traits in relation to adaptations to bird pollination: one has no apparent adaptations to birds, whereas the other shows a floral syndrome indicative of bird pollination according to our preliminary observations. We choose such two species because the damage might vary with stages on the evolutionary pathway to bird pollination if bird bills do impose damage on ovaries. Second, we reviewed community-level studies involving bird pollination to test the relationship between bird pollination and ovary position. Specifically, according to the inferior ovary protection hypothesis, the ovaries will be damaged when the flowers are visited by birds and there will be reduced fruit set due to this damage; bird pollination tends to occur more frequently in plants with inferior ovaries.

We quantified floral syndromes and pollination systems of the two *Cerasus* spp. Then we used this information to ask three specific questions. (1) Do birds damage the superior ovaries of *Cerasus* spp. with their bills and reduce fruit set? (2) If this is the case, what is the mechanism behind this? For example, do birds' bills prick and damage the ovaries? (3) Does bird pollination occur in plants with superior ovaries relatively infrequently?

MATERIAL AND METHODS

STUDY SPECIES AND SITES

Cerasus cerasoides (D.Don) S.Ya.Sokolov. (= *Prunus cerasoides* D.Don) is a tree that blooms from late November to early February. It has pink flowers that do not emit a distinct scent but secrete noticeably ample nectar. *Cerasus conradinae* (Koehne) Yu & Li (= *Prunus conradinae* Koehne) is a tree that flowers in March. It has white flowers that emit strong fragrance and always present quite small amounts of nectar. Our study sites are Kunming (25º8'48.9" N, 18 102º44'41.2" E, 1788m) and Baihualing (25°30'42.1"N, 98°78'30.3"E, 1500 m altitude). *Cerasus cerasoides* can be found in both sites, whereas *C. conradinae* is only present in Kunming. Both species occur in subtropical broad-leaved deciduous forests in mountains. The floral scent, colour, nectar and morphology of *C. cerasoides* were quite similar between the two sites and we only reported the results for the Baihualing population. Voucher specimens were deposited in the herbarium of Kunming Institute of Botany, Chinese Academy of Sciences under the following accession numbers: *C. cerasoides* (LCQ 201601), *C. cerasoides* (LCQ 201602) and *C. conradinae* (LCQ 201603).

FLOWER-VISITING ANIMALS AND FLORAL TRAITS

Floral visitor observations

Floral visitors were observed on four days per site when each study species was in full bloom. Observations started at dawn. Each observation session lasted 30 min for birds and 20 min for insects and each tree received one observation. Floral visitors to *C. cerasoides* were observed in December from 2013 to 2015 in Kunming and February in 2015 and 2016 in Baihualing. Flower visitors to *C. conradinae* were observed in March from 2014 to 2016 in Kunming. Birds and insects were observed separately because if we were too far from the observed flowers insects would not be seen clearly and if we were too close birds would not visit the observed flowers. Birds were observed with binoculars. We counted all the flowers in an observed branch before an observation session began to calculate visitation rates later. The number of observed flowers ranged from 700 to 3400 for *C. cerasoides* and 70 to 150 for *C. conradinae*, depending on year and site, because visitation rates varied substantially with year and site and we had to ensure that we could count the visits clearly. All observed flowers in one observation belonged to one tree and all the observations were conducted in different trees. The bird and insect visitation rate (per flower per hour) was estimated as the number of visits per observation multiplied by two and three, respectively, and divided by the number of observed flowers. The numbers of observation sessions (N) were 24 for birds on *C. cerasoides* in Kunming in 2013 and 16 for both birds and insects on *C. cerasoides* in Kunming in 2014. For all other cases $N = 20$ (sessions).

Scent

Floral scent of *C. cerasoides* and *C. conradinae* was collected in 2016. The scent collection was conducted from 11:00 to 13:00 h when bird and insect pollinators were both active. Seventy flowers per tree were sampled and six trees per species were used. Branches containing 70 flowers were cut and enclosed in a Tedlar bag (Dupont, USA). The inflorescence peduncles were wrapped in absorbent cotton soaked in a 10% sucrose solution. Volatiles were drawn from the bags into glass tubes with adsorbent Porapak Q (100 mg, mesh 80–100, Waters Associates, Inc.) using a pump with an inlet flow rate of 300 ml/min. The adsorbent Porapak Q was anchored inside the tubes by small balls of cleaned glass fibre so that it would not be blown out of the tubes when the pump was working. The absorbed volatiles were eluted with 300 µl *n*-hexane to which 3000 ng *n*-nonane was added as internal standard. The total of volatiles was calculated with the percentage of the internal standard in the extract.

The extracts were concentrated to 60 µl by a gentle stream of nitrogen (200 ml/min) and kept at –20 °C in a refrigerator before analysis. These extracts were analysed by HP 6890 gas chromatography (Agilent Technologies, USA), with a HP-5MS column (30 m × 0.25 mm, 0.25 µm film thickness) and linked to an HP 5973 mass spectrometer (Agilent Technologies, USA). Chen *et al.* (2012) give more details of the procedure.

Colour

Colour measurement: Petal reflectance spectra of *C. cerasoides* and *C. conradinae* were measured using a spectrophotometer (USB Ocean Optics 2000+), equipped with a UV-VIS light source (DH-2000, both by Ocean Optics Inc., Dunedin, FL). Each sample was obtained by measuring three flowers from each plant to determine the average. In addition, as both *Cerasus* spp. are hysteranthous, leaves from 20 plant species found in the natural habitat were measured to represent the background. During measurement, the probe was held at 45° to the target surface, to avoid any glare. PTFE (polytetrafluoroethylene) material WS-1 (Ocean Optics) was used as white reference. Before analysis, the raw floral reflectance spectra were processed to 1-nm interval smoothed curves from 300 to 700 nm using the R package pavo (Maia *et al.*, 2013).

