Delineating the calling pattern of *Oecanthus indicus* from native and non-native plant species (#82788)

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Delineating the calling pattern of *Oecanthus indicus* from native and non-native plant species

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The study intends to understand the effect of the host plants on the call parameters of native tree cricket, *Oecanthus indicus* (Order: Orthoptera, Sub-order: Ensifera, Family: Gryllidae) while calling from native (*Justicia adhatoda*) and non-native host plant species (*Lantana camara* and *Hyptis suaveolens*). The study was conducted at five locations across India. Calls of ~~*Oecanthus*~~ *indicus* were recorded on these host plants in the field and spectral and temporal parameters of calls were analyzed. Additionally, the calling site along with the microhabitat was noted. The results suggested that the peak frequency and syllable period varied across the host plant species. The peak frequency varied among the two non-native plant species while the difference in temporal pattern between the native and non-native host plants was observed only in the syllable period. The study also quantified the choice of microhabitat site of calling insects from the three host species. The native *O. indicus* chose non-native *H. suaveolens* leaves extensively as a preferable site to baffle (37%). Differences in the call parameters and choice of host plant by insects may ultimately affect the preference and performance of insects. The study would aid in exploