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Why are some plant–nectar robber interactions commensalisms?

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Many plants that bear hidden or recessed floral nectar experience nectar robbing, the removal of nectar by a floral visitor through holes pierced in the corolla. Although robbing can reduce plant reproductive success, many studies fail to find such effects. We outline three mechanistic hypotheses that can explain when interactions between plants and nectar-robbers should be commensal rather than antagonistic: the non-discrimination (pollinators do not avoid robbed flowers), visitor prevalence (robber visitation is rare relative to pollinator visitation), and pollen saturation (stigmas receive sufficient pollen to fertilize all ovules with one or very few pollinator visits) hypotheses. We then explore these mechanisms in the North American subalpine, bumble bee-pollinated and nectar-robbed plant *Corydalis caseana* (Fumariaceae). We first confirmed that the effects of nectar robbing on female reproductive success were neutral in *C. caseana*. We then tested the three mechanisms underlying these neutral effects using a combination of observational studies and experiments. We found evidence for all three mechanisms. First, consistent with the non-discrimination hypothesis, pollinators failed to discriminate against experimentally robbed flowers or inflorescences even though naturally robbed flowers offered significantly lower nectar rewards than unrobbed flowers. Second, *C. caseana* was more commonly visited by pollinators than by nectar robbers, in accordance with the visitor prevalence hypothesis. Third, stigmas of unvisited flowers as well as those visited once by pollinators were saturated with pollen, with all stigmas bearing pollen loads several orders of magnitude higher than the number of ovules per fruit, consistent with the pollen saturation hypothesis. Our investigation of the mechanisms driving the commensal outcome of nectar robbing in this system deepens our understanding of the ecology of nectar robbing and contributes to a more general understanding of the variation in the outcomes of interactions between species.

Keywords: nectar robbing, commensalism, *Corydalis caseana*, plant reproduction

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Introduction

Mutualisms are prone to exploitation when individuals collect a reward or obtain a service from their partner without reciprocating. The fitness effects imposed by exploiters have traditionally been assumed to be negative (Jones et al. 2015). For example, in an early description of the exploitation of nectar rewards in flowers by non-pollinating visitors, Darwin supposed that "...all plants must suffer in some degree when bees obtain their nectar in a felonious manner…" (Darwin 1876). Indeed, exploitation can be detrimental to host fitness because the resources invested in the reward or service are lost, potentially making future interactions with mutualist partners less likely (Irwin and Brody 1998), and/or increasing the metabolic cost of reward production for species that replenish rewards (e.g. nectar) upon removal (Pyke et al. 1988). However, the outcomes of species interactions depend on the interplay between traits and processes unique to the particular web of interaction partners and the larger community in which they are imbedded and may not coincide with the predictions we might make based on first principles. There is growing recognition that exploiters of mutualisms do not always, or even typically, impose negative fitness effects on their hosts (Jones et al. 2015). In these cases, the exploiter may be acting as a commensal: that is, it may profit from its partner, while the partner experiences neither positive or negative fitness consequences from the interaction. For example, some non-pollinating fig wasps consume sterile fig tissue and exact no reproductive cost on their plant hosts (Bronstein 1991). While a great deal of research has explored the causes and consequences of negative species interactions (predation, competition, parasitism) (Gurevitch et al. 2000) and, to growing extent, positive species interactions (mutualism and facilitation) (Bronstein 2015), relatively little work has explored commensalism, despite its ubiquity in nature (Palumbi 1985, Sáyago et al. 2013).

One of the best-studied examples of exploitation of mutualisms is the interaction between animal-pollinated plants and nectar robbers (reviewed by Irwin et al. 2010). Nectar robbers are floral visitors that feed on nectar via holes made in flowers, often without transferring pollen. The effect of nectar robbers on plant reproduction ranges from negative to neutral to positive (Olesen 1996, Maloof and Inouye 2000, Irwin et al. 2001). Plants can experience direct negative effects of robbing through damage to floral reproductive tissues (McDade and Kinsman 1980), and indirect negative effects through decreased attractiveness of robbed flowers to pollinators (Irwin and Brody 1999). Conversely, when visitation by pollinators does not limit seed production, decreased attractiveness due to nectar removal by robbers may actually benefit plant reproduction by increasing pollinator flight distances between plants, possibly reducing rates of self-pollination and bi-parental inbreeding (Zimmerman and Cook 1985, Maloof 2001). Robbers may also positively affect plant reproduction if they pollinate flowers while robbing (Olesen 1996, Maloof and Inouye 2000). Many studies document both negative and positive effects of robbing, and several have explored the mechanisms underlying these effects (Inouye 1983, Burkle et al. 2007). However, while roughly one third of the studies of nectar robbing find no effect of robbing on plant fitness (Maloof and Inouye 2000) and some of these offer plausible post hoc explanations for it (Inouye 1983, Hazlehurst and Karubian 2016), few studies have directly explored mechanisms driving neutral effects (but see Morris 1996). Here we explicitly formulate and test mechanistic hypotheses that might explain neutral effects of nectar robbing on plant reproduction.

We suggest that at least three, non-mutually exclusive hypotheses could explain neutral effects of nectar robbing. First, pollinators may not discriminate between robbed and unrobbed flowers (the non-discrimination hypothesis). Nectar-robbed flowers often have lower nectar standing crops than unrobbed flowers (Richardson and Bronstein 2012). While pollinators sometimes avoid robbed flowers due to low nectar volumes (Dohzono et al. 2008, Zhang et al. 2009), such behavior is not ubiquitous (Fumero-Cabán and Meléndez-Ackerman 2013) and may be dependent on the pollinator species (Irwin et al. 2001). This hypothesis predicts that robbing has a neutral effect on plant reproduction even in pollen-limited populations, because robbing does not change the behavior of pollinators. Second, the visitor prevalence hypothesis predicts that if the ratio of robber-to-pollinator visitation frequency is low enough, then robbing may have a neutral effect even if there is some pollinator discrimination against robbed flowers. This mechanism may be especially relevant for female mating success, which often peaks with fewer visits from pollinators than male mating success (Carlson 2007). Third, the pollen saturation hypothesis predicts that even moderate to large reductions in pollinator visitation to nectar-robbed plants and flowers may not translate into differences in female reproductive success. This mechanism could operate when plant reproduction is not pollen-limited, either due to high pollen receipt relative to ovules per flower or due to autogamous selfing in self-compatible species with little inbreeding depression (Burkle et al. 2007). The visitor prevalence and pollen saturation hypotheses predict the same outcome (visitation by pollinators is high enough to avoid pollen limitation). However, they are distinct from one another because the mechanisms driving that outcome differ. The visitor prevalence hypothesis relies on a community-based mechanism, while the pollen saturation hypothesis relies primarily on floral design and plant mating system. While these three mechanisms have, to some extent, been suggested previously and partially explored, no studies have formalized a discrete set of hypotheses regarding mechanisms driving neutral effects of robbing or to test such a set of hypotheses together in a single system.