Colour perception model: To examine the detectability of flower colour through the eyes of pollinators, we estimated the chromatic and achromatic contrast of flowers against leaf background based on the colour perception of birds and bees, respectively. To compare the results of bird and bee colour perception, we used the logarithm version of a receptor noise-limited model (Vorobyev & Osorio, 1998) to estimate the colour perception of pollinators. For the bee model we used the data for *Apis* provided by Peitsch (1992), with receptor noise values as follows: eUV = 0.13, eB = 0.06 and eG = 0.12. A colour hexagon model (Chittka, 1992) was used to visualize colour loci in the colour space for bees. For the bird model we used the data for blue tits (*Cyanistes caeruleus*), provided by the R package pavo (Maia *et al.*, 2013). This model represents a UVS colour perception system that also applies to Asian Passeriformes. A trichromatic and a tetrachromatic model were used to calculate the floral colour loci for bees and birds, respectively. Detailed calculations can be found in the appendix of Renoult, Kelber & Schaefer (2017). Daylight D65 (ICE) was used as the irradiance spectrum.

Chromatic contrast: For both models, chromatic contrast was indicated by the Euclidean distance from colour loci to the origin of coordinates, in units of just noticeable differences (JND). Increasing distance

indicates increasing chromatic conspicuousness in the perception system.

Achromatic contrast: For bees, the achromatic contrast (ΔS) was estimated by the contrast in the L(green)-receptor (Hempel De Ibarra *et al.*, 2000; Reisenman & Giurfa, 2008), calculated by the quantum catch of the L-receptor produced by a stimulus divided by that produced by the background (Giurfa *et al.*, 1997). For birds, this mechanism involves the similar contrast (Δf_i) in double cones (Cuthill, 2006), and the noise values ω_D were set to 0.05.

$$\Delta S = \left| \Delta f_i / \omega_D \right|$$

Nectar

We measured nectar volume and concentration of one flower from each of 20 trees for both species with capillary tubes and a pocket refractometer at 07:00 h. Sugar content of nectar was used to estimate the amount of nectar given that it reflects the energy value for visitors (Corbet, 2003). It was calculated with the methods introduced by Corbet (2003). Nectar sugar composition of one flower from each of ten trees for both species was analysed with high performance liquid chromatography (Agilent 1100 Series, USA) and a carbohydrate analysis column (Agilent ZORBAX, USA).

Morphology

Floral tube length of one flower from each of 20 trees for both species was measured with a digital calliper from the bottom the hypanthium to its entrance to examine the fit between flowers and visitors.

MORPHOLOGICAL FIT BETWEEN FLOWERS AND POLLINATORS AND DAMAGE TO OVARIES BY BIRDS

Pollination treatments

To assess the different roles of birds and insects in the pollination of *C. cerasoides* and *C. conradinae* and to examine the possible damage to ovaries by bird bills, five pollination treatments were conducted in 2015 for *C. cerasoides* in Baihualing and 2016 for *C. conradinae* in Kunming: open pollination; visitor exclusion; hand cross pollination; bird exclusion and hand cross pollination together with bird exclusion. If ovaries were damaged by bird bills, hand cross pollination would result in significantly lower fruit set than hand cross pollination with bird exclusion. In the bird exclusion treatment, birds were excluded and insects were retained as flower visitors (see Fang, Chen & Huang, 2012 for the method). In the visitor exclusion treatment, fine-mesh voile bags (apertures: 0.3 × 0.3 mm) were used to exclude all floral visitors. On each tree we randomly chose five branches each of which had 35–80 flowers and applied the five treatments and each branch received one of the five treatments. The treatments for *C. cerasoides* were conducted in Baihualing because floral visitors were more abundant there. We harvested the fruits and calculated fruit set 45 days after all treated flowers wilted. To assess possible damage to ovaries by bird bills, we examined the surfaces of the fruits from the two treatments in which flowers were available to birds for mechanical injuries with a magnifying glass. Moreover, in order not to neglect evidence for possible early ovary abortion caused by bird bills, on each tree we examined 100 immature fruits that dropped soon after the flowers wilted.

Pollen deposition by birds and insects

According to our preliminary observations, birds and honeybees visiting the flowers contacted the reproductive organs of *C. cerasoides* and *C. conradinae* at quite different rates because of morphological differences, potentially leading to different rates of pollen deposition on stigmas. To test this hypothesis, we examined whether pollen was deposited on stigmas for both *Cerasus* spp. (single-visit pollen deposition) immediately after the flowers were visited by each of the two types of animal. The fresh stigmas were cut off the styles and each one was put on a microscope slide. Then one or two drops of sodium hydroxide solution were used to soften the stigma for an hour and a coverslip was used to cover and squash the stigma. The deposited *Cerasus* pollen was examined using a dissecting microscope. Tiny amounts of deposited pollen could be enough to pollinate a flower since *Cerasus* has only a single ovule per ovary. The examined flowers were bagged before they started to open to make sure that they were virgin flowers before they were used in our experiments. The visitation rate of birds to *C. cerasoides* was too low to permit this design so we used our six caged birds (see below for bird care and maintenance) to examine single-visit pollen deposition. Each bird was allowed to visit a small branch with 20 flowers freely to pick pollen up before they started visiting the flowers the stigmas of which we used to examine pollen deposition. Stigmas of 17 flowers visited by each bird were used. All the other three examinations (birds on *C. cerasoides*, honeybees on both *Cerasus* spp.) of single-visit pollen deposition were conducted using visitors outdoors instead and ten flowers of each of ten branches from different trees were used for each examination. Birds tended to visit flowers of *C. cerasoides* on high branches and visited less frequently in Kunming than in Baihualing probably because the environment

was more disturbed, posing great difficulty for the experiment. Thus, for this species, we examined single-visit pollen deposition in Baihualing.

Mechanisms behind treatments

Bird care and maintenance: Our preliminary observations suggested that *Zosterops palpebrosa* (Oriental white-eye) was the most common or only bird visitor to flowers of our study plant species. Six individuals of this bird species were captured with a combination of mist-nets and cage traps baited with fruit in Kunming during early March in 2016. Each pair of birds was kept in a cage (33 × 30 × 44 cm) and fed on a daily diet of fruits (apples, pears and bananas) supplemented with Elvish-Soony white-eye pellets (Minlong Products, Zhangzhou, Fujian, China), fresh water and mealworms. To make sure they acclimatized to the new conditions, they were placed outdoors in quiet woodland in Kunming Institute of Botany. They were used in experiments two weeks later and were consequently released.

Nectar extraction by the bills of birds: To present the details of whether and how a bird bill contacts and potentially damages ovaries, it was necessary to film the process of extracting nectar. First, we trained the birds to drink nectar from transparent plastic centrifuge tubes (0.5 mL) and glass tubes (5 mm long) that simulate the floral tubes of *C. cerasoides* and *C. conradinae*, respectively. We fixed those tubes in cardboard with holes surrounded by a flower-shaped paper model to make artificial flowers (Supporting Information, Fig. S1). To induce birds to drink from them, we filled them until they were so full that the meniscus bulged above the rim of the tube and birds could notice that there was liquid in the tubes. After the birds were conditioned to this device, we placed a camera (Nikon, COOLPIX, P900s) beside the cage to record birds drinking nectar. The tubes were filled with sugar solution that simulated the nectar volume, concentration and sugar composition in *C. cerasoides* and *C. conradinae*. Then we played the films back slowly, selecting the clearest feeding event for each bird. We measured how far the tongue of the bird extended beyond the bill and compared this with the ovary length to estimate whether the bill could contact the ovaries in the process of extracting nectar. The ovary length of one flower from each of 20 trees was measured.

BIRD POLLINATION AND OVARY POSITION IN COMMUNITY-LEVEL STUDIES

To test whether bird pollination occurs in plants with superior ovaries less frequently than in plants with inferior ovaries, we performed a literature search on community-level studies involving bird pollination and investigated the relationship between bird pollination and ovary position (inferior or superior) using those studies. We defined the ovary of a plant species as inferior or not according to the descriptions in *The Families and Genera of Vascular Plants* (Kubitzki), http://angio.bergianska.se/ (Johansson) and http://delta-intkey.com/angio/ (Watson & Dallwitz). Whether bird pollination occurred in a plant species was determined on the basis of the results from those community-level studies. Here we considered 'inferior' as being completely inferior and 'superior' as being not completely inferior, given that only being completely inferior can really exclude contact between bird bills and ovaries. Where we could not determine whether the ovary was inferior or not by consulting the information sources (e.g. morphologies vary substantially in a genus), those species were excluded from the survey. We also excluded all species for which pollinators were unknown. Pollinating birds in the New World and the Old World differ dramatically in behaviour and body size (Cronk & Ojeda, 2008), which might have resulted in different evolutionary patterns of bird pollination. Region (Old World vs. New World) was therefore included as a factor with ovary position in our statistical analysis.

STATISTICAL ANALYSIS

Independent samples *t*-tests were used to compare colour perception by bees and birds between the two *Cerasus* spp. in both colour models and to compare the mean values for floral traits (except scent) for which equal variances were not assumed. Chi-square (χ^2) tests were applied to analyse pollen deposition on stigmas. The amounts of collected scent, flower visitation rates of different animal groups, lengths of bird tongues extending beyond the bills and ovary lengths were analysed using a Mann–Whitney test as those data were not normally distributed. A generalized linear model with a binomial distribution (events occurring out of a set of trials) and a logit link function was used to compare fruit sets of pollination treatments and to compare the proportions of bird-pollinated species in plants with and without inferior ovaries in community-level studies. All the statistical analysis was conducted in SPSS 20.0.

RESULTS

FLOWER-VISITING ANIMALS AND FLORAL TRAITS

Floral visitor observations

Floral visitors to both *Cerasus* spp. were insects and birds. Insect visitors were all pollen-gathering (mostly

on *C. cerasoides*) or nectar-feeding honeybees (*Apis cerana*) (Fig. 1) in both sites, although some hoverflies and butterflies visit *Cerasus* flowers rarely, outside our observation sessions. Bird visitors to *C. cerasoides* in Kunming were principally *Zosterops palpebrosa* (Fig. 1) (72.8% of 5559 visits in 2013, 68.4% of 4473 visits in 2014, 83.5% of 5785 visits in 2015) and to a lesser extent brown-breasted bulbul (*Pycnonotus xanthorrhous*). Both of these can be defined as generalist flower-visiting birds (Johnson & Nicolson, 2008). Bird visitors to *C. cerasoides* in Baihualing were *Z. palpebrosa* (90.4% of 7720 visits in 2015, 87.9% of 6839 visits in 2016) and *Aethopyga gouldiae* (Mrs. Gould's sunbird), *Minla cyanouroptera* (blue-winged minla) and, more rarely, some *Pycnonotus*, *Phylloscopus* (willow warbler) and *Garrulax* (babbler). All bird visitors to *C. conradinae* were *Z. palpebrosa*. We compared the bird visitation rate to *C. cerasoides* in December with that to *C. conradinae* in the following March (e.g. December 2013 vs. March 2014) (Fig. 2) because the two months are closer than December and March in the same calendar year. Birds visited *C. cerasoides* significantly more frequently than *C. conradinae* (December 2013 vs. March 2014: $Z = -2.48$, $P = 0.013$; December 2014

vs. March 2015: $Z = -2.86$, $P = 0.004$; December 2015 vs. March 2016: $Z = -2.91$, $P = 0.004$) in Kunming, whereas honeybee visits to *C. cerasoides* were significantly less frequent than or not significantly different from those to *C. conradinae* (December 2013 vs. March 2014: $Z = -1.859$, $P = 0.063$; December 2014 vs. March 2015: $Z = -1.633$, $P = 0.103$; December 2015 vs. March 2016: $Z = -3.333$, $P = 0.001$) (Fig. 2).

