

The floriphilic katydid, *Phaneroptera brevis*, is a frequent flower visitor of non-native, flowering forbs

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Abstract

Distribution of consumers in a patch of vegetation can be predicted by resource availability and explained by the resource-concentration and optimal-foraging hypotheses. These hypotheses have not been explored for flower-visiting Orthoptera because they are deemed less economically or ecologically important. Some flower-visiting orthopterans can provide pollination services, which warrants more attention. We studied a Singaporean, floriphilic katydid, *Phaneroptera brevis*, to investigate the following questions: 1) how frequently does *P. brevis* visit flowers compared to other flower visitors and 2) what factors predict the abundance of *P. brevis*? We collected abundance data for *P. brevis* and other flower-visiting arthropods and quantified seven environmental parameters, including flower abundance and host-plant species richness. We found that *P. brevis* frequents flowers significantly more often than some common and expected flower visitors such as hoverflies. In line with the prediction of the resource-concentration hypothesis, the abundance of *P. brevis* was positively correlated with a higher flower abundance. Owing to the limited information on unexpected wild flower visitors and pollinators, especially from the understudied tropics of Southeast Asia, we propose that *P. brevis* can be a model organism for future studies to answer fundamental questions on flower visitation.

Key words

florivores, flower visitor, optimal foraging, Orthoptera, resource concentration

Introduction

Resource availability (such as that of a floral resource) can help to predict how consumers (including pollinators and florivores) are distributed in a patch of vegetation, and this consumer-resource relationship has been studied extensively under various theoretical frameworks (e.g. resource-concentration hypothesis) to examine the interactions between insects and plants (e.g. Otway et al. 2005, Andersson et al. 2013). The resource-concentration hypothesis (Root 1973) was one of the earliest hypotheses proposed to explain insect-plant interactions, particularly of insect pests on monocultures and polycultures of agricultural crops (Andow 1991, Rhoads and English-Loeb 2003). It predicts that an insect occurs at a higher density when its host-plant species occurs at a greater density or patch size (Kareiva 1983, Rhoads and English-Loeb

2003). A mechanism to explain such a relationship is the optimal-foraging hypothesis, which predicts that the insect can forage more optimally or efficiently in a patch with a greater density of host plant species since the insect is more likely to find and utilize its host plant, for example for feeding and as a reproduction substrate, while spending less time and energy on travelling and exposing itself to predation while travelling (e.g. Pyke 1984, Sowig 1989).

The resource-concentration and optimal-foraging hypotheses have been tested extensively on various flower-visiting insects, particularly mutualistic pollinators such as bees (e.g. Real 1981, Sowig 1989, Goulson 2000, Westphal et al. 2003, Vrdoljak et al. 2016), probably owing to the importance of these insects in fruit farming. However, not all flower-visiting insects are equally well-studied, especially those deemed to be less economically or ecologically important. Examples of these understudied flower-visiting insects include the orthopterans. Although orthopterans are probably more diverse flower-visitors than previously thought (Tan et al. 2017a), they are rarely considered as important flower visitors in ecological studies. This is partly because there are few studies on how their abundances can be predicted by floral resources or other biotic and abiotic factors.

Phaneroptera brevis (Serville, 1838) (Fig. 1) is a tropical floriphilic katydid from Southeast Asia which has been observed to visit and feed on the flowers of many host-plant species (Tan et al. 2017a). Although Tan and Tan (2018a) recently also observed that the gentle foraging behavior can help with pollination in an insectary setting, we are unaware of how abundant these flower-visiting katydids are in their natural environment, how frequently they visit flowers, and why. Without these data, it is not possible to assess the importance of these flower-visiting katydids in flowering communities and their pollinating efficiency.

In this study, we aim to investigate the following two research questions: 1) how frequently does *P. brevis* visit flowers compared to other flower visitors and 2) what factors predict the abundance of *P. brevis*? We counted the types of flower-visiting arthropods (including *P. brevis*) and measured environmental and resource parameters in a wasteland site in Singapore that is representative of the habitat of *P. brevis*. We predicted that *P. brevis* is a frequent flower visitor and that its abundance can be predicted by resource abundance in accordance to the prediction of the resource-concentration hypothesis.