The goal of this study was to test these three hypotheses empirically in a native North American plant, *Corydalis caseana* (Fumariaceae), which is both robbed and pollinated by bumble bees. Prior research on this species documented neutral effects of nectar robbing on female components of plant reproduction (Maloof 2000, 2001); thus, this system provided an opportunity to test the mechanisms driving these

effects with respect to female reproductive success. Given the consistency of evidence for spatio–temporal variation in the outcome of species interactions (Chamberlain et al. 2014), we first conducted observations and experiments to verify that the effects of robbing on female components of *C. caseana* reproduction were neutral in the populations and years in which we worked. We then used a series of observations and experiments to explore the mechanisms driving these effects. We first assessed whether there was a reward-based motivation for pollinators to discriminate against robbed plants and flowers, by testing the assumption that nectar standing crops differ between robbed and unrobbed flowers. We confirmed that robbed flowers had significantly lower nectar standing crops compared to unrobbed flowers. We then tested the non-discrimination hypothesis through a field experiment designed to answer the question: Do pollinators discriminate against robbed plants and flowers? If pollinators visit robbed and unrobbed flowers at similar rates, as the non-discrimination hypothesis predicts, then robbing status should not influence pollen receipt and seed set, barring any physical damage to the gynoecium or androecium during robbing. To test the visitor prevalence hypothesis, we asked: how common are pollinator visits relative to nectar robber visits? Plants may escape the negative effects of robbing if robber visits are rare relative to those from pollinators. Finally, we tested the pollen saturation hypothesis by asking: how do single visits from pollinators affect stigmatic pollen loads? High single-visit pollen receipt, as well as high levels of autogamous pollen transfer, in self-compatible species could negate any possible plant-reproduction effects of pollinator discrimination between robbed versus unrobbed flowers. Our results demonstrate how nectar robbing can produce a commensal outcome, using general hypotheses that may be relevant to all plant–pollinator-robber interaction webs.

Material and methods

Study system

Our field sites were in the Elk Mountains of Gunnison County, Colorado, USA near the Rocky Mountain Biological Laboratory (RMBL). We worked in three sites: Kebler Pass (38°86′55.8″N, –107°10′52.8″W; 3086.40 m a.s.l.), Poverty Gulch (38°95′61.5′N, –107°07′71.3″W; 2917.55 m a.s.l.), and Washington Gulch (38°95’99.7″N, –107°03′37.9″W; 3149.80 m a.s.l.). All sites were in wet subalpine meadows with similar floral communities and bee assemblages. *Corydalis caseana* (Fumariaceae) is an herbaceous hermaphroditic perennial occurring in wet meadows, seeps and drainages of the subalpine zone of North America's mountain west. It grows in dense stands with stalks reaching 1–1.5 m in height, and mature plants can bear approximately 20 stalks (Maloof 2000). Stalks bear numerous terminal racemose, occasionally branching, inflorescences with approximately 5–70 flowers each (Maloof 2000). The bilaterally symmetrical flowers bear a single nectar spur. The flowers are hermaphroditic and do not exhibit dichogamy or herkogamy (Maloof 2000). While pollen is readily transferred to the stigmas autogamously, flowers are only partially self-compatible, with seed set approximately 1.5 times higher in outcrossed flowers; open pollinated flowers produce a mean of 5 ± 0.8 seeds fruit^{-1} (± 2 SE) (Maloof 2000). Flowers produce nectar (35% sugar) at a rate of approximately 2 µl day^{-1} (Maloof 2000). In the West Elk Mountains, bumble bees (*Bombus* spp.) are the most common floral visitors to *C. caseana*. *Bombus appositus* is the most common pollinator, responsible for >50% of all visits to the species in some years (Maloof 2000). Less frequent, more spatially and temporally variable visitors include *Bombus flavifrons, B. bifarius, B. balteatus, B. mixtus, B. frigidus, B. rufocinctus, B. nevadensis* and *B. fervidus,* as well as some non-*Bombus* bees, hummingbirds and butterflies.

Corydalis caseana is also commonly nectar-robbed by at least two bumble bee species, *Bombus occidentalis* and *B. mixtus*. *Bombus occidentalis* is historically the most common nectar robber on *C. caseana,* and was responsible for approximately 30% of all floral visits observed in some sites and years (Maloof 2000). *Bombus occidentalis* and *B. mixtus* can act both as primary nectar robbers (making robbing holes in flowers and removing nectar) and as secondary nectar robbers (removing nectar from holes already present) on *C. caseana*. These robbers do not damage reproductive or nectar-producing structures while primary or secondary robbing; thus, robbers do not directly interfere with fertilization or seed development in this species. *Corydalis caseana* is consistently and heavily robbed, with > 90% of flowers bearing robbing holes in many years and sites and experiences high levels of secondary robbing (Irwin and Maloof 2002). Despite heavy nectar robbing, a previous study found neutral effects of robbing on *C. caseana* fruit and seed set (Maloof 2001). The mechanisms driving these neutral effects are unknown, and we investigated them here.

Field methods

Are the effects of nectar robbing on female function neutral?