Scent

The amount of volatiles collected in two hours from 70 flowers was significantly lower in *C. cerasoides* than in *C. conradinae* (Table 1), corresponding with the fact that flowers of *C. cerasoides* are virtually scentless, whereas those of *C. conradinae* smell strongly fragrant. Analysis of floral scent revealed only six compounds from flowers of *C. cerasoides* and 33 compounds from flowers of *C. conradinae* (Table 2).

Colour

The flowers of the two species differed in their reflectance spectra (Fig. 1). (1) *Chromatic contrast*.
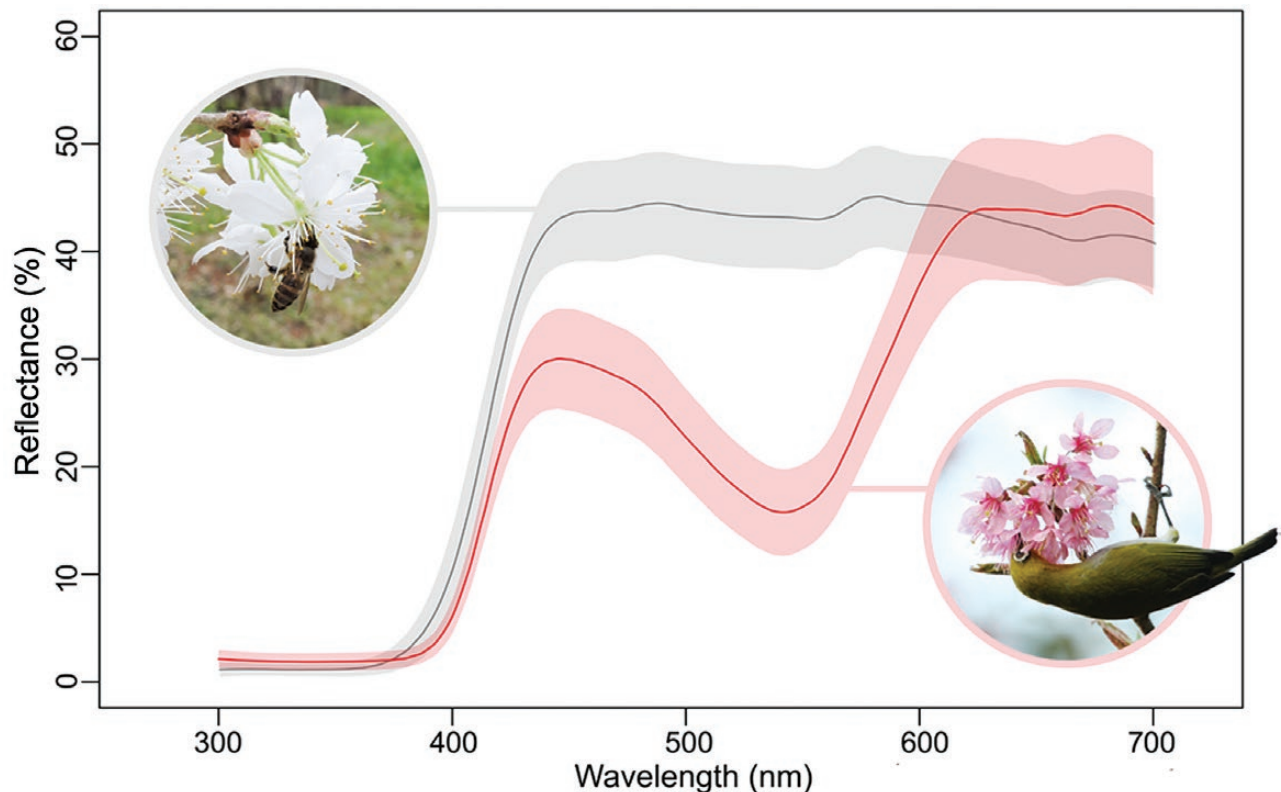
Figure 1. Spectral reflectance of *Cerasus conradinae* (white, with a visiting honeybee, *Apis cerana*) and *Cerasus cerasoides* (pink, with a visiting white-eye, *Zosterops palpebrosa*). The line represents the mean and the shading represents the standard deviation.
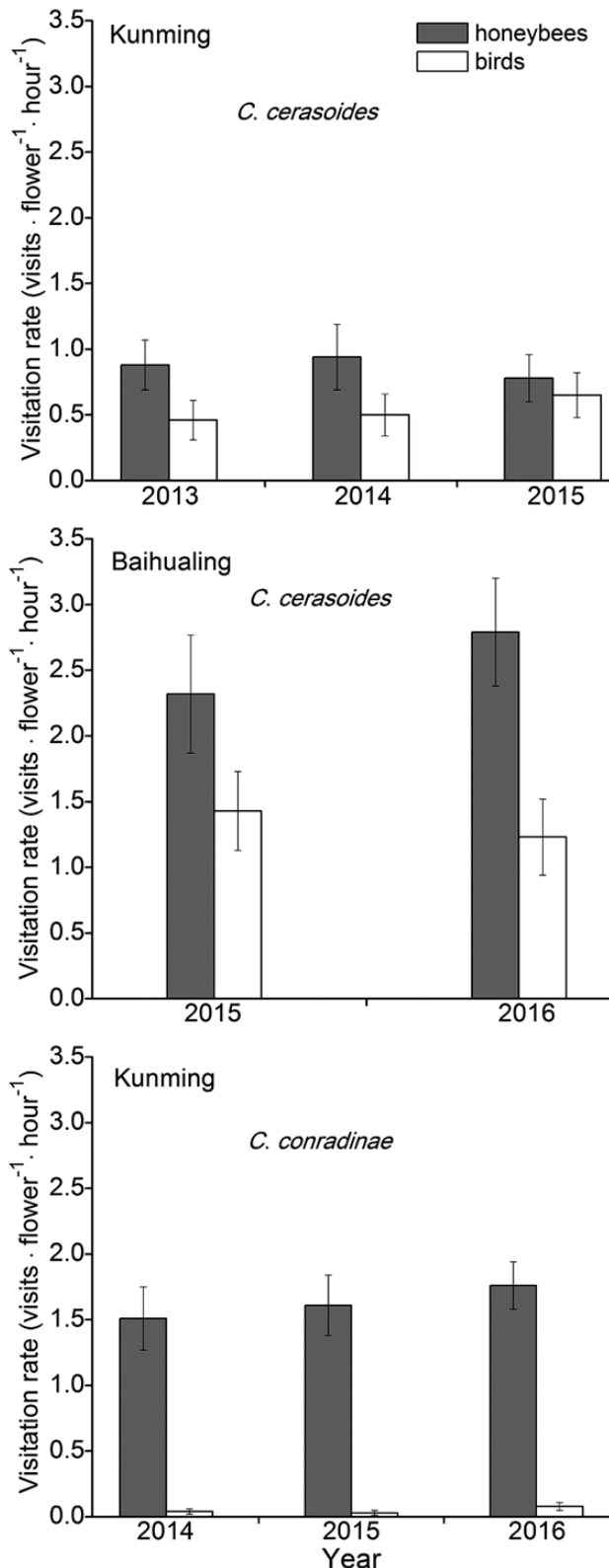
Figure 2. Mean ± s.e. of visitation rates of birds and honeybees to the two *Cerasus* species.