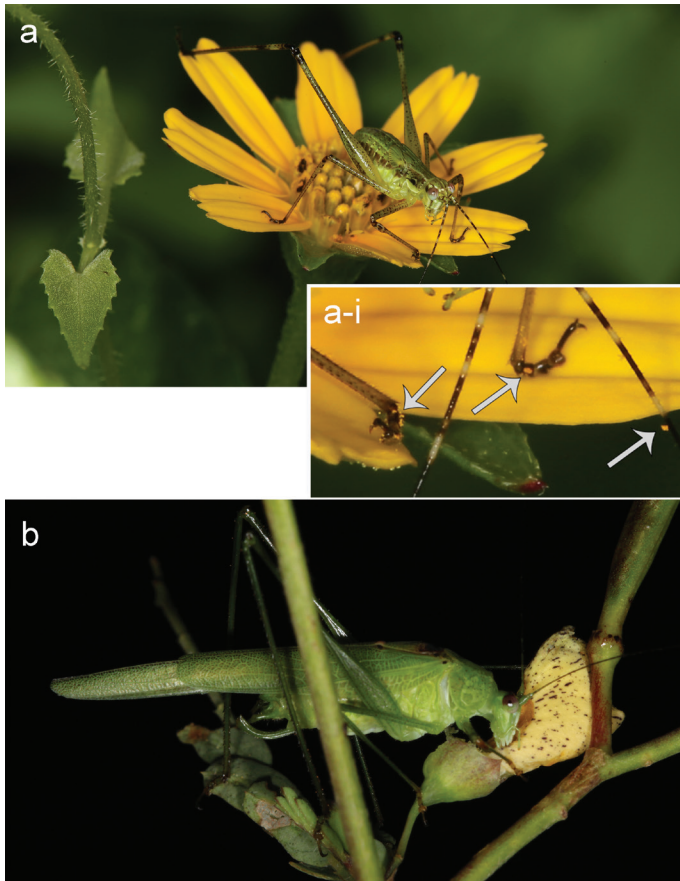


Fig. 1. A. Immature and B. Adult male individuals of *Phaneroptera brevis* visiting a capitulum of *Sphagneticola trilobata* (A) and an inflorescence of *Sesbania sesban* (B) at the study site in Singapore in the day (A) and at night (B). The arrows in the inset (a-i) indicate pollen grains attached to the body of the individual.

Materials and methods

Study subject.—*Phaneroptera brevis* belongs to the subfamily Phaneropterinae which is a group of katydids known to visit flowers. Native to Southeast Asia, *P. brevis* has been observed to visit and feed on the flowers of at least 13 species (Tan et al. 2017a). In Singapore, it is relatively common in open grasslands and forest edges that contain many flowering forbs, particularly on sites which contain *Bidens pilosa* L. (Asteraceae), *Sphagneticola trilobata* (L.) Pruski (Asteraceae), and *Neptunia plena* (L.) Benth. (Fabaceae) (Tan et al. 2017a). Although little is known about the life history of this katydid, several studies have examined the foraging behavior of *P. brevis* (e.g. Tan and Tan 2017, Tan et al. 2017b) and showed that this katydid prefers flowers to leaves (Tan and Tan 2017) and that its foraging performance can be influenced by flower abundance (Tan et al. 2017b).

Study locations and sampling.—Sampling for flower-visiting arthropods was conducted in a wasteland site of about 2,390 m² in Lorong Lada Hitam, off Mandai Road, Singapore (N1.41846°, E103.79164°). This site is dominated by non-native, naturalized weedy plants including *Bidens pilosa* and *Neptunia plena*. Surveys were conducted about once a week on non-rainy days at three broad time periods: in the morning (10 am–12 pm), afternoon

(3–5 pm), and evening (7–9 pm). The surveys were conducted between August and September 2018. The same surveyor was involved in observing and recording the data throughout the surveys.

Data collection.—To minimize sampling bias, we first generated randomized points within the 2,390 m² wasteland site using QGIS software version 2.18.7 (QGIS Development Team 2019). A circular PVC hoop (i.e. hula hoop) of 70 cm interior diameter was used to delineate sampling quadrats, with the center of the hoop placed over the location of the GPS coordinates of the randomized points. We used a circular quadrat (area 0.385 m²) because it has a lower perimeter-to-edge ratio than a square quadrat. For each survey, six quadrats were sampled. The hoop was gently placed over the vegetation with minimal disturbance. The hoop was then left for at least 20 min for the insects to acclimatize to the hoop before sampling began. Two methods were then employed (in the following order) to ensure a comprehensive survey of the flower-visiting insects:

- 1) Snapshot method (Garbuzov and Ratnieks 2014). For 30 s we counted and visually identified flower-visiting insects within each hoop. Earlier trials suggested that 30 s provided more than sufficient time for a snapshot survey of the flower-visiting insects for the size of the hoop used. This method allowed for a comprehensive sampling of the most prominent but fleeting flower-visiting insects such as Lepidoptera (butterflies and moths), Aculeata (bees and wasps), and Diptera (including hoverflies).
- 2) Timed interval method. While the snapshot method allowed a comprehensive sampling of Lepidoptera and Aculeata, less-fleeting and more well-camouflaged flower visitors (e.g. *P. brevis* and crab spiders) may be overlooked. To compensate for this, for the next 5 min we did a more thorough search for more cryptic insects, which included *P. brevis*, within the hoop. As it was impracticable to count the number of ants within the hoop, we only recorded the absence or presence of ants.

To obtain the total number and species of flower-visiting insects within each sampling point, data from both methods were pooled together. Only active flower-visiting insects, defined as any insect that intentionally moved in or on an inflorescence thereby touching the reproductive organs of the flower (Knop et al. 2018), were included. The total number of *P. brevis* adults and immatures inside the hoop was counted and we took note of whether the katydid was on a flower or on the leaves.

We grouped the flower-visiting arthropods into broad flower visitors:

1. Crickets and other katydids (suborder Ensifera, order Orthoptera);
2. Grasshoppers (suborder Caelifera, order Orthoptera);
3. Bees and wasps (subclade Aculeata, suborder Apocrita, order Hymenoptera, but not including the ants);
4. Ants (family Formicidae, suborder Apocrita, order Hymenoptera);
5. Floriphilic hoverflies (family Syrphidae, order Diptera);
6. All other flies (order Diptera);
7. Butterflies and moths (order Lepidoptera);
8. Cockroaches (order Blattodea);
9. Beetles (order Coleoptera);
10. True bugs (order Hemiptera);
11. Flower-visiting crab spiders (family Thomisidae, order Araneae).

The vegetation was also sampled within the hoop. Specifically, the number of plant species was recorded. For flowering

species, the number of flowers was also counted for each species. For Asteraceae and Fabaceae species, inflorescences were counted instead of individual florets or flowers, respectively. We excluded the data for the Poaceae (grasses) owing to the vastly different floral morphology. Poaceae from the site are also mostly wind-pollinated so do not usually attract insect visitors (Culley et al. 2002). Environmental variables, including the brightness and temperature, were recorded using a HOBO pendant temperature/light 64K data logger. In total, 36 quadrats were sampled for altogether 107 times (over three time periods). One quadrat did not have complete data over the three time periods because of the presence of aggressive territorial dogs in the evening.

Data analysis.—To examine how frequently *P. brevis* visited flowers in comparison with other flower-visiting insects, we compared the frequency of visits to flowers for each type of flower-visiting insect. This was done by fitting a generalized linear mixed-effects model (GLMM) with the Poisson error via the log-link function using the `glmer` function from the R package `lme4` (Bates et al. 2014). The flower visitor group was used as a fixed effect. The plot number was used as a random effect since each plot was sampled three times over the three time periods. We compared the least-square means of the frequency of visits to flowers between *P. brevis* and the different flower visitors using the `emmeans` function of the R package `emmeans` (Lenth 2018).