To confirm that the effects of nectar robbing on female reproduction were neutral in the populations in our study, consistent with Maloof (2000) from field work conducted in 1996, we used observations and experiments in 2014 and 2015 to compare pollen receipt, pollen-tube growth, fruit set, and seed set between robbed and unrobbed plants and flowers.

I. Observational study

The number of pollen tubes per stigma is a proxy for female mating success, as the number of pollen tubes in a stigma sets an upper limit on the number of ovules that can be fertilized in an ovary. We compared pollen tube growth in unrobbed and naturally robbed *C. caseana* flowers collected near peak bloom (population-level) from three sites in 2014 (Kebler Pass on 14 July, Poverty Gulch on 10 and 15 July, and Washington Gulch on 11 July). We sampled up to

10 plants per site and collected up to five robbed (bearing at least one robbing hole) and five unrobbed flowers of similar age from each plant. We collected 311 styles from 32 plants, and successfully processed 249 styles from 29 plants.

In the field, we fixed each flower in 3:1 (volume : volume) 95% ethanol : glacial acetic acid to arrest pollen-tube growth. In the lab, we rinsed pistils in DI water and transferred them to new vials containing 4:1 (volume : volume) 1% basic fuchsin : 1% fast green to stain pollen tubes for visualization via white light transmission. After 24 h, we rinsed pistils in DI water and transferred them to vials with 88% lactic acid to clear and soften them. After 5 d in lactic acid, we mounted the styles on microscope slides using clear fingernail varnish (Kearns and Inouye 1993). Using a compound microscope, we counted the number of pollen tubes at the receptacle end of each style at 1000× magnification. For each plant, we calculated the mean number of pollen tubes in robbed versus unrobbed flowers.

Statistical analysis. We performed all statistical analyses (here and below) in R ver. 3.4.0 (<www.r-project.org>). We compared mean number of pollen tubes between robbed and unrobbed flowers using a mixed effects model, fit by maximum likelihood (ML), with robbing status (robbed versus unrobbed) as a fixed effect and site and plant as random effects, with plant nested within site. To assess the effect of robbing status on pollen tube count, we performed a likelihood ratio test by comparing the full model to a model with the same random effects, but with intercept as the only fixed effect. We constructed the generalized linear mixed effects models (GLMM) in 'lme4' (Bates et al. 2015) in R (here and below) and used 'lmerTest' (Kuznetsova et al. 2015) to perform inference tests for GLMMs.

II. Experimental study

We experimentally manipulated the frequency of nectar-robbed flowers at one site (Kebler Pass) and measured subsequent effects on pollen receipt, fruit set and seed set from 2–24 July 2015. We haphazardly assigned plants to one of three treatments with five plants per treatment: no robbing (control), flowers robbed one time (primary robbing – PR), and flowers robbed daily (continuous robbing – CR). Because of the large number of flowers that *C. caseana* individuals bear (Maloof 2001), it was not possible to treat every flower on a plant. Instead, we treated a subset (10–20%) of the flowers within each of five lateral racemes on each plant. We tracked treated flowers by placing a small mark on their corollas using a permanent marker. Marking corollas in this way does not affect visitation by pollinators or robbers (Maloof 2000).

To apply robbing treatments, we made a small hole in the corolla with dissecting scissors and removed nectar with 5 µl microcapillary tubes. This method of artificial robbing mimics natural robbing by bumble bees (Irwin and Brody 1998, Burkle et al. 2007, Richman et al. 2017). We fit clear plastic collars over the nectar spur of each flower to prevent any robbing for the control (unrobbed) treatment and secondary robbing for the PR treatment. We cut small windows in the collars we used for the CR treatment to control for the effects of the collars on the other treatments while allowing subsequent experimental robbing with a microcapillary tube each day until flowers senesced. Collaring flowers in this way does not deter pollinators (Morris 1996, Irwin and Brody 1999). By using both the PR and CR treatments, we were able to test whether daily robbing in the CR treatment resulted in any additional plant fitness effects beyond the initial robbing event in the PR treatment (akin to Richman et al. 2017).

To measure pollen receipt, we collected the stigmas from focal flowers upon corolla senescence. At this point, pollen should have grown down the style and fertilized the ovules, so stigma collection should not have affected fruit or seed set. We mounted fresh stigmas on microscope slides using basic fuchsin gel (Kearns and Inouye 1993). We imaged slides with a digital compound microscope and counted conspecific pollen using 'Count Tool' in Adobe Photoshop Creative Cloud. We calculated average pollen receipt per flower per raceme.

To assess fruit and seed set, we monitored each flower until flower abscission, fruit abortion, or fruit set. We then collected mature fruits and counted the number of seeds per fruit. We estimated female function as 1) proportion fruit set per raceme (no. of mature fruits/no. of mature and aborted fruits) and 2) seed set per raceme (total no. of seeds per raceme).

Statistical analyses. We tested whether robbing treatment affected mean conspecific pollen receipt per flower per raceme using a linear mixed effects model (ML) with robbing treatment (control, PR, CR) and the number of flowers per raceme as fixed effects. Because we sub-sampled racemes within plants, we included plant as a random effect in all models to prevent pseudoreplication. We square-root transformed mean pollen receipt to meet the assumption of Gaussian error distribution. We tested how robbing treatment affected proportion fruit set and seed set per raceme using linear and generalized linear mixed effects models, respectively. We included robbing treatment as a fixed effect, number of flowers per raceme as a covariate in the proportion fruit set model, and number of mature fruits per raceme as a covariate in the seed set model. To test significance of fixed effects in all models, we ran likelihood ratio tests comparing the full models to null models with the same random effects but with intercept as the only fixed effect.

Non-discrimination hypothesis: are nectar rewards diminished by robbing?

To assess the nectar reward availability in robbed and unrobbed flowers, we used 5 µl microcapillary tubes to measure the nectar standing crop of each flower that we collected for the pollen tube growth study (n = 32 plants across three sites). For each plant, we calculated the proportion of robbed and unrobbed flowers without nectar (treating nectar as either present or absent) and the mean nectar standing crop in robbed and unrobbed flowers.