Estimated by the colour perception model for bees, there was no significant difference in detectability (distance from petal colour loci to the background) between *C. cerasoides* ($N = 14$) and *C. conradinae* ($N = 10$) (Fig. 3) ($9.51 ± 0.19$ vs. $9.23 ± 0.18$ JNDs, $t = 1.01$, d.f. = 22, $P = 0.32$). To the eyes of a bird, however, *C. cerasoides* showed significantly higher detectability than *C. conradinae* ($18.12 ± 0.42$ vs. $13.07 ± 0.40$, $t = 8.35$, d.f. = 22, $P < 0.001$). The colour loci of these two species are shown in Fig. 3. (2) *Achromatic contrast*. For both bees ($2.78 + 0.14$ vs. $5.32 + 0.18$, $t = -11.28$, d.f. = 22, $P < 0.001$) and birds ($23.12 ± 0.94$ vs. $33.81 ± 0.67$, $t = -8.55$, d.f. = 22, $P < 0.001$), the contrast in the L-receptor was greater in *C. conradinae* than in *C. cerasoides*. Both the colour models showed that white flowers have significantly higher achromatic contrast than reddish pink ones.

Nectar

The nectar (Table 1) of *C. cerasoides* was more dilute than that of *C. conradinae*. The nectar volume and sugar content per flower was greater in *C. cerasoides* than that in *C. conradinae*. *Cerasus cerasoides* had a lower proportion of sucrose in the nectar sugar than *C. conradinae*. All the three nectar traits in *C. cerasoides* and *C. conradinae* are characteristic of flowers pollinated by generalized birds and long-tongued bees (see Johnson & Nicolson, 2008; Willmer, 2011).

Morphology

The floral tubes of *C. cerasoides* was significantly longer than that of *C. conradinae* and the two species differs in the arrangement of stamens and styles (Table 1, Fig. 1). The difference in tube length corresponds with the difference in mouthparts of their main pollinators (see Zhao, 2001; Willmer, 2011).

MORPHOLOGICAL FIT BETWEEN FLOWERS AND POLLINATORS AND DAMAGE TO OVARIES BY BIRDS

Pollination treatments

No fruits were produced in the visitor exclusion treatment for either *C. cerasoides* or *C. conradinae*. This treatment was not included in the subsequent statistical analysis. Fruit set differed between the four pollination treatments in *C. cerasoides* (Wald $\chi^2 = 139.145$, d.f. = 3, $P < 0.001$, $N = 16$ for all treatments) (Fig. 4). Pairwise comparisons indicated that the fruit set from the bird exclusion treatment was significantly lower than those from the other three treatments (all $P < 0.001$) and the average of fruit set from the bird exclusion treatment was less than half of that from any one of the other three treatments (Fig. 4), suggesting that birds played

Table 1. Comparison of floral syndromes in two *Cerasus* species. The numbers represent mean ± s.e. Refer to Results for detailed colour analysis and to Table 2 for detailed scent composition analysis. SS = Stamens and styles. The 'one whorl' of stamens and styles (Fig. 1) does not mean a morphological whorl but a functional whorl

	C. cerasoides	*C. conradinae*	Statistical results
Floral display traits			
Colour	Pink	White	See Results
Scent (ng/2 h)	188 ± 63	10 842 ± 512	Z = −2.882, P = 0.004
Morphology			
Tube length (mm)	9.0 ± 0.1	4.8 ± 0.1	$t = 25.393$, d.f. = 38, $P < 0.001$
SS arrangement	One whorl	Irregular	
Nectar			
Concentration (%)	13.4 ± 0.5	43.3 ± 1.5	$t = 18.548$, d.f. = 38, $P < 0.001$
Volume (μL)	7.57 ± 0.96	0.53 ± 0.07	$t = 7.331$, d.f. = 38, $P < 0.001$
Sugar content (μg)	1.08 ± 0.15	0.27 ± 0.04	$t = 5.377$, d.f. = 38, $P < 0.001$
Sucrose (%)	9.0 ± 0.6	91.7 ± 1.5	$t = 13.571$, d.f. = 18, $P < 0.001$

a more important role in the pollination of this species than insects. The other three treatments did not differ in fruit set (all $P > 0.05$). There is no significant difference among pollination treatments in *C. conradinae* (Wald $\chi^2 = 4.365$, d.f. = 3, $P = 0.225$, $N = 20$ for all treatments) (Fig. 4), suggesting that honeybees alone could assure sufficient pollination of this species. There was no evidence for pollen limitation in either species since the fruit set from the open pollination was not significantly different from that from the hand cross pollination. The fruit set from hand cross pollination was not significantly different from that from hand cross pollination together with bird exclusion, suggesting that bird visitation did not reduce fruit set in these *Cerasus* spp., as would have been expected if the ovary was damaged by the bill of the bird. No mechanical damage was found on the fruits from the two treatments in which flowers were available to birds and the 100 dropped immature fruits from each treated tree.

Pollen deposition by birds and insects

Birds deposited pollen onto stigmas of *C. cerasoides* (98 of 100 visits) more frequently than onto *C. conradinae* (23 of 102 visits) ($\chi^2 = 119.677$, $P < 0.001$), whereas honeybees deposited pollen onto stigmas of *C. cerasoides* (17 of 100 visits) less frequently than onto *C. conradinae* (58 of 100 visits) ($\chi^2 = 117.69$, $P < 0.001$). These results indicate that flower morphologies of *C. cerasoides* and *C. conradinae* are more adapted to birds and honeybees respectively.

Mechanisms behind treatments

The playback of short films showed that the birds did not peck at the artificial flowers, but just extended their tongues to extract nectar (Supporting Information, Videos S1, S2). The length of tongue

extended beyond the bill tip was 3.51 ± 0.05 (mean ± s.e.) mm ($N = 6$) in the process of extracting nectar from artificial flowers simulating *C. cerasoides* (Supporting Information, Video S1), which was significantly longer than the ovaries (mean ± s.e. 1.84 ± 0.05, $N = 20$) of this species ($Z = −3.651$, $P < 0.001$). The length was 2.35 ± 0.03 mm (mean ± s.e. $N = 6$) in the process of extracting nectar from artificial flowers simulating *C. conradinae* (Supporting Information, Video S2), which was significantly longer than the ovaries (mean ± s.e. 1.48 ± 0.04, $N = 20$) of this species ($Z = −3.653$, $P < 0.001$).

BIRD POLLINATION AND OVARY POSITIONIN COMMUNITY-LEVEL STUDIES

Bird pollination did not occur more frequently in plants with inferior ovaries (mean ± s.e. 9.0 ± 1.8%) than with superior ovaries (mean ± s.e. 7.7 ± 1.4%, Wald $\chi^2 = 0.836$, d.f. = 1, $P = 0.361$), suggesting that there was no tendency for bird pollination to concentrate on plants with inferior ovaries. No significant interaction (Wald $\chi^2 = 1.051$, $P = 0.305$) between region and ovary position indicated that the Old World ($N = 10$) and the New World ($N = 17$) do not differ in the relationship between bird pollination and ovary position in plants with inferior ovaries. The plant species with inferior ovaries and/or pollinated by birds in the collected studies were listed in Supporting Information, Review S1.

DISCUSSION

Cerasus cerasoides and *C. conradinae* exhibit a floral syndrome suggestive of bird pollination and insect pollination, respectively. *Cerasus cerasoides* was more dependent on birds for pollination, despite bird and insect visitation to both species. The superior ovaries

Table 2. Average relative amounts (mean ± s.e. %) of floral scent compounds from *C. cerasoides* and *C. conradinae*. Lilac aldehydes and lilac alcohols both contain three isomers. "–", not detected.

| Compound	*C. cerasoides*	*C. conradinae*
FATTY ACID DERIVATIVES		
Alcohols		
2-Ethylhexanol	14.13 ± 3.42	–
Alkanes		
Dodecane	3.24 ± 0.51	–
Tetradecane	–	0.08 ± 0.05
Esters		
Octyl acetate	1.97 ± 0.64	–
Benzenoids		
Benzaldehyde	14.56 ± 4.27	21.90 ± 2.01
Benzyl alcohol	–	1.77 ± 0.75
4-Ethylbenzaldehyde	–	0.06 ± 0.06
Ethyl 4-methoxybenzoate	–	3.65 ± 1.16
4-Methoxybenzaldehyde	–	0.24 ± 0.13
Methyl benzoate	–	4.77 ± 1.21
Phenylacetaldehyde	–	20.98 ± 1.07
Phenylethanol	–	2.32 ± 0.64
Methyl salicylate	–	1.58 ± 0.39
Ketones		
6-Methyl-5-hepten-2-one	–	0.36 ± 0.09
ISOPRENOIDS		
Monoterpenoids		
α-Camphene	–	0.24 ± 0.24
p-Cymene	–	0.14 ± 0.10
4,8-Dimethyl-l,3,7-nonatriene	–	6.08 ± 1.79
Lilac alcohols	–	4.73 ± 1.04
Lilac aldehydes	–	8.85 ± 2.69
Limonene	41.48 ± 4.52	0.31 ± 0.14
Linalool	–	4.57 ± 1.71
Myrcene	–	0.32 ± 0.15
allo-Ocimene	–	0.31 ± 0.15
cis-β-Ocimene	–	3.33 ± 0.92
trans-β-Ocimene	–	2.07 ± 0.65
α-Phellandrene	–	0.56 ± 0.38
α-Pinene	24.61 ± 3.96	0.54 ± 35
α-Thujene	–	0.19 ± 0.12
Sesquiterpeniods		
δ-Cadinene	–	0.03 ± 0.03
β-Caryophyllene	–	0.10 ± 0.08
β-Elemene	–	0.04 ± 0.04
(*E,E*)-α-Farnesene	–	4.49 ± 1.75
Germacrene D	–	1.84 ± 1.35
Nerolidol	–	1.59 ± 0.35
CAROTENOID DERIVATIVES		
Dihydro-β-ionone	–	0.13 ± 0.09
β-Ionone	–	1.81 ± 1.5

were not damaged by bills and there was no decline in fruit set after bird visitation in either of the *Cerasus* spp. The bird tongues extended beyond the tip of the bills by a distance significantly greater than the height of the ovaries, so bills probing in flowers probably did not contact ovaries. Our review of community-level pollination studies revealed no tendency for bird pollination to be constrained in plants with superior ovaries.

Flowers of *C. cerasoides* and *C. conradinae* exhibit a dichotomy in floral syndromes (Table 1; Figs 1, 3) associated with pollination by generalist birds and large bees, respectively (Johnson & Nicolson, 2008; Willmer, 2011), and our study confirmed the prediction of their differential dependence on birds and bees for pollination (Fig. 4). Although bird visitation and pollination in Rosaceae has been mentioned elsewhere (Proctor, Yeo & Lack, 1996; Fang, Chen & Huang, 2012), as far as we know, *C. cerasoides* is the first reported species of Rosaceae with a typical floral syndrome of bird pollination and a pollination system mainly involving birds. *Eriobotrya japonica* is another member of Rosaceae in the pollination of which birds play a significant role (Fang, Chen & Huang, 2012), but its flowers retain white petals and strong scent and are visited by a much broader range of insects. Birds may also act as principal pollinators of some other species of Rosaceae producing abundant nectar as in *C. cerasoides* (Fig. 1) in tropical and subtropical Asia (unpubl. data). *Cerasus conradinae* remains a typical insect-pollinated species as is usual in Rosaceae, but birds can transfer pollen between flowers if they visit the flowers. In these *Cerasus* spp., which seem to be at different stages of an evolutionary pathway to bird pollination, however, we found no evidence for bird bill-mediated damage to the superior ovaries as predicted by the inferior ovary protection hypothesis (see Grant, 1950). The absence of damage to ovaries cannot be attributed to other possible morphological protective traits proposed by Grant (1950) because none of them is present in the two species. These findings indicate that compared with superior ovaries, inferior ovaries may not be a special trait to enhance adaptation to bird pollination.

Our investigation of the process of extracting sugar solutions from artificial flowers demonstrated that the bird bill might not contact ovaries at all because the tongues extended as birds drank liquid. This presents a plausible explanation for why the bird bills did not damage the superior ovaries and may also be the case for other important flower-visiting birds such as hummingbirds and honeyeaters, which can extend their tongues much further than *Z. palpebrosa* here (see Grant, 1992; Kim *et al.*, 2012). No published data
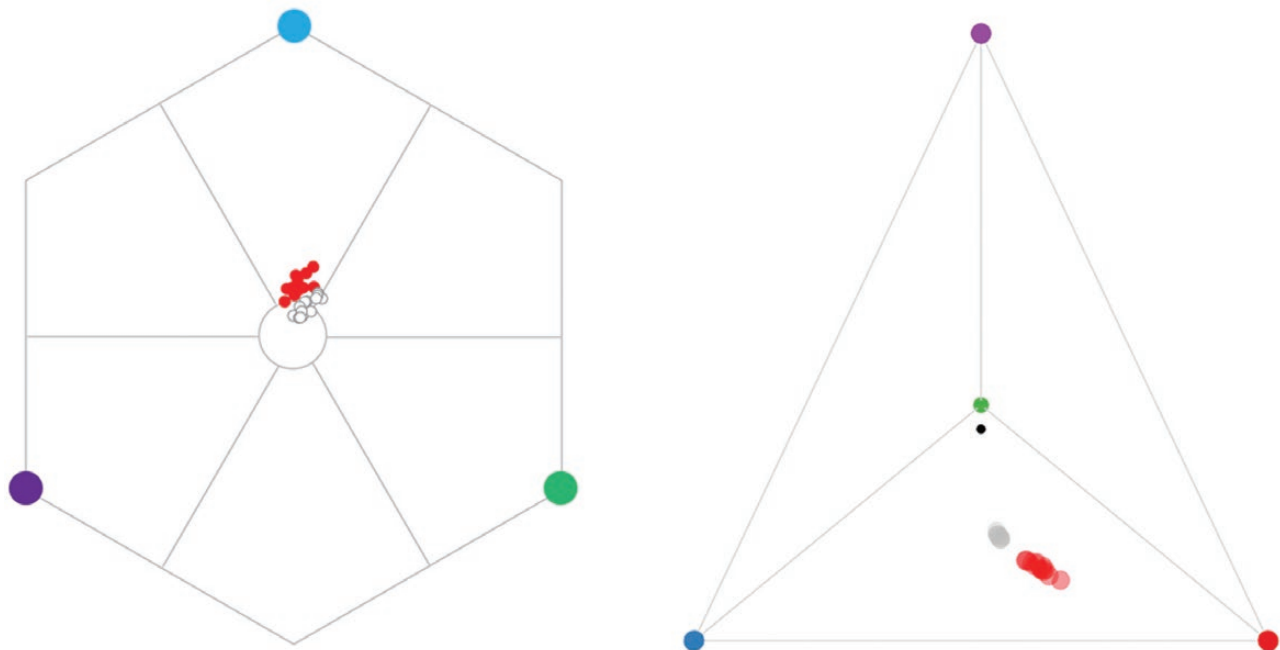
Figure 3. Visualized colour loci in bee (left) and bird (right) colour perception models. Increasing distance [in units of JNDs (just noticeable differences)] between loci and the origin of coordinates indicates increased detectability of the colour. Red: *C. cerasoides*. Grey: *C. conradinae*.
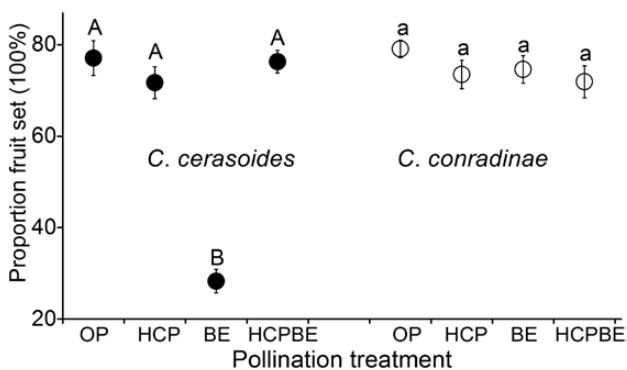
Figure 4. Mean ± s.e. of fruit set in four pollination treatments: open pollination (OP), hand cross pollination (HCP), bird exclusion (BE), hand cross pollination and bird exclusion (HCPBE). For each species, means sharing the same letters are not significantly different (*P* > 0.05).

were found about how long sunbirds extend their tongues when they are feeding on nectar. However, we have taken a photograph of a female sunbird (*Aethopyga saturata*) visiting flowers of *Colquhounia elegans* Wall. (Supporting Information, Fig. S2) in the field, which showed that at least 5 mm of her tongue were beyond the tip of the bill (estimated from the average bill length of this species; see Zhao, 2001). Sunbirds (Asia and Africa), hummingbirds (America) and honeyeaters (Oceania) are predominant bird

pollinators in the world (Cronk & Ojeda, 2008). It seems reasonable to predict that superior ovaries are probably not often damaged by those birds. Although we only scrutinized the feeding details of *Z. palpebrosa* in this study, we could infer that other birds visiting *Cerasus* in this study may also extend their tongues and do not damage the ovaries because of the fully intact *Cerasus* ovaries after their visitation.

One might imagine a possibility that birds do not damage inferior ovaries but damage superior ovaries when they are puncturing perianths and robbing nectar because an inferior ovary is completely below the perianth. Nectar robbing by birds is rare and sporadic in bird-adapted *C. cerasoides* (and did not occur every year) and absent in insect-adapted *C. conradinae* so it would be almost impossible to examine this hypothesis in detail with the two *Cerasus* species in this study. We did find out 140 flowers with punctures in total in 2014 and 115 ovaries from those flowers developed into fruits without signs of scars or with tiny obscure signs of scars. This suggested that birds did not cause significant damage to the superior ovaries even if they robbed nectar, although such a scenario lacks statistical power because all the 140 robbed flowers concentrated on only three neighbouring trees on the campus of Yunnan Agricultural University, Kunming. All the other robbed flowers we found were too few and sparse to deserve investigation. No mechanical damage by bird bills occurred either in three other

bird-pollinated plant species we studied in Yunnan Province, *Colquhounia elegans*, *Mayodendron igneum* Kurz and *Rhododendron vialii* Delavay & Franch. (unpubl. data), despite frequent nectar robbing. Moreover, Grant (1950) himself mentioned various examples of flowers damaged by birds, but did not provide any example of damage to superior ovaries by birds robbing nectar in the study in which he proposed the inferior ovary protection hypothesis. Thus, damage to superior ovaries caused by nectar robbing might not be common though it needs to be examined in more plant species.

A tendency for bird pollination to concentrate on plants with inferior ovaries has generally been mentioned (e.g. Primack, Duke & Tomlinson, 1981; Proctor, Yeo & Lack, 1996; Luteyn, 1989; Turner, 2001; Willmer, 2011; Fang, Chen & Huang, 2012) since Grant (1950), but our review of community-level studies involving bird pollination found no evidence for this prediction based on the inferior ovary protection hypothesis, suggesting that superior ovaries do not constrain floral adaptation to bird pollinators and inferior ovaries do not promote it. The discordance between the results of our review and the general impression of some pollination ecologists and botanists might arise from the possibility that those pollination ecologists and botanists since Grant (1950) were particularly impressed by some angiosperm lineages that are rich both in species with inferior ovaries and in ones with bird pollination systems. One example is the New World Ericaceae, in which bird pollination predominates in genera with inferior ovaries, whereas insect pollination predominates in those without (Luteyn, 1989). At first sight, this seems to conform with the prediction that bird pollination tends to occur in plants with inferior ovaries. However, it should be noted that the New World genera of Ericaceae without inferior ovaries mostly occur at higher latitudes, where hummingbirds as pollinators are probably not as reliable as those in the Tropics (Luteyn, 1989). Pollinator-mediated floral divergence is substantially dependent on the biogeographical distribution of pollinators (Stebbins, 1970; Johnson & Raguso, 2016), so the uneven occurrence of bird pollination among genera of the New World Ericaceae may result from the difference in local pollinator climates and does not necessarily result from the different ovary morphologies. A second remarkable example is that bird pollination prevails in the New World Gesneriaceae, which have inferior ovaries, whereas bird pollination may be much less common in the Old World Gesneriaceae, which have superior ovaries (Weber, 2004). On the other hand, Myrtaceae might go against the prediction of inferior ovary protection hypothesis. Bird pollination seems common in this large family in Oceania, where typical inferior ovaries seem rare, whereas bird pollination may be rare in the New World Mytaceae, despite the prevalence of typical inferior ovaries as our review suggests (Supporting Information, Review S1). Thus, ovary position may not account for the uneven distribution of bird pollination between the New and Old World in Gesneriaceae. In a word, it is problematic to consider inferior ovaries as a trait closely related to bird pollination.

In conclusion, the inferior ovary protection hypothesis has long been put forward, but this study found no evidence that superior ovaries are vulnerable to bird bills, implying the absence of a protective role of inferior ovaries. We also found no tendency for bird pollination to be precluded in plants with superior ovaries, which is also predicted by this hypothesis. Absence of bird-mediated damage to the superior ovaries of the two *Cerasus* spp. is probably attributable to the fact that birds extended lengths of the tongue beyond their bills and the bills did not contact ovaries. This scenario apparently may apply to many other common flower-visiting birds and their feeding flowers.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Artificial flowers for birds to visit.
Figure S2. A female *Aethopyga saturata* visiting *Colquhounia elegans* flowers, with her tongue out.
Review S1. Plants with inferior ovaries and/or pollinated by birds.
Video S1. Birds visiting artificial flowers simulating *Cerasus cerasoides*.
Video S2. Birds visiting artificial flowers simulating *Cerasus conradinae*.