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Comparison of two criteria on the essential number calculation of *Andrena camellia*

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Abstract

Andrena camellia Wu is one of the primary pollinators of *Camellia oleifera* A. in China. In this paper, the essential number of individuals for efficient pollination by this species was calculated via two criteria, based on various indicators including counts of pollen grains in provisions, from single visits, and from single foraging trips overall; single flower visit duration; single flight period duration; number of eggs laid by a single female over their lifetime; and the average number of flowers per plant. Based on the number of pollen grains collected per flower visit, the essential number of females necessary is 2107 in a 1-ha *Camellia oleifera* garden with 1800 plants, while only 1998 female individuals are essentially needed when estimated based on the mean number of pollen grains collected in a single flight period. We argue that the essential number estimated by the former method is more reasonable and accurate for practical applications.

Introduction

Roughly 90% of plant species are pollinated by animals and insects play an especially important role in pollination (Bawa, 1990; Linder, 1998; Ollerton *et al*., 2011). For example, most Apocynaceae are insect-pollinated, with only a few records of bird pollination (Ollerton, 2018). Among pollinating insects, bees play a dominant role in most ecosystems and many species have been identified as the most-effective pollinators for various kinds of plants (Crane and Walker, 1984; Pernal and Currie, 2001; Winfree *et al*., 2007). Further, 90% of the world's 107 most-important crops depend on bees for pollination (Potts *et al*., 2016). For example, the managed honey bee *Apis mellifera* is famous for the portable pollination services they provide, more easily enhancing the yields of the target plants while improving the quality of their fruits (Morse and Calderone, 2000; Klein *et al*., 2007).

In recent years, native bees have become a prominent focus due to honey bee declines and potential ecological consequences of their high abundance (Roubik *et al*., 1986; Steffan-Dewenter and Tscharntke, 2000; Paini, 2004; Aizen *et al*., 2008; Allsopp *et al*., 2008; Rader *et al*., 2009; Suzuki *et al*., 2009; Kleijn *et al*., 2015; Frier *et al*., 2016). However, more research is needed to understand the dynamics of pollination throughout most cropping systems in China and monitoring data are also lacking generally for wild pollinators (Liu *et al*., 2018). To date, the majority of studies have focused on managed honey bees (Teichroew *et al*., 2017). For example, *Apis cerana* was among 18 flower-visiting insect taxa observed in cabbage fields and was the focus of the study (Johnson *et al*., 2017). Of these, the order Hymenoptera constituted 59.40% and 40.70% in honey bee introduced and control fields, respectively. It is crucial that we investigate the specific visitors in systems like this because species differ not only in their effectiveness but also their specialization (or oligolecty), such that many may only visit a small number of plants (Gauld and Bolton, 1988; Cane and Sipes, 2006).

The case of the economically-important tea oil plant, *Camellia oleifera* (Theaceae) is especially interesting because it requires cross-pollination but seemingly discourages pollinators (Zhuang, 1998; Huang *et al*., 2017). Not only does this species bloom during winter in China when few pollinators are available, it is also chemically defended, causing losses to honey bee colonies used to pollinate it (Zhang and Chen, 2013). These factors may contribute to pollen limitation, leading to the observed phenomenon of 'with a thousand flowers and only one fruit' observed by He *et al*. (2002).

Given these challenges, few species are thought to be effective pollinators of *C. oleifera* (Lin and Li, 1991; Qiu *et al*., 2018). Among them, *Andrena camellia* Wu (Hymenoptera, Apoidea, Andrenidae) is an oligolectic species and a primary pollinator of *C. oleifera* based on their unusual activity period, peaking during the bloom of *C. oleifera* and extensive observations of floral visitation and nesting density among *Camellia* fields (Wu, 1977; Ding *et al*., 2007; Huang *et al*., 2008; Xie *et al*., 2013; Qiu *et al*., 2018). Shortages of this crucial pollinator could result in limited visitation and, therefore, pollen limitation causes diminished fruit

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production of *C. oleifera*. Conversely, the fruit setting rate could be improved by increasing the abundance and density of bees that pollinate *C. oleifera* such as *Andrena camellia*, *Colletes gigas* Cockerell, *Andrena striata* Wu, and *Andrena hunanensis* Wu (Lin and Li, 1991; Kunin, 1997; Zhuang, 1998). Recent studies reported the nesting biology, the biological features and behaviors of *A. camellia* (Ding *et al*., 2007; Huang *et al*., 2008). However, up to the present, its flower foraging habits remain poorly known and unquantified, preventing us from building a framework to evaluate and better manage the pollination services that *A. camellia* and other species provide for this vital crop.