Statistical analysis. We compared the proportion of robbed and unrobbed flowers that were empty of nectar using a linear mixed effect model (REML) with robbing status (robbed versus unrobbed) as a fixed effect and plant as a random effect. We used a similar model with mean nectar standing

crop in robbed and unrobbed flowers as the response. We dropped one individual from the analysis because a Grubbs test (using the R package 'outliers'; Komsta 2011) revealed that the nectar standing crop value (4.17 µl) was an outlier ($G = 6.39$, $p < 0.0001$).

Non-discrimination hypothesis: do pollinators discriminate between robbed and unrobbed flowers?

To test the prediction that plants escape negative effects of robbing because pollinators do not avoid robbed flowers, we measured pollinator visitation to experimentally robbed and control (unrobbed) flowers and stalks. At the Washington Gulch site on 29 and 30 June and 6 July 2016, we haphazardly assigned two treatments, robbed and unrobbed, to paired stalks on 77 plants. Each plant was only used for one day and was marked with flagging tape to prevent resampling on subsequent days. For flowers on stalks in the robbing treatment, we artificially robbed all flowers but did not place collars on flowers after robbing. We handled, but did not cut holes in or remove nectar from, flowers on unrobbed stalks. We recorded the number of open flowers on each stalk (2 – 116 flowers stalk^{-1}, mean = 29.5 ± 1.5 SE). Once treatments were applied, we observed the patch for all floral visitors to marked stalks for 2 consecutive hours (between 10:00 and 16:00) on sunny to partly cloudy days, using multiple observers, resulting in >69.65 person-hours of observation. We used digital voice recorders to record the number of pollinator bouts received by each treatment stalk, the number of flowers visited per stalk per bout, the time spent per flower, and the identity of visitors. We identified pollinators to family for non-bumble bee pollinators and to species for bumble bees. We identified pollinators on the wing to the lowest taxonomic level we could achieve without netting them.

Statistical analyses. We tested how robbing treatment affected pollinator foraging behavior using GLMM (ML) for count data (total bouts received) and using liner mixed effects models (ML) for continuous data (mean time spent per flower and proportion of flowers visited per stalk). Count data were over-dispersed and zero-inflated; thus, we fit a zero-inflated GLMM with a negative binomial error distribution (Brooks et al. 2017). We constructed the generalized linear mixed effects models (GLMM) using 'glmmTMB' and used 'lmerTest' to preform inference tests (Brooks et al. 2017). For all models, we performed backward model selection and compared AIC values to determine best fit models. Initial predictors included date, robbing treatment (robbed versus unrobbed), and number of flowers open per stalk as fixed effects, and plant as a random effect (to account for pairing). For mean proportion of flowers probed and mean time spent per flower, we only used data from plants for which we observed visitation to both stalks (robbed and unrobbed), and we dropped one plant from the analysis because a Grubbs test revealed that the mean time per flower was an outlier (14.5 and 4.85 s on the robbed and unrobbed flowers respectively), ($G = 6.69$, $p < 0.0001$). We natural-log transformed mean flowers visited and mean time spent per flower to meet the assumption of Gaussian error distributions.

Visitor prevalence hypothesis: how common are pollinator relative to nectar-robber visits?

To determine relative visitation frequencies by pollinators and robbers (both primary and secondary) at the plant population level, we recorded floral visitation to *C. caseana* on 16 days at three sites (5–6 days per site) between 2 July and 9 August, 2014 for approximately two and a half h per site per day. The sampling period spanned roughly from just before the peak to the end of the flowering season of *C. caseana* at these sites. We used voice recorders to record each flower visit we observed to *C. caseana* and the type of visit, with each observer tracking only one kind of visitor (robbers or pollinators) during an observation session. We followed each visitor until it flew out of sight.

Statistical analyses. We summed visits of each type (robber or pollinator) across all visitors on each day of sampling. While this method fails to capture variation in the relative abundance of each visitor species, it is sufficient to describe the variation in visitation important to our question, specifically, the ratio of robbing to pollinating visits experienced by *C. caseana*. To control for differences in sampling effort, we used corrected visitation rate (visits observed per minute of sampling) as our response. We used a paired t-test to compare corrected pollinator and robber visitation rates with day as the unit of replication.

Pollen saturation hypothesis: how do single visits from pollinators affect stigmatic pollen loads?

We performed a single-visit pollen receipt study (31 July and 4 and 5 August 2015) to estimate how many pollinator visits to *C. caseana* flowers are required to saturate stigmas with pollen and thus maximize female mating success, and to estimate autogamous pollen transfer rates. One to three days before each sampling date, we covered one haphazardly chosen stalk on each of three haphazardly chosen plants with bridal veil bags to prevent any floral visitation. Before bagging, any open flowers were removed, allowing us to use only virgin flowers. On each day of sampling, we removed the bag from stalks and immediately sampled two virgin flowers per stalk (autogamy controls), placing them in individually-labeled glassine envelopes and storing them on ice. These unvisited flowers allowed us to assess the amount of pollen that is transferred to the stigmas through autogamous self-pollination in the absence of pollinator visitation. We then observed the stalks until they were visited by a pollinator. Immediately after the pollinator departed, we collected two to four of the flowers visited and placed them in individually labeled glassine envelopes, storing them on ice. Each plant was only sampled once. We measured single-visit pollen deposition from the flowers of 10 plants, and all pollinator visits were by *Bombus* spp. In the lab, we mounted stigmas on microscope slides using basic fuchsin gel (Kearns and Inouye 1993) and counted all conspecific pollen grains under a compound microscope at 100× magnification.

Stigma–pollen saturation (Ashman et al. 1993) occurs when a stigma receives at least one viable conspecific pollen grain per ovule, and thus serves as a proxy for the upper limit

of female mating success. To estimate the number of pollen grains necessary to reach stigma saturation for *C. caseana*, we collected five to six ovaries from each of 13 *C. caseana* plants on 5 July 2016 (n = 77 total ovaries). We collected ovaries into 70% ethanol in the field. To fix the ovaries, we transferred them to 80% lactic acid for 48 h at room temperature. We then rinsed them with DI water and stored them in 70% ethanol until dissections. We counted the ovules in each ovary under a dissecting microscope by pulling the ovary walls apart using fine tip forceps which revealed the fixed ovules.

