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SHORT COMMUNICATION

Competition for nectar resources does not affect bee foraging tactic constancy

ELINOR M. LICHTENBERG,[1,2,3†] SARAH K. RICHMAN,[1,4†] REBECCA E. IRWIN[5,6] and JUDITH L. BRONSTEIN[1] [1]Department of Ecology & Evolutionary Biology, University of Arizona, Tucson, Arizona, U.S.A, [2]Department of Integrative Biology, The University of Texas at Austin, Austin, Texas, U.S.A, [3]Department of Biological Sciences and Advanced Environmental Research Institute, University of North Texas, Denton, Texas, U.S.A, [4]Department of Biology, University of Nevada, Reno, Reno, Nevada, U.S.A, [5]Department of Applied Ecology, North Carolina State University, Raleigh, North Carolina, U.S.A. and [6]Rocky Mountain Biological Lab, Crested Butte, Colorado, U.S.A.

Abstract. 1. Competition alters animal foraging, including promoting the use of alternative resources. It may also impact how animals feed when they are able to handle the same food with more than one tactic. Competition likely impacts both consumers and their resources through its effects on food handling, but this topic has received little attention.

2. Bees often use two tactics for extracting nectar from flowers: they can visit at the flower opening, or rob nectar from holes at the base of flowers. Exploitative competition for nectar is thought to promote nectar robbing. If so, higher competition among floral visitors should reduce constancy to a single foraging tactic as foragers will seek food using all possible tactics. To test this prediction, field observations and two experiments involving bumble bees visiting three montane Colorado plant species (*Mertensia ciliata*, *Linaria vulgaris*, *Corydalis caseana*) were used under various levels of inter- and intra-specific competition for nectar.

3. In general, individual bumble bees remained constant to a single foraging tactic, independent of competition levels. However, bees that visited *M. ciliata* in field observations decreased their constancy and increased nectar robbing rates as visitation rates by co-visitors increased.

4. While tactic constancy was high overall regardless of competition intensity, this study highlights some intriguing instances in which competition and tactic constancy may be linked. Further studies investigating the cognitive underpinnings of tactic constancy should provide insight on the ways in which animals use alternative foraging tactics to exploit resources.

Key words. *Bombus*, food handling, foraging, mutualism, nectar robbing, pollination.

Introduction

Resource competition has a profound influence on animal foraging. As competition increases, preferred resources may become less available. Competition promotes the use of alternative resources (Schoener, 1974) and may also impact how animals feed. Flower foragers can experience intense competition for nectar (Pyke, 1982). Increasing densities of flower visitors (henceforth 'co-visitors') can increasingly limit nectar availability and restrict bumble bee population sizes (Bowers, 1986). In the face of resource competition, flower-visiting insects such as bees may increase their feeding through holes at the base of tubular flowers or nectar spurs (nectar robbing) to access otherwise inaccessible nectar (e.g. nectar in long spurs or corollas; Pyke, 1982) or the last dregs of nectar (Barker *et al.*, 2018). Insects that rob flowers are typically also capable

Correspondence: Elinor M. Lichtenberg, Advanced Environmental Research Institute, University of North Texas, 1155 Union Circle #310559, Denton, TX 76203-5017, U.S.A. E-mail: elichten@unt.edu
†Co-first authors.

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of visiting those same flowers 'legitimately', through the floral opening (Barker *et al.*, 2018; Lichtenberg *et al.*, 2018). Research has begun to reveal that bees exhibit constancy in their foraging tactic, i.e. the way in which they handle flowers while feeding (Bronstein *et al.*, 2017). Thus, three strategies are available to bee foragers: constant to robbing, constant to legitimate visitation, or inconstant. We investigated the impacts of competition for nectar among co-visitors on the choices bees make among these three strategies.

Conventional wisdom posits that nectar robbing allows bees to avoid competition with other bee species by giving them access to otherwise inaccessible nectar (Wratt, 1968; Pyke, 1982). By extension, increasing competition for nectar should increase the use of nectar robbing by bees who can utilise it. However, by not considering the strategies by which bees combine foraging tactics, this extension may be too simple. We predicted that, as competition increases, foragers will begin to access food in any way possible. This could manifest as high constancy to nectar robbing (Pyke, 1982) or as inconstancy as foragers mix food-handling tactics. The latter pattern would be consistent with what is known about choices of what flower species to visit in high-competition environments. Flower-visiting insects often forage exclusively on one species, even when more rewarding alternatives are available (floral constancy; Grüter *et al.*, 2011), but bees are known to decrease their floral constancy in environments with higher con- and hetero-specific competitor abundances (Heinrich, 1979; Fontaine *et al.*, 2008; Baude *et al.*, 2011). Conversely, low-competition environments (e.g. those in which floral rewards are abundant) promote floral constancy (e.g. Grüter *et al.*, 2011; Keasar *et al.*, 2013).

We used three lines of inquiry in subalpine Colorado, U.S.A., to explore how competition affected tactic constancy. First, we determined how nectar robbing constancy in three bumble bee species (*Bombus*, Apidae) on three plant species changes with nectar standing crops (total available nectar volume per flower within a patch) and flower visitation rates under field conditions (Inquiry 1). Second, we re-analysed data from a foraging experiment that investigated the effects of nectar standing crop on the foraging strategy used by individual *Bombus bifarius* Cresson, 1878 foragers (Inquiry 2). Finally, we assessed tactic constancy of a second bumble bee species, *Bombus flavifrons* Cresson, 1863, under experimentally manipulated abundances of conspecific and hetero-specific co-visitors (Inquiry 3). Table S1 summarises the three approaches.

Methods

We conducted this research during June to Aug 2014–2016 near the Rocky Mountain Biological Laboratory (RMBL; 2886 m elevation) in Gunnison County, Colorado. The region is characterised by open meadows dominated by perennial flowering plants that host diverse pollinator assemblages. These include *Corydalis caseana* (Fumariaceae), *Linaria vulgaris* (Plantaginaceae), and *Mertensia ciliata* (Boraginaceae), which are commonly nectar-robbed and legitimately visited by the bumble bees *Bombus occidentalis* Greene, 1858; *B. bifarius*; and *B. flavifrons*. The system is described in detail elsewhere (Richman *et al.*, 2017a; Lichtenberg *et al.*, 2018).

To measure the effects of the competition for nectar on tactic constancy, we made the common assumption (addressed in Results and Discussion) that increased co-visitors and decreased nectar standing crop were associated with increased competition for nectar. Inquiry 1 examines both of these factors; Inquiries 2 and 3 examine nectar standing crop and co-visitors, respectively. In each line of inquiry, we recorded the foraging tactic that each individual bee used on every flower it visited and asked whether competition affected tactic constancy. We classified each individual as either constant (if it only exhibited one tactic) or inconstant (if it both robbed and visited legitimately).

In Inquiry 1, we determined food-handling tactic constancy of free-flying *B. bifarius*, *B. flavifrons*, and *B. occidentalis* visiting *C. caseana*, *M. ciliata*, and *L. vulgaris* in meadows in 2014. We observed *B. occidentalis* on *L. vulgaris* and the other two bee species on all three plant species. Multiple observers followed worker bees, focusing on one individual until it flew out of sight (a 'bout') and recording the foraging tactic used at each flower in the bout. We also calculated the total number of visits to the focal plant species across all observed flower co-visitors (mainly bees but also flies and butterflies) and the number of observation minutes summed across all observers collecting data during each observation period. We divided the total number of flower visits observed by the number of observer minutes within the period to estimate flower co-visitation rate as a measure of competition level. At each site, we also determined nectar standing crop by measuring the nectar volume on the flowers of 4–21 (median 7) plants per observation period, with a range of 1–10 (median 10) flowers measured per plant and a total of 19–212 (median 58) flowers measured per observation period. We measured nectar standing crop using microcapillary tubes, typically on the same day of observation and at the same time of day (morning or afternoon). On three site-day instances for *C. caseana* (16 bouts) and two for *L. vulgaris* (10 bouts), we measured nectar standing crop within 3 days and at the same time of day as the observations. Excluding these data had no qualitative effect on the results, and so, we present results of the full dataset. We investigated impacts of nectar standing crop and visitation rates on the probability that individual bouts were constant via logistic regressions that also included focal bee species and the number of flower visits in each bout as fixed effects. *Mertensia ciliata* and *L. vulgaris* analyses included both competition factors in a single analysis (variance inflation factors, or VIFs, for both terms in each model were ∼1; Spearman's rank correlation: *M. ciliata* $r = -0.37$, $S = 164.00$, $p = 0.34$; *L. vulgaris* $r = -0.12$, $S = 917.06$, $p = 0.64$). Because of collinearity between nectar standing crop and co-visitation rates (VIFs ∼3; $r = 0.70$, $S = 49.30$, $p = 0.02$) at *C. caseana* sites, we analysed the impacts of each factor in a separate analysis. Analyses here and below only included foraging bouts when the individual bee visited at least five flowers to ensure sufficient visitation for assessing constancy. This and all following analyses were performed using R version 3.6.1 (R Core Team, 2018).

In Inquiry 2, we reanalysed data from Richman *et al.* (2017a) to determine the effects of nectar standing crop on flower-handling tactic constancy by *B. bifarius* visiting *L. vulgaris*. Inside a large flight cage (2.4 × 3.1 × 2.1 m, WeatherPort

Shelter Systems, Delta, Colorado) located in the RMBL townsite, we presented individual *B. bifarius* workers with 30 *L. vulgaris* stalks that each bore 20 flowers. We artificially robbed the flowers on 80% of stalks by piercing flowers' nectar spurs with forceps, a technique used successfully in other studies (Richman *et al.*, 2017b). Bees were exposed to either a high competition treatment (nectar removed from robbed flowers) or a low competition treatment (nectar present in robbed flowers, $n = 10$ bees/treatment with three bees that visited fewer than five flowers in the low competition treatment removed from this analysis). We observed individual foraging bouts, recording the foraging tactic a bee used at each flower. Bees were marked with indelible ink after observations and returned to a nearby meadow to ensure they were not used more than once. We used Fisher's exact test to determine whether constancy probability varied with competition treatment.

Inquiry 3 focused on how foraging by *B. flavifrons* visiting *C. caseana* flowers changed in response to conspecific and hetero-specific densities of co-visitors, conducting new analyses of data originally presented in Richman (2018). Data were collected between late June and early August in 2015 and 2016. We determined the nectar-robbing constancy of 58 individual *B. flavifrons* foragers feeding inside a 3 m × 3 m × 2.5 m portable field cage (E-Z Up Sierra II, E-Z Up, Norco, California) that enclosed an individual, large *C. caseana* plant (bearing ~500–1000 open flowers). Each *B. flavifrons* foraged in the presence of zero to nine co-visitors. The hetero-specific co-visitor used was *Bombus appositus* Cresson, 1878, a common legitimate visitor to *C. caseana* that does not rob this species (Maloof, 2000). We manipulated densities of both *B. flavifrons* and *B. appositus* using a response surface experimental design (Inouye, 2001) that included all pairwise combinations of zero, one, three, or five conspecific or hetero-specific foragers. We recorded food-handling tactics of a single focal *B. flavifrons* individual for all density combinations that contained either both species or only *B. flavifrons* individuals. We determined, via logistic regression, whether the probability that an individual was constant depended on the total density of both conspecific and hetero-specific co-visitors.

Results and discussion

Across all inquiries, tactic constancy was high: 83–100% of recorded bouts included a single flower-handling tactic (Figs 1 and 2; raw data in Figs S1 and S2). We did find evidence for decreased constancy in more competitive environments from the observational data (Inquiry 1). Consistent with our prediction, *B. bifarius* and *B. flavifrons* visiting *M. ciliata* exhibited lower tactic constancy when more co-visitors were present (Fig. 1b). However, other bee–plant combinations in Inquiry 1 did not exhibit this pattern, nor was it seen in either of the two experiments (Inquiries 2 and 3). Neither nectar standing crop nor flower co-visitor activity predicted whether free-flying bumble bees were constant to a single flower-handling tactic when visiting either *C. caseana* or *L. vulgaris* (Inquiry 1; Fig. 1c-f). In Inquiry 2, 90% of *B. bifarius* foraging on *L. vulgaris* flowers exhibited only one tactic at each nectar standing crop level (Fig. 2a; Fisher's exact test: odds ratio = 0.68, $p = 1$). In Inquiry 3, *B. flavifrons* foraging on *C. caseana* flowers also exhibited high tactic constancy across all bee densities (Fig. 2b; 75–100%; logistic regression: $\chi_1^2 = 0.37$, $p = 0.54$). Results across all plant species in Inquiry 1 did not reflect differences in the mean or variability of visitation rates among these plants (Table S2; LMM with valley, site, and date as random effects; likelihood ratio test: $\chi_2^2 = 2.50$, $p = 0.29$; Brown-Forsythe test of homogeneity of variance: $F_{2,59} = 2.60$, $p = 0.08$).

Intriguingly, our results also indicate that bee species do not have absolute preferences for one tactic over another. In Inquiry 1, each bout tended to contain one tactic, but the predominant constant tactic exhibited by a bee species varied across plant species (Fig. 1, black vs. white boxes; Lichtenberg *et al.*, 2018). Both *B. bifarius* and *B. flavifrons* robbed nectar in a majority of bouts when visiting *C. caseana* but were more likely to forage legitimately when visiting *L. vulgaris* and *M. ciliata*. Individuals in Inquiries 2 and 3 varied in tactic choice (Fig. 2, black and white boxes).

We suggest two possible explanations for our finding that tactic constancy is, with a few exceptions, insensitive to competition for nectar. First, the energetic payoff from frequently switching tactics to escape competition may not be high enough to overcome the associated learning costs. For instance, if bees use the robbing hole as a search image to find nectar, it may be inefficient to use, at the same time, a second search image for the part of the flower where they legitimately forage (Goulson, 2000). Second, when competition is high, bees may prefer to forage from more flowering plant species rather than use more feeding tactics on any one species (i.e. exhibit higher tactic constancy than floral constancy). Consistent with this hypothesis, bees in Inquiry 1 that visited more than one plant species in a single bout were more likely to be constant to one tactic (19 bouts) than to mix tactics (3 bouts; $\chi_1^2 = 11.64$, $p = 0.0006$).

Our results could reflect an inability to capture realistic signatures of competition, but we find this unlikely. Nectar availability limits bumble bee population sizes in our study region, with the degree of limitation varying across sites (Pleasants, 1981). Because competition was present at all sites assessed by Pleasants (1981), including those with the highest nectar standing crop or lowest co-visitor densities, we made the reasonable (and common) assumption that nectar is more limited at sites with lower standing crops or higher co-visitation. Our experimental and field conditions covered a wide range of nectar availabilities. Meadow (Inquiry 1) nectar standing crops ranged from 0.002 to 0.42 µl (median 0.08 µl) per flower, and co-visitation rates from 0.16 to 8.58 bees/min (median 2.51). In Inquiry 3, nectar standing crops ranged from 0 to 1.23 µl (median 0.14 µl) per flower. Furthermore, we found minimal change in food-handling tactic constancy rates across competition levels even though we estimated competition levels in multiple ways.

Previous studies have reported low floral constancy under high competition (Heinrich, 1979; Fontaine *et al.*, 2008; Baude *et al.*, 2011). Therefore, our finding of high tactic constancy independent of competition level calls into question prior research suggesting that floral and tactic constancy have similar proximate causes (reviewed in Barker *et al.*, 2018). One possible explanation for this discrepancy is that the cognitive

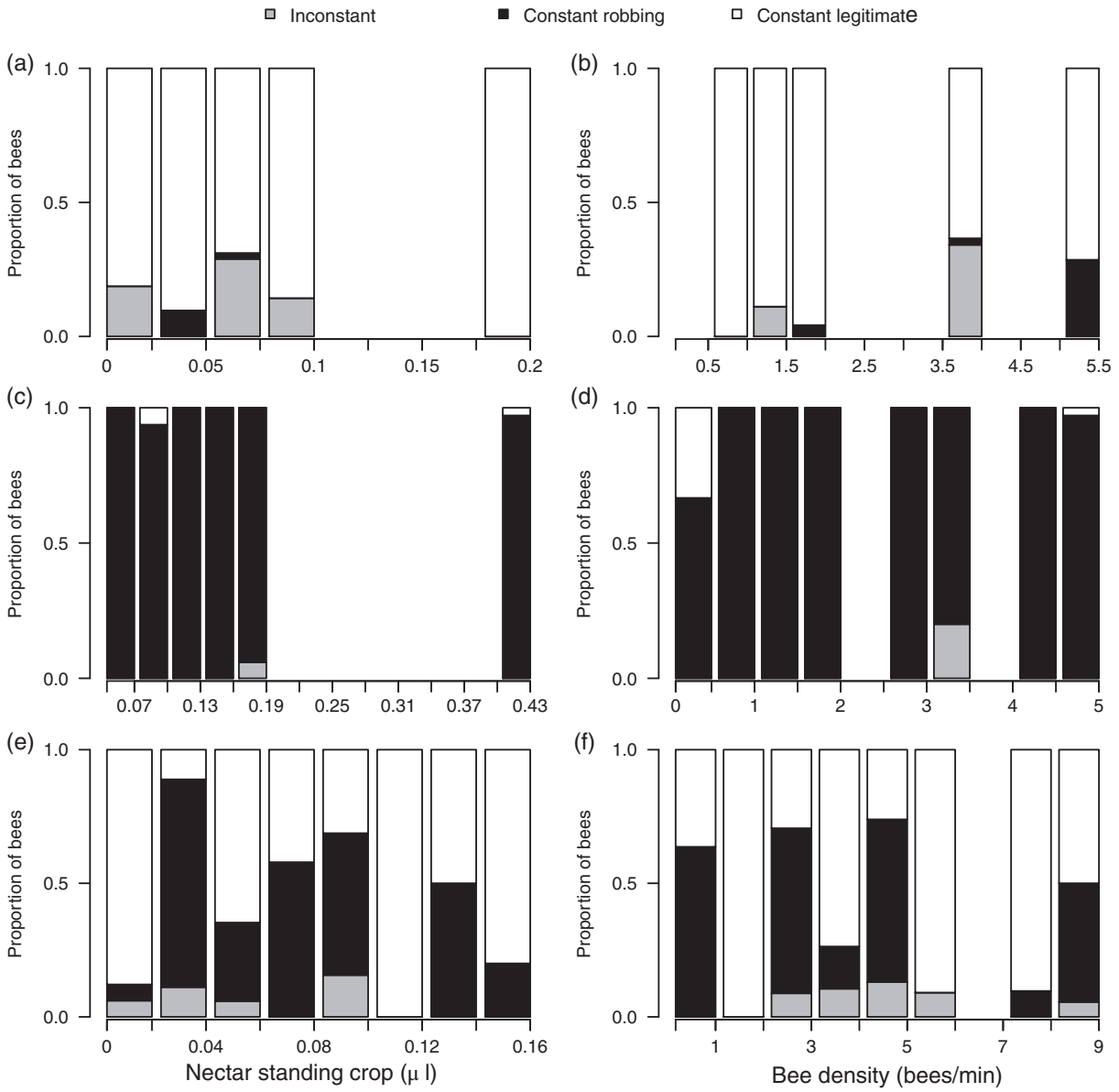


Fig. 1. Inquiry 1. Intra-bout tactic constancy across natural variation in competition (estimated via nectar standing crop or co-visitor density) exhibited by bumble bees visiting *Mertensia ciliata* (a, b), *Corydalis caseana* (c, d), and *Linaria vulgaris* (e, f) flowers. Bars show the proportion of bees exhibiting each strategy across nectar standing crops (a, c, e) or co-visitor densities (b, d, f). Logistic regression likelihood ratio tests: (a) $\chi_1^2 = 0.85$, $p = 0.36$; (b) $\chi_1^2 = 5.43$, $p = 0.02$; (c) $\chi_1^2 = 0.07$, $p = 0.79$; (d) $\chi_1^2 = 0.12$, $p = 0.73$; (e) $\chi_1^2 = 0.43$, $p = 0.51$; (f) $\chi_1^2 = 0.35$, $p = 0.56$.

mechanisms underpinning floral constancy may be more plastic than those driving tactic constancy. If so, strong tactic constancy may influence bees to visit flowers that they handle in the same way when they switch among plant species. Observations by Stout *et al.* (1998) are consistent with this prediction. Reliance on higher-level neurological processes to regulate tactic than floral constancy could also explain such differential plasticity (Stamps, 2016). However, it is unclear why food-handling constancy would require higher-order neurological processes than would floral constancy, which combines food handling with plant species recognition. Further research into the cognitive mechanisms underpinning floral versus tactic constancy are needed as they may point to the ways in which flexible resource acquisition is constrained in some contexts but not others and to how bees process the myriad of information they encounter while foraging.

In summary, a bumble bee foraging in this system is typified by constancy to particular foraging tactics. Tactic constancy rates are high and are largely insensitive to estimated nectar competition levels. Whether tactic constancy is sensitive to other ecological contexts (e.g. plant community composition, individual or colony-level nutritional requirements) and why

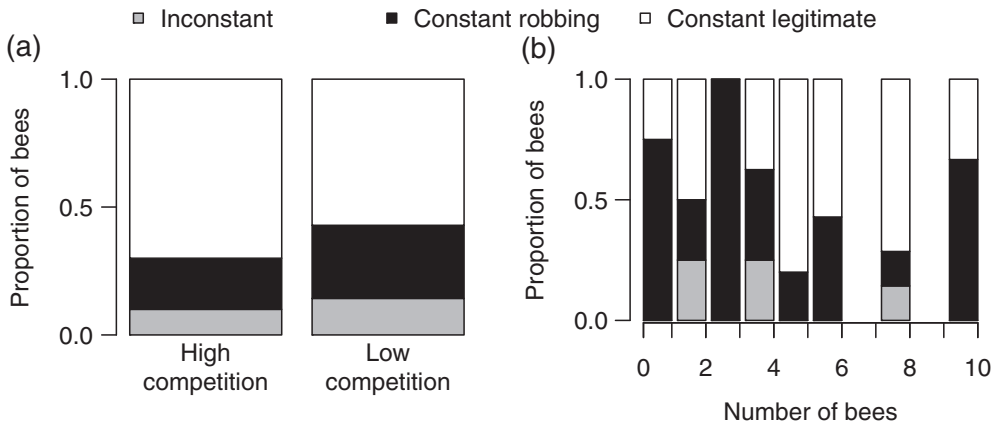


Fig. 2. *Bombus bifarius* visiting *Linaria vulgaris* (a, Inquiry 2) and *Bombus flavifrons* visiting *Corydalis caseana* (b, Inquiry 3) showed high food-handling tactic constancy independent of experimentally manipulated competition levels. Bars show the proportion of bees exhibiting each strategy across competition levels.

bees exhibit such high constancy remain open questions. Further studies of nectar robbing from the bee's perspective, as we have reported here, should provide insights into the cognitive mechanisms driving different types of foraging constancy. It will also improve our ability to predict how changing densities of co-visitors – due to phenomena such as increasing use of high densities of managed pollinators or phenologically driven shifts within wild bee communities – alter pollinator foraging constancy and thus both animal and plant fitness.

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Contribution of authors

EML and SKR conceived the project. SKR, REI, and JLB collected the field data. EML analysed the data, and EML and SKR led the writing. All authors contributed to conceptual development and text editing.

Supporting information

The supporting information includes Table S1, a summary of approaches used in each Inquiry, and S2, summaries of nectar standing crops and co-visitor densities used in Inquiry 1. It also contains two supplemental figures that show the raw numbers that Figs 1 and 2 present as proportions.

Data availability

The data that support the findings of this study are openly available in Zenodo at https://zenodo.org/record/3704938 (DOI: 10.5281/zenodo.3704938).

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1. Supporting information

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