Quantitative pollination ecology has gained attention in recent years, based mainly on a need to increase agricultural sustainability for production (Lonsdorf *et al*., 2009). Although many studies have taken top-down approaches to estimate ecosystem services, seeking to determine total pollination based on correlations with landscape or other factors, bottom-up methods that calculate service provision species-by-species are a powerful way to incorporate interspecies variation in effectiveness (Joseph *et al*., 2020). As an example, the essential numbers of *Osmia cornifrons* and *Osmia excavata* per unit area were estimated using both flower-foraging habits and foraging trip duration, but the results were quite different between these metrics (Wei *et al*., 2000). This may be due to various factors such as debilitating weather or low density of plantings, both of which can greatly reduce the amount of time that an insect is actually pollinating within a given foraging period. Studies must also incorporate measures of pollination efficiency, the comparative ability of individuals to provide pollination services (Traveset, 1999; Young, 2002). Foraging frequency is also an important index of pollination efficiency and some studies have found that the effective foraging frequency is lower than that of total foraging frequency. Some studies have tried to control for this, for instance, only if the time spent on a flower exceeds 5 s and there is nectar- or powder-gathering behavior, will an effective visit be counted (Luo *et al*., 2019). Consequently, it is vital that we include the amount of pollen transported, as it does not matter how long a bee spends on a flower if it is not carrying any suitable pollen or contacting floral reproductive structures.

Here, we report new advances in the incorporation of these factors into the calculation of the essential number of pollinators for *C. oleifera*. To this end, we report the foraging habits of *Andrena camellia* and provide two methods to determine their essential number per unit forest area, incorporating both foraging time and the number of pollen grains carried as metrics. This represents an important first step to building a holistic model of pollination service provision for *C. oleifera* and other crops that require animal pollination.

Material and methods

Study species

Camellia oleifera Abel (family Theaceae is an important woody oil plant used in China for both human consumption and industries such as textile manufacture) having originated in China, is now extensively planted in 16 provinces in southern China as well as other countries such as Vietnam (Zhuang, 1998). Currently, the total planted area of *C. oleifera* in China is about 1 million hectares (http://www.forestry.gov.cn/). The flowering period of *C. oleifera* ranges mainly from the middle of October to the end of December.

Study area

Field investigations were carried out in two *C. oleifera* sample plots located in Jiangxi province, China, from October 2015 to December 2018. The sample plot was located in Xinyu city (115°04′ E, 28°04′ N). The *C. oleifera* have been growing for 10 years and have consistently high yields. The numbers of *C. oleifera* per hectare to determine the planting density and the numbers of flowers on each target plant were counted.

Sampling programme

A cubic net measuring 4 m × 2.5 m × 2.5 m (Devkota and Thapa, 2005) was used to collect 60 *A. camellia* individuals. After each foraging trip, the numbers of pollen grains carried on the body was counted. One foraging period was measured for the 60 collected females every 2 h from 8:00 am to 18:00 pm under natural conditions. For each individual, the total foraging time in 1 day was measured using a cup placed over the nest (fig. 1a); In the morning, we take the lid off, let the bees out of the nest, count the time, and close it when it is time to go back to its nest, so that it stays around its nest and cannot get in. This has been observed in our previous research, so we designed the device (Huang *et al*., 2008). The data on 60 female individuals were recorded every day for 10 days. Finally, 60 homing females were collected returning to their nests and the number of pollen grains carried by each was counted under a microscope (100×).

Based on nest excavations, 100 fresh pollen balls made by *A. camellia* were collected and the number of pollen grains contained in each pollen ball was counted out under a microscope (100×). One hundred newly-hatched individuals collected from nests using covering cups were examined under a microscope (100×) for whether any residual pollen grain existed on their body surfaces.

For each relevant treatment, to collect the pollen grains from females, their bodies were washed with 75% (v/v) alcohol solution repeatedly. From these samples, representative 0.01 ml samples were slide mounted and the pollen grains were counted under a microscope (100×), with total amounts per body then calculated based on the total volume related to this subsample. The criteria for determining sex were based on a previous study, drones are small, with a body length of 8.501 ± 0.244 mm, and with no pollen picking organs (corbiculate). The female bee has a large body length of 10.233 ± 0.365 mm, has a special pollen-collecting organ (corbiculate) to collect pollen and suck nectar without harming flowers, and its body surface is hairy and easy to get pollen (Huang *et al*., 2008).

Data analysis

The essential number of bees per unit area was calculated according to the number of flowers in the *Camellia oleifera* plantation located in Xinyu city. The plants in this area were planted with a density of 1800 ha^{-1}. The following six parameters were used for calculating the essential number of bees: speed of processing (time spent per flower), duration of a single flight period, mean number of pollen grains carried in one foraging instance (during the time spent on a single flower), mean number of pollen grains carried in a single total foraging period, mean number of pollen grains contained in one pollen ball, and mean number of eggs laid by one female over their lifetime.

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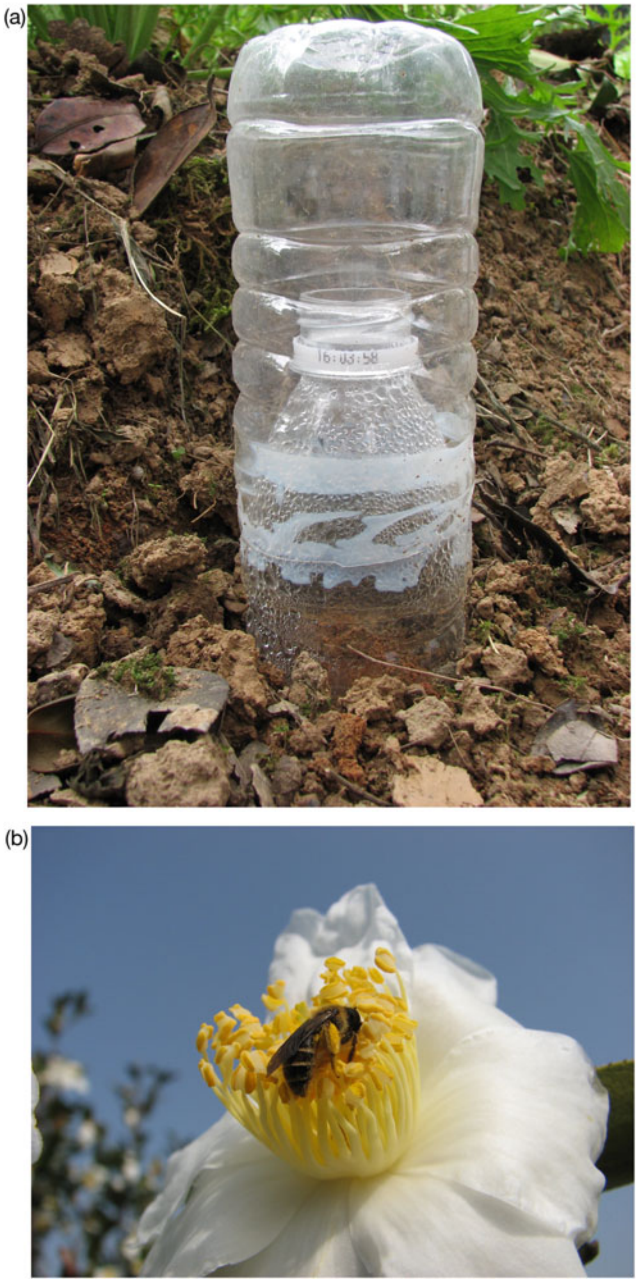

Figure 1 (a) Cup trap for measuring the total foraging time in 1 day. (b) A female *Andrena camellia* on a flower of *Camellia oleifera*.

Results

Essential number of pollinators based on foraging time

The observation of 60 nests of *A. camellia* showed that the foraging frequency of a female individual on a sunny day ranged from one to four trips, averaging 2.98 trips ± 0 (mean ± SD, $n = 60$). The time that 60 homing females spent in a single period (SFT) was 2644 s ± 120 (44.06 mins ± 2) (mean ± SD, $n = 60$), and the mean number of pollen grains collected from one foraging periods (NPSF) was 90,692.5 ± 80 (mean ± SD, $n = 60$). The mean number of time spent per flower for 100 female visits (SP) was 79.26 s ± 7 (mean ± SD, $n = 60$). A female bee needs about 51 flights to collect sufficient pollen grains during its lifetime, considering average fecundity and the pollen balls required for its offspring (Table 1). The number of plants foraged on in one foraging period (NFOF) was conservatively set to one in this formula. In this case, about 1998 *A. camellia* female individuals were essential to the efficient pollination of 1800 (NPH) *C. oleifera* plants in 1 ha of garden.

Based on foraging time:

$$\begin{aligned}&(\text{Essential number of pollinators})\ \text{ENP}\\&=\frac{\text{NPH}\times\text{NFP}\times\text{NFOF}\times\text{SP}\times\text{NPSF}}{\text{SFT}\times\text{NPFL}}\end{aligned}$$

where ENP is the essential number of *A. camellia* per hectare (essential number of pollinators), NPH is the mean number of plants per hectare; NFP is the mean number of flowers per plant, NFOF is the mean number of flowers foraged on in one foraging period, SP is the mean time spent per flower (S) (Speed of Processing), NPSF is the mean number of pollen grains collected from one foraging period, SFT is the mean time of single flight period (min), and NPFL is the mean number of pollen grains collected by a female throughout lifetime

$$\text{NPFL}=\left(\frac{1}{4}\right)\times(\text{NE})\times(\text{NPS})+\left(\frac{3}{4}\right)\times(\text{NE})\times(\text{NPL}).$$

Essential number of pollinators based on quantity of pollen carried

The mean number of pollen grains collected by a female individual from one flower (NPOF) was 2876 ± 28 (mean ± SD, $n = 60$). The mean number of pollen grains contained in big (NPL) and small pollen balls (NPS) were 384,900 ± 15,800 (mean ± SD, $n = 60$) and 282,440 ± 8700 (mean ± SD, $n = 60$), respectively. The mean number of eggs laid by a female in its lifetime (NE) was 17, with each pollen ball sustaining one offspring (Table 1). The sex ratio of female-to-male among these eggs was approximately 3:1. In order to estimate the essential number of pollinators, it is assumed that there are only *A. camellia* pollinators in 1 ha of *C. oleifera* garden with 1800 6-year old plants (NPH) and each flower only needs one individual for successful pollination. The number of plants foraged on in one foraging period (NFOF) was conservatively set to one in this formula. Pollen carried in all parts of the body should be considered effective pollen of the belt as shown in fig. 1b (Qiu *et al.*, 2018). Under this circumstance, atleast 2107 female individuals are estimated to be required to complete the whole pollination task.

Based on pollen grains' numbers:

$$\begin{aligned}&(\text{Essential number of pollinators})\ \text{ENP}\\&=\frac{\text{NPH}\times\text{NFP}\times\text{NFOF}\times\text{NPOF}}{(1/4)\,(\text{NE}\times\text{NPS})+(3/4)\,(\text{NE}\times\text{NPL})}\end{aligned}$$

where ENP is the essential number of *A. camellia* per hectare (essential number of pollinators), NPH is the mean number of plants per hectare, NFOF is the mean number of plants foraged on in one foraging period, NFP is the mean number of flowers per plant, NPOF is the mean number of pollen grains collected from one flower, NE is the mean number of eggs laid by a female, NPS is the mean number of pollen grains in a small pollen ball, and NPL is the mean number of pollen grains in a big pollen ball.

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Table 1. Data for the essential individual numbers of *Andrena camellia* per unit area of *C. oleifera*

Code	NPL	NPS	NPOF	NPSF	SP(s)	SFT(s)	NE	FFD	NFP
1	394,400	271,200	2960	96,360	70	2220	17	3	2310
2	358,400	243,600	2652	89,280	155	3180	16	2	1978
3	420,400	244,800	2944	103,280	123	2940	16	3	1568
4	414,400	277,600	2704	98,880	230	2700	15	3	2284
5	372,000	313,600	3164	91,360	95	2580	13	1	1930
6	362,800	262,000	2964	83,680	40	3220	15	4	2542
7	403,200	278,400	2768	87,400	85	2660	16	3	2776
8	426,400	301,200	1912	89,560	65	2880	20	3	2670
9	371,200	269,600	3552	79,120	49	2040	16	2	2424
10	369,600	274,800	2656	102,080	76	3480	12	3	2132
11	413,200	317,600	2708	87,220	73	1920	18	4	1586
12	384,800	289,600	3224	91,360	65	3300	18	3	2044
13	352,400	307,200	3266	88,560	51	2840	19	3	3189
14	342,800	268,600	2596	94,040	75	2400	17	3	2544
15	404,800	244,600	2768	90,780	72	2940	16	4	1834
16	403,200	276,200	3304	89,360	80	1960	17	3	2618
17	420,400	317,400	2636	97,960	94	3180	18	2	2944
18	361,600	285,400	2912	91,360	65	2880	17	2	2790
19	408,400	306,400	2788	96,560	54	3160	19	4	3186
20	408,400	291,200	2830	88,280	54	2700	19	2	1956
21	368,500	280,600	2640	91,360	76	2520	16	3	2173
22	364,400	274,300	2845	89,660	73	2500	18	3	3668
23	383,600	305,600	2712	94,040	76	2880	16	4	2286
24	426,400	286,800	2854	90,780	51	3120	13	3	1956
25	371,200	302,200	3068	89,360	75	2160	19	4	3546
26	369,600	270,600	2762	93,870	67	3060	16	3	2776
27	393,200	285,700	3010	92,390	80	2880	18	3	1798
28	354,300	276,400	2528	94,580	82	1740	16	3	2456
29	367,300	304,400	2851	93,720	58	2400	17	4	3598
30	342,800	215,400	2906	89,320	108	2880	18	3	2786
31	404,800	286,200	2524	93,910	64	3240	21	2	2178
32	403,200	292,000	3045	92,050	76	2520	19	3	2689
33	421,600	271,200	3556	94,530	59	2340	20	2	2543
34	414,800	300,200	2462	89,210	85	3180	18	3	3031
35	366,000	264,400	3312	91,560	78	2880	16	3	1918
36	362,800	274,800	2622	89,660	56	2460	18	2	2141
37	403,200	302,100	3219	94,210	69	2740	20	3	2790
38	416,900	289,600	2672	90,780	78	2280	19	4	2186
39	375,200	300,200	2921	10,310	135	2460	20	3	1910
40	363,300	268,600	2734	92,060	74	2160	16	3	1978
41	413,200	254,100	2522	91,280	83	2400	12	3	2256
42	344,800	266,900	3002	89,670	72	2340	18	4	2288
43	352,400	301,200	2796	95,360	80	2600	15	3	1968

(*Continued*)

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Table 1. (*Continued.*)