Statistical analyses. To assess single visit deposition, we used a paired t-test to compare the mean stigmatic pollen loads of virgin flowers within each plant with the means of the flowers that received a single pollinator visit. We qualitatively compared mean stigma pollen receipt from single pollinator visits to the number of ovules in flowers to assess the degree to which stigmas were saturated with pollen after a single pollinator visit.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.bh6hs70> (Heiling et al. 2018).

Results

Are the effects of nectar robbing on female function neutral?

As we predicted, using both observational and experimental approaches, we found no significant effects of nectar robbing on estimates of female function in *Corydalis caseana*, suggesting that the effects of nectar robber were neutral.

I. Observational study
There was no difference in pollen tube count between unrobbed and robbed flowers ($\chi^2_1 = 2.81$, $p = 0.09$). Unrobbed flowers had 60.4 + 2.7 (mean + SE) pollen tubes per pistil, and robbed flowers had 57.6 + 2.2 pollen tubes per pistil.

II. Experimental study
There was no difference in pollen receipt between experimentally robbed and unrobbed flowers ($\chi^2_1 = 4.39$, $p = 0.11$). Unrobbed flowers received 24.83 ± 0.96 (square-root transformed mean + SE) conspecific pollen grains per flower per raceme, while flowers in the PR and CR treatments received 28.16 ± 1.01 and 28.54 ± 0.88 pollen grains, respectively. Likewise, we found no effect of experimental robbing on proportion fruit set ($\chi^2_2 = 2.05$, $p = 0.36$) or seed set per raceme ($\chi^2_2 = 0.37$, $p = 0.83$). Proportion fruit set in unrobbed plants was 0.74 ± 0.04 (mean ± SE), in PR plants was 0.73 ± 0.05, and 0.83 ± 0.04 in CR plants. Mean seed set per raceme was 7.56 ± 0.83 (mean ± SE) for unrobbed plants, 6.73 ± 1.04 for PR plants, and 8.65 ± 1.64 for CR plants.

Non-discrimination hypothesis: are nectar rewards diminished by robbing?

Within plants, approximately 15% more unrobbed flowers bore nectar than did robbed flowers ($t_{30} = 3.35$, $p = 0.002$) (Fig. 1a). Not only were robbed flowers more likely to be empty, they also had approximately half the amount of nectar on average relative to unrobbed flowers ($t_{30} = -4.77$; $p < 0.0001$) (Fig. 1b).

Non-discrimination hypothesis: do pollinators discriminate between robbed and unrobbed flowers?

Our final model for the total number of bouts received by robbed and unrobbed pairs of stalks included robbing treatment and number of flowers per stalk as fixed effects and plant as a random effect for the conditional model, and a uniform probability of producing a structural zero in the final zero-inflation model. Our final models for the mean time spent per flower and the mean proportion of flowers visited per stalk included treatment as a fixed effect and plant as a random effect.

Over nearly 70 person-hours of observation, we observed 611 flower visits by pollinators, with 571 flower visits by *Bombus appositus*, 24 by *B. flavifrons*, 13 by *B. bifarius*, and three by an Andrenid species. Across all analyses, results suggest that pollinators did not discriminate between robbed and unrobbed stalks. There was no effect of robbing treatment on total bouts received per stalk ($\chi^2_2 = 0.78$; $p = 0.68$). Unrobbed stalks received 1.24 ± 0.13 bouts per stalk (mean + SE) and robbed stalks 1.07 ± 0.15 bouts per stalk. We found no significant effect of robbing treatment on mean proportion of flowers visited per stalk ($\chi^2_1 = 0.27$, $p = 0.60$) and mean time spent per flower ($\chi^2_1 = 0.04$; $p = 0.84$). The mean proportion of flowers visited per stalk (ln transformed mean + SE) was 1.47 ± 0.18 in the unrobbed treatment and 1.08 ± 0.15 in the robbed treatment. Bees spent (mean ± SE) 0.08 ± 0.09 s flower^{-1} in unrobbed flowers and 0.05 ± 0.6 s flower^{-1} in robbed flowers.

Visitor prevalence hypothesis: how common are pollinator visits relative to nectar robber visits?

In 78 person-hours of observation (across 16 d), we recorded 9709 individual flower visits. Pollinating species included *B. appositus*, *B. bifarius*, *B. flavifrons*, *B. nevadensis*, *B. rufocinctus*, and a small number of unidentified non-*Bombus* bees, with *B. appositus* being the most common pollinator (approximately 52% of all pollinating visits observed). Robbers included *Bombus bifarius*, *B. flavifrons*, *B. frigidus*, *B. kirbiellus* and *B. occidentalis*, with the latter being the most common robber (approximately 34% of all robbing visits observed). Of the 9709 total visits, 6709 were pollinating visits and 3000 were robbing visits, making pollinator visitation to *C. caseana* more than twice as common as robber visitation ($t_{15} = -4.1$, $p < 0.001$) (Fig. 2).

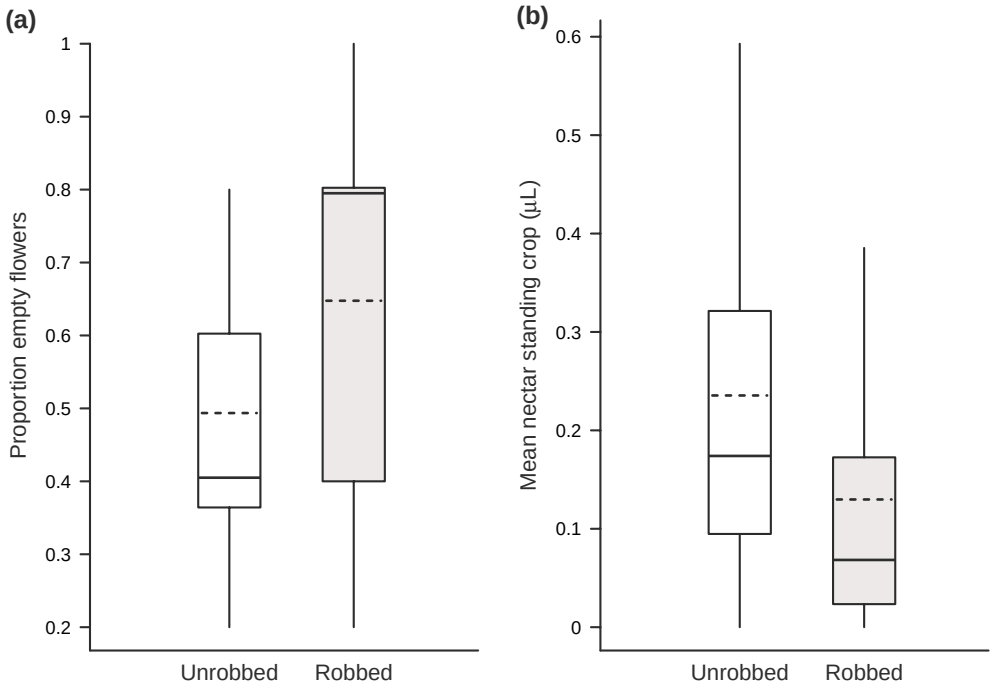

Figure 1. Nectar robbing was associated with reduced nectar rewards. (a) Robbed flowers were more often empty of nectar than were unrobbed flowers on the same plant, and (b) robbed flowers had lower nectar standing crops than unrobbed flowers on the same plant. Bars are boxplots, with lower and upper ends of boxes depicting the lower and upper quartiles, respectively. Solid bands indicate medians, dashed bands indicate means. Whiskers extend across the data range, excluding outliers. n = 31 plants.

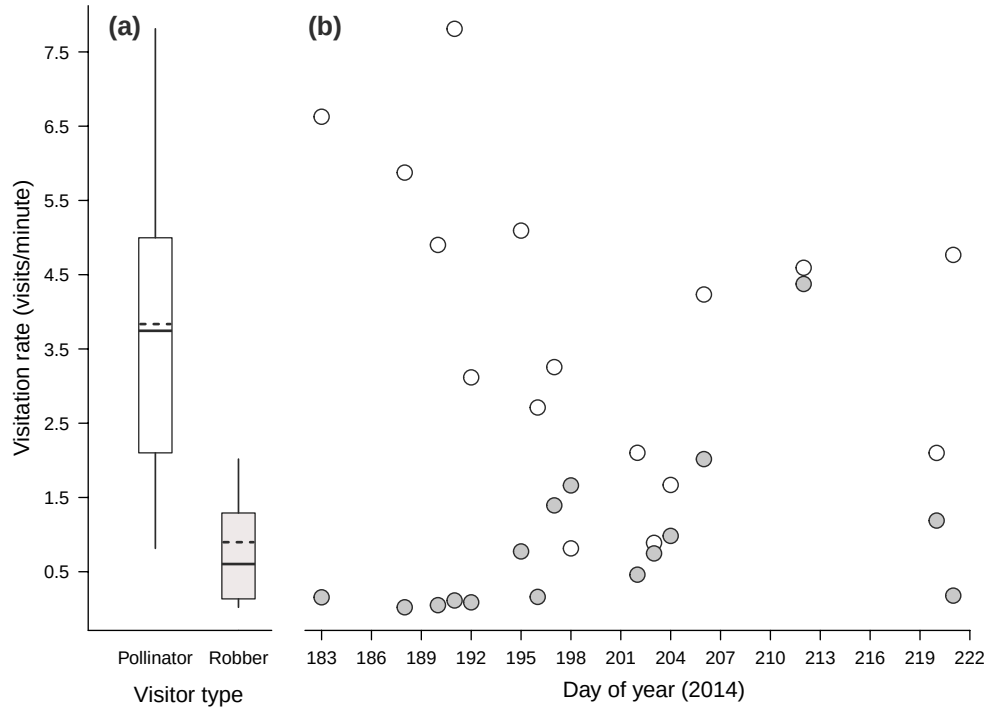

Figure 2. Visitation rates (standardized by sampling effort) by pollinators and nectar robbers in a *Corydalis caseana* population across 16 days of observation. To standardize visitation rate by sampling effort, we divided the number of visits of each type (pollinator or robber) observed each day by the effort (minutes) spent on observations that day. Pollinator visits were more than twice as common as robbing visits. (a) Boxes are box plots depicting quartiles, median, mean, and data range as in Fig. 1. (b) Points are paired visitation rates for each day of sampling; empty points are pollinator visitation rates and gray points are robber visitation rates. n = 16 days of sampling.

This pattern was consistent both within days as well as across the dates sampled (Fig. 2). An analysis at the site level showed the same pattern as the global analysis (data not shown).

Pollen saturation hypothesis: how do single visits from pollinators affect stigmatic pollen loads?

We found that ovaries contained 4–12 ovules each (mean + SE = 6.96 ± 0.18 ovules per ovary). Thus, stigma saturation in *C. caseana* should occur after the receipt of a fairly low number of viable pollen grains.

All of the *C. caseana* stigmas that we sampled bore copious amounts of pollen. Across virgin and single-visit flowers, conspecific pollen counts on *C. caseana* stigmas ranged from 1706–11 692 grains, indicating that it is unlikely that these *C. caseana* populations are pollen limited. Virgin stigmas bore large quantities of conspecific pollen (Fig. 3), suggesting autogamous self-pollination. The stigmas of virgin flowers had approximately twice as many pollen grains as stigmas of flowers that received a single visit from a pollinating bumble bee ($t_8 = 3.31$, $p = 0.01$) (Fig. 3).