To investigate which factors predict the abundance of *P. brevis*, we performed a model selection via the information-theoretic approach (see Suppl. material 1 for more details). We first proposed a total of 39 candidate models with the abundance of *P. brevis* as the response (see Suppl. material 1 for the details and explanation of each proposed model). Each model contained a different combination of the following predictors: 1) abundance of all flower-visiting insects, 2) abundance of ambush predator crab spiders, 3) abundance of main competitors (bees, see Lindström et al. 2016), 4) presence or absence of ants, 5) time period of sampling (see Knop et al. 2018), 6) total flower abundance, and 7) plant species richness. We ensured that all models were biologically meaningful and not overfitted. We then ranked the models using the small sample size-corrected version using the Akaike information criterion (AICc) and the Akaike weights using the R package `MuMIn` (Barton and Barton 2015) (see Suppl. material 1 for how they were used to compare the models).

All statistical analyses were conducted using R software v.3.5.1 (R Core Team 2018).

Results

We observed that *P. brevis* frequents flowers significantly more often than some common and expected flower visitors such as hoverflies (Fig. 2); only bees and crab spiders visited flowers more frequently. *P. brevis* also frequents flowers more than lepidopterans, although this difference is not significant (Fig. 2). We did not observe any flower-visiting grasshoppers, beetles, and true bugs. Ants were encountered in 23 of 107 samples.

The best performing model for explaining the abundance of *P. brevis* (among 39 proposed models) contained flower abundance and the presence or absence of ants as important variables ($R^2_{\text{GLMM}(m)} = 0.06$, $R^2_{\text{GLMM}(c)} = 0.22$) (Table 1). Specifically, a high abundance of *P. brevis* was found to be associated with

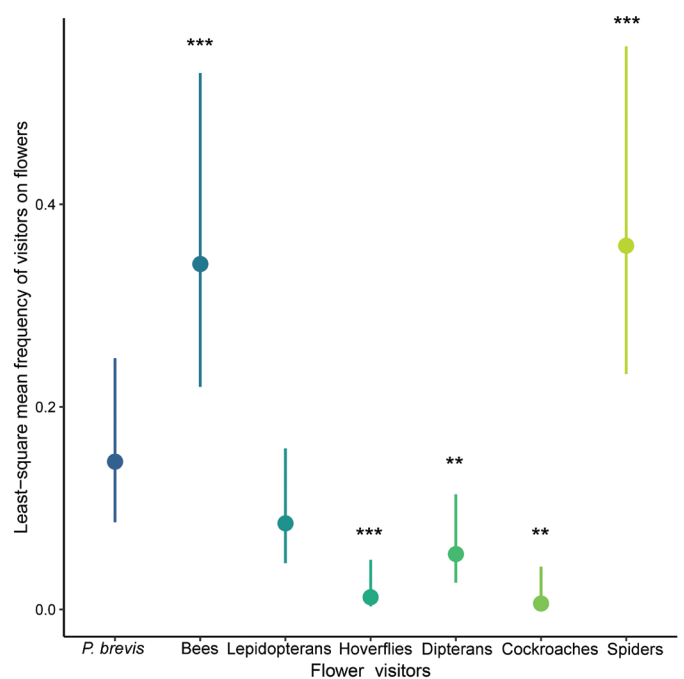


Fig. 2. Comparison of the least-square means of the frequency of visitors on flowers between *P. brevis* and other flower visitors. A generalized linear mixed-effects model with Poisson errors was fitted with different flower visitor as the fixed effect and the replicate number as the random effect. The significance between *P. brevis* and each flower visitor group is denoted as follows: ** $P < 0.01$; *** $P < 0.001$.

Table 1. Summary of the top 10 models (out of 39 models) predicting the abundance of *P. brevis*. Generalized linear mixed-effects models with Poisson errors were fitted with replicate number as the random effect.

Models	df	AICc	Delta	Weight
~ total flower abundance + presence or absence of ants	4	177.4	0.0	0.50
~ total flower abundance × presence or absence of ants	5	179.6	2.2	0.17
~ total flower abundance + total flower abundance ²	4	181.2	3.8	0.08
~ total flower abundance + abundance of crab spiders	4	181.5	4.0	0.07
~ total flower abundance	3	182.2	4.8	0.05
~ plant species richness + presence or absence of ants	4	183.3	5.9	0.03
~ total flower abundance + time	5	183.5	6.1	0.02
~ total flower abundance × abundance of crab spiders	5	183.6	6.2	0.02
~ total flower abundance + abundance of all flower-visiting insects	4	184.2	6.8	0.02
~ plant species richness × presence or absence of ants	5	184.6	7.2	0.01

high flower abundance (estimate = 0.07, p-value = 0.011, 95% CI [0.02, 0.13], $n = 107$, Fig. 3). There was, however, no evidence of the effect of presence or absence of ants on the abundance of *P. brevis* (estimate = 0.17, p-value = 0.632, 95% CI [-0.55, 0.86], $n = 107$).

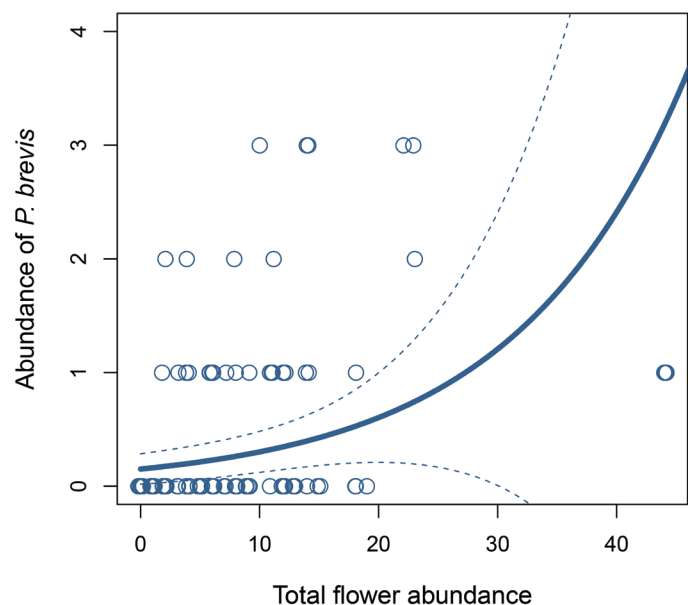


Fig. 3. High flower abundance was associated with high abundance of *P. brevis* (estimate = 0.07, p-value = 0.011, 95% CI [0.02, 0.13], $R^2_{\text{GLMM}(m)} = 0.06$, $R^2_{\text{GLMM}(c)} = 0.22$, $n = 107$). Generalized linear mixed-effects models with Poisson errors were fitted with the replicate number as the random effect.

Discussion

The major finding of our study is that *P. brevis* can be a considerably frequent flower visitor. This suggests that floriphilic orthopterans can play important roles in flowering communities both as florivores and potential pollinators, contrary to the generalization that orthopterans are unimportant flower visitors (Wardhaugh 2015, Ollerton 2017).

As a frequent flower visitor of non-native and potentially invasive species, *P. brevis* can help to reduce the spread of these weeds by feeding on the flowers. Florivory can directly and indirectly reduce reproductive success by causing damage to the reproductive parts and reducing attractiveness of the flowers to pollinators (McCall and Irwin 2006, Tan and Tan 2018b). Owing to *P. brevis* visiting flowers more frequently than other florivores (i.e. cockroaches, beetles, and true bugs), the katydid can be more efficient at weed control compared to other florivores. This, however, requires further validation given that the feeding efficiency of *P. brevis* can be variable (e.g. Tan and Tan 2017, Tan et al. 2017b) and the feeding efficiency of other florivores has not been measured and compared.

On the other hand, Tan and Tan (2018a) had previously demonstrated that *P. brevis* can forage gently on pollen grains without causing extensive damage to the reproductive parts. This may suggest that even though *P. brevis* visits flowers frequently, each individual may not be that efficient in damaging the reproductive parts and controlling weeds. Tan and Tan (2018a) also postulated that such behavior can help with pollination, but there is hitherto no direct evidence on how *P. brevis* can improve reproductive success of non-native weeds. Since *P. brevis* feeds mainly on non-native species, it is also unlikely that *P. brevis* has adapted to pollinating them and that any transfer of pollen is probably an artefact of its opportunistic feeding strategy. Therefore, in addition to the

insectary experiment (Tan and Tan 2018a) and our observational study, controlled nursery or greenhouse experiments will also be needed to investigate more explicitly and quantify the feeding and pollination efficiencies of *P. brevis* to better understand their roles as flower visitors.

That high flower abundance is associated with higher *P. brevis* abundance is consistent with the predictions of the resource-concentration hypothesis and the optimal-foraging theory. A patch with a large quantity of floral resource may indicate a more favorable habitat for *P. brevis*, thus attracting the fully-winged adults to feed and lay eggs so that the nymphs can subsequently feed on the flowers. Although the juveniles are unlikely to disperse far, the adults of *P. brevis* can travel to and forage in vegetation patches with more resources. According to the prediction of the optimal-foraging theory, the adults should prefer to forage in patches of high flower abundance having travelled a great distance (Cresswell et al. 2000).

That more flowers attract more *P. brevis* individuals is not surprising since such a pattern has been observed in other flower visitors. Given that 1) there is a lack of descriptive studies on the relationships between the distribution of floral resources and the visitation activity of wild insects at the local scale and that 2) the existing literature tends to focus on monocultures and agricultural insect pests rather than natural communities (Otway et al. 2005, Scheper et al. 2015; but see Vrdoljak et al. 2016), our observations extend these hypotheses to include overlooked wild flower-visiting insect responses in relation to variation in floral resource density within vegetation patches. Furthermore, owing to the fact that *P. brevis* (and possibly other floriphilic katydids) were observed to be active and visit flowers day and night (although many other katydids are more nocturnal) (Tan et al. 2017a), its overall importance as a flower visitor may have been underestimated and overlooked in many studies which focused only on diurnal species (e.g. Garbuzov and Ratnieks 2014).

A limitation of our study is that sampling was conducted at only one site. Nonetheless, the site was selected because it is representative of the natural habitats of *P. brevis* and of forest edges in Singapore, thus providing a microcosm to answer our research questions on flower-visiting insect responses in relation to variation in floral-resource density within vegetation patches. Moreover, we restricted our study to one population of *P. brevis* because a concurrent study showed that individuals from different populations can exhibit consistent inter-population differences in behavior across time and/or contexts, which can in turn influence how they forage and respond to floral resources (Tan and Tan 2019). Since we did not also quantify population-level traits of *P. brevis* in this study, future investigations incorporating the traits of these different *P. brevis* populations can provide more insight into how different populations can respond differently to their environments (Tan and Tan 2019).

Our observations on understudied wild flower visitors from the tropics can also inspire unanswered ecological and evolutionary questions. First, the importance of floral resources, biotic interactions (e.g. predators and competitors), and abiotic predictors (e.g. time period) is likely to vary among flower visitors and in different systems (Hegland and Boeke 2006, Vrdoljak et al. 2016). There is currently insufficient ecological and behavioral data on the neglected flower visitors (including the orthopterans), especially in the tropics, to allow the explicit testing of many ecological hypotheses and to have a more generalizable understanding of flower visitors and their responses to floral resources in the tropics. We propose *P. brevis* as a model organism for studies on

overlooked wild flower visitors and pollinators, especially in the understudied tropical habitats of Southeast Asia, to answer fundamental questions on flower visitation.

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Supplementary material 1

Authors: Ming Kai Tan, Hui Lee, Hugh Tiang Wah Tan

Data type: DOCX file

Explanation note: Supplementary Information on Statistical Analysis.

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