Code	NPL	NPS	NPOF	NPSF	SP(s)	SFT(s)	NE	FFD	NFP
44	362,200	223,100	2664	91,880	78	2580	19	2	2542
45	404,800	286,400	3374	96,540	76	2820	17	4	2741
46	403,500	262,000	2638	90,280	76	2460	18	2	2173
47	420,400	267,400	2712	91,240	56	2880	16	3	3424
48	372,500	306,200	3232	89,750	67	2580	18	3	2275
49	360,600	279,700	2636	94,640	76	2540	17	3	3384
50	403,600	274,800	2940	91,740	96	2640	21	3	2546
51	420,400	317,600	3345	88,350	76	3000	19	4	3181
52	391,200	289,600	2712	93,270	78	1920	16	3	2544
53	372,600	307,200	3454	95,320	75	2400	18	3	1834
54	403,400	268,600	2668	94,580	67	2460	16	3	2314
55	344,800	274,900	2762	93,720	89	2640	13	2	1986
56	352,400	296,200	3310	89,660	82	2400	19	3	2790
57	342,800	317,400	2528	93,420	86	2580	16	3	3186
58	406,400	265,800	2751	89,570	88	2520	18	4	2567
59	393,300	306,400	2975	91,240	68	2840	14	3	2721
60	362,800	288,600	3016	96,200	84	2460	17	3	2684

NPL, mean number of pollen grains in a big pollen ball; NPS, mean number of pollen grains in a small pollen ball; NPOF, mean number of pollen grains collected from one flower; NPSF, mean number of pollen grains collected from one foraging period; SP, mean time spent per flower (S) (Speed of Processing); SFT, mean time of single flight period (min); NE, mean number of eggs laid by a female; FFD, frequency of flight per day; NFP, mean number of flowers per plant.

Discussion

At present, research on quantification of pollinator populations remains incipient. Crucially, there has too often been a disconnect between the calculation of pollination services at either the field level, which is relevant to farmers, or at the individual level, where important information about specific pollinators and their effectiveness can be more readily detected (Perrot *et al.*, 2019; Jauker *et al.*, 2012). By scaling up from the individual to the field level, however, we can satisfy practitioners while still incorporating variation in efficiency both within and across different pollinator species.

In quantifying the essential number of pollinators, prior studies have relied primarily on flight period data alone (Wei *et al.*, 2000). However, this is problematic because it does not account for time spent foraging for nectar vs pollen, nor does it account for time spent off flowers. The number of bees visiting flowers on a daily basis can be affected by many climatic factors, such as temperature. In addition, the time spent by bees on any single flower depends on many factors, including the size of flower and the amount of nectar or pollen present, the latter two being directly related to time of day and how many resources other visitors have already removed (Joshi and Joshi, 2010; Field *et al.*, 2012). Given that pollen carrying capacity is an important characteristic value of statistical pollination efficiency, determining fitness outcomes for both the pollinator and the plant, this experiment has improved this method on the basis of selecting stable flowering stage and estimated the effective pollinator quantity based on pollen quantity.

The critical issue with using total foraging period time is that it tends to overestimate the time spent pollinating, thereby underestimating the essential number of pollinators. Here, flight period-based analyses suggest that only 1988 females are required, but the integration of pollen quantity instead suggests that at least 2107 females are required. If underestimations based on flight period were followed, insufficient pollination services may result, impacting grower profits and, on larger scales, this could potentially lead to food or product shortages. At present, however, these estimates may be high or low, given that the exact amount of pollen needed for successful pollination was not measured, nor was the rate of deposition; it may be that only a small amount of pollen is necessary, but we do not know how much is successfully transferred. Future work should also more directly incorporate the amount of pollen required for optimal fruit production on the individual level, as well as single visit deposition trials to confirm that each individual visit by *A. camellia* is sufficient for fruit set (King *et al.*, 2013).

Summary and future perspectives

The number of pollinating insects present during a given crop's flowering period plays a central role in improving fruit setting rate, fruit shape index and fruit quality overall, and efforts to enhance their numbers are necessary to ensure food security in developing countries such as China. Quantifying the insects present and their value as ecosystem service providers is a crucial first step to this type of management. Our study significantly improves upon previous approaches, demonstrating the importance of methods which directly incorporate flower visiting activity into essential number calculation. In addition, this study provides foundational data for the rearing and management of *A. camellia*, a crucial pollinator of *C. oleifera*. In the future, by extending this method to additional pollinators in this or other cropping

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systems, it will finally be possible to build an integrative, holistic scheme for managing wild pollinators in crops to ensure optimal pollination.

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