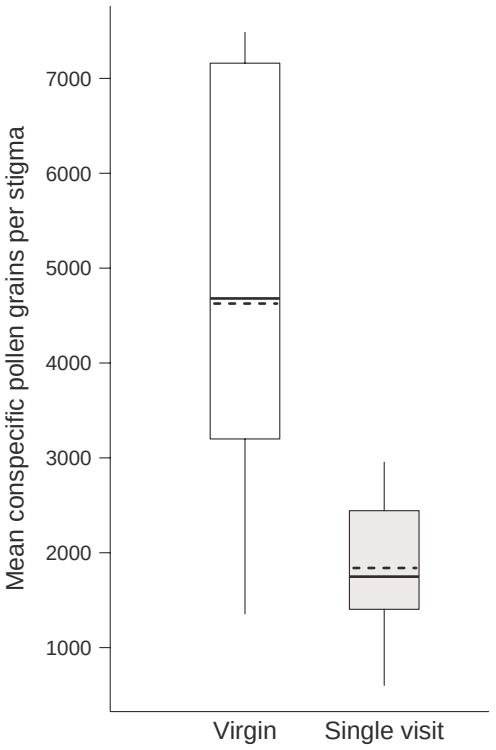

Figure 3. Virgin, unvisited flowers of *Corydalis caseana* had nearly twice as many pollen grains as flowers on the same plant that received a single visit by a pollinating *Bombus* spp. Boxes are box plots depicting quartiles, median, mean, and data range as in Fig. 1. n = 9 plants.

Discussion

Most studies of species interaction focus on interactions that yield mutually negative, mutually positive, or mixed positive and negative outcomes for the species involved (Sih et al. 1985, Goldberg and Barton 1992, Hoeksema and Bruna 2000), whereas commensalisms are poorly studied relative to their frequency in nature (Palumbi 1985, Maloof and Inouye 2000, Sáyago et al. 2013). Although 'exploitation' implies a negative interaction, some studies show that exploitation of pollination mutualisms can be commensal, possibly benefiting the exploiter at no cost (or benefit) to the plant (Morris 1996, Fumero-Cabán and Meléndez-Ackerman 2013). Here we also show that exploitation of nectar by robbing bees has neutral effects on female function of *Corydalis caseana*. These results are consistent with those of Maloof (2001) who showed thirteen years earlier in some of the same *C. caseana* populations that robbing was common but had no detectible effect on female function. Our goal here was to mechanistically explain why nectar robbers are commensals in this system. To understand the mechanisms driving these neutral effects, we empirically evaluated three non-mutually exclusive hypotheses, and found evidence consistent with each of them.

Non-discrimination hypothesis

While the lower reward levels we observed in robbed *C. caseana* flowers could serve as a motivation for pollinators to avoid them, we found no evidence that pollinators did in fact discriminate against robbed flowers. These results are consistent with results in some other bee- and bird-pollinated systems (Rust 1979, Fumero-Cabán and Meléndez-Ackerman 2013). For example, in *Linaria vulgaris* (Plantaginaceae), robbing reduces nectar standing crop by >50%, but there is no evidence that *Bombus pascuorum* or *B. hortorum* pollinators discriminate between robbed and unrobbed flowers (Stout et al. 2000). Likewise, Rust (1979) found that artificially robbed *Impatiens capensis* (Balsaminaceae) flowers did not experience reduced pollination success relative to unrobbed flowers and found no evidence that bee pollinators differentiated between flowers on the basis of robbing status. Bee pollinators can make foraging decisions based on nectar availability (Pleasants 1981). Why pollinators discriminate in some systems and not in others is not fully understood, though it may depend on underlying variation in reward levels within the plant species. For example, theoretical and empirical work addressing the occurrence of unrewarding flowers within otherwise rewarding plants suggests that, above some threshold reward frequency or concentration at the plant or population level, pollinators may not avoid unrewarding flowers because it is more energetically costly to do so than it is to visit them (Bell 1986). That is, if variation in reward levels is high, whether they are robbed or not, avoiding robbed flowers may not increase foraging efficiency even if they do tend to contain less nectar. This may be especially true in systems where nectar production varies substantially throughout

anthesis, and in systems in which flowers refill at a constant rate (as in *C. caseana*). Indeed, this could be the case in the *C. caseana* system, as nectar production continues throughout a flower's six- to seven-day lifetime. However, we limited our sample to flowers of roughly the same age (approximately one to two days post anthesis), and so were unable to test for any age-dependent differences in the relative nectar volumes of robbed and unrobbed flowers in this dataset. It is important to note, however, that in some cases, pollinators do discriminate between robbed and unrobbed flowers, especially in bird-pollinated systems (Arizmendi et al. 1996, Irwin and Brody 1998) and in some bee-pollinated systems (Zimmerman and Cook 1985, Dohzono et al. 2008, Zhang et al. 2014). Understanding the proximate cues that pollinators use to perceive robbed flowers and the cognitive constraints they face may yield mechanistic insight into why they discriminate against robbed flowers in some cases and not others.

Visitor prevalence hypothesis

The ratio of robber visitation to pollinator visitation was low at the site and in the year that we conducted the study, consistent with the pollinator prevalence hypothesis. The timing of interactions between a species and its mutualists and exploiters is generally critical to determining the outcomes of those interactions (Barker and Bronstein 2016). Thus, it is important to note not only the ratio of robber-to-pollinator visits, but also the timing of those visits relative to each other. We found that not only across days, but also within days, plants were more likely to be visited by a pollinator than a robber (Fig. 2). Additionally, we found no evidence that robbers and pollinators partitioned the day, though such partitioning has been observed in other systems (Rust 1979). While the lack of discrimination by pollinators against robbed flowers in this system would likely dampen any potential effects related to the timing of interactions relative to one another, a similar lack of a temporal pattern in pollinator and robber visitation may be important to neutral effects of robbing on plant reproductive outcomes in other systems. Alternatively, for systems in which robber visits tend to occur before pollinator visits, and pollinators discriminate against robbed flowers, if neutral effects of robbing are observed, they would not be explained by the visitor prevalence hypothesis.

Robbing 'frequency' is often estimated only by the number of robbed flowers per individual plant in a population. However, this is only a proxy for robber visitation frequency, especially when considering secondary robbing (since it leaves no evidence behind that it has taken place). Assessing the visitor prevalence hypothesis requires information on the actual frequencies of floral visits by robbers and pollinators. Counting robbing holes alone can over- or underestimate the prevalence of robbers in a visitor community. For example, Stout et al. (2000) found that while 96% of *Linaria vulgaris* flowers at their site in southern England had robbing holes, visits by nectar robbers only accounted for approximately 62% of all floral visits. Likewise, in two populations of *Impatiens capensis* in Delaware, USA, Rust (1979) found that up to 72% of flowers were robbed on 12 sampling dates, but robbers accounted for only half of all visitors observed. These results suggest that counting robbing holes in flowers may not be a sufficient way to assess the severity of robbing activity relative to other floral visitation, and that observing the real-time activity of pollinators and robbers is necessary to assess the visitor prevalence hypothesis.

Pollen saturation hypothesis

The pollen saturation hypothesis predicts that if plant reproduction is not pollen-limited, small to moderate reductions in pollinator visitation to nectar-robbed plants and flowers may not translate into differences in female reproductive success (Burkle et al. 2007). We found that all *C. caseana* stigmas that we examined were saturated with pollen, bearing pollen loads well in excess of the number of ovules available, consistent with the pollen saturation hypothesis. The high frequency of pollinator visits combined with the high autogamous self-pollination suggests that pollen limitation is unlikely in these populations of *C. caseana*. Indeed, working in some of the same populations, Maloof (2000) found that open-pollinated *C. caseana* were not pollen limited, as measured by pollen-supplementation experiments.

Surprisingly, stigmas of *C. caseana* were saturated with pollen even without pollinator visitation, suggesting that *C. caseana* flowers receive significant amounts of autogamous pollen. *Corydalis caseana* anthers are positioned in contact with the stigma (Maloof 2000) and shed pollen directly onto the stigma upon dehiscence or manipulation of the corolla; thus, autogamous pollen transfer could explain the universally high stigmatic pollen loads that we observed. As copious self-pollen is shed directly onto stigmas in *C. caseana*, autogamous pollen transfer may represent a bet-hedging strategy for this self-compatible species. Such a strategy may result in reduced outcrossing in exchange for some insured fertilization at low visitation frequencies. Yet, *C. caseana* receives relatively high pollinator visitation rates (here and Maloof 2000). Thus, it is not clear whether such a bet-hedging strategy would help or hinder outcrossed pollination, warranting additional investigation of *C. caseana* reproductive biology.

Interestingly, stigmas from flowers visited once by pollinators bore a mean of 3838 ± 273 (SE) pollen grains while stigmas from virgin (unvisited) bore approximately twice as much, with a mean of 6651 ± 774 (SE) grains. This result suggests that, for at least the first few visits to a flower, pollinators remove large numbers of self-pollen grains from stigmas. Thus, the stigma may serve dual roles as both a pollen receiving organ and a secondary pollen presentation surface in *C. caseana*, similar to other stylar presenters, such as in some members of the Marantaceae and Polygalaceae (Howell et al. 1993). It is likely that there is a threshold of pollinator visits that must occur before outcross pollen is able to gain access to the stigmatic surface relative to self-pollen. One limitation to the interpretation of our results is that we did not emasculate flowers prior to measuring single-visit pollen

deposition (as in Geber 1985); thus, the pollen we counted is a mixture of outcrossed and self-pollen, and we do not know the exact number of pollen grains a visitor deposits in a single visit. Repeating this single-visit pollen deposition study using emasculated flowers would yield additional ecological insight, though conducting such a study using emasculated flowers would be exceptionally challenging given the fusion of the androecium and gynoecium.

Nectar robbing as a commensal species interaction

Here we demonstrate multiple avenues through which the effects of nectar robbing on the fitness of robbed plants can be mitigated. These buffers allow an apparently antagonistic interaction to function in nature as a commensalism. At least three areas of further work are important to understanding nectar robbing commensalisms. First, in cases where robbers do not damage the reproductive or nectar-producing structures while robbing, the sign of the plant–nectar robber interaction should be context dependent. Inter- and intra-annual variation in the relative frequencies of robber and pollinator abundance are common in plant-pollinator–nectar robber systems (Irwin and Maloof 2002). For example, *B. occidentalis* accounted for only about 1.2% of all floral visits by *Bombus* species (120 out of 9709 floral visits) to *C. caseana* in our 2014 data; compare this to the 30% *B. occidentalis* visitation rate (63 of 205 total visits) observed by Maloof in some of the same sites in 1996 (Maloof 2000). Such variation could cause the extent to which a plant population experiences robbing to fluctuate dramatically between years and locations, and these fluctuations could cause the magnitude of any robbing effects to vary accordingly. The sign and magnitude of such effects should depend both on the degree to which pollinators in the system discriminate against robbed plants, and how sensitive the plant species is to pollen limitation. However, surprisingly few studies have measured spatio-temporal variation in the fitness effects of nectar robbing in plant-robber–pollinator systems, and so we do not know how commonly the interaction shifts among commensalism, antagonism, and mutualism. Second, we focused on measuring the effects of robbing on female components of plant reproduction, but most flowering plants are hermaphrodites. Assessing the degree to which the effects of robbing are neutral for plants requires the measurement of both female and male components of plant fitness. While in some cases species interactions can have similar effects on male and female function (reviewed by Schaeffer et al. 2013), in other cases species interactions can promote sexual conflict, driving strongly divergent effects on the two sexual functions (Zhang et al. 2009). Because the effects of nectar robbing often manifest through effects on pollinator behavior, and because male function can be more sensitive to pollinator behavior than is female function (Stanton et al. 1986), measuring both sexual functions is critical for fully assessing the degree to which robbing affects plant reproduction. Including measurement of male function may also require the development of additional hypotheses to explain neutral effects. Third, it remains unresolved how nectar robbers should be included in networks of interactions between plants and floral visitors, especially in cases where the interaction is commensal, as the effects of nectar robbers may be quite weak overall. Weak interactions can be important in stabilizing food webs (McCann et al. 1998), and weak and commensal interactions between plants and robbers may be important in promoting community stability and persistence in plant–floral visitor webs. However, the degree to which this occurs is unknown and warrants further research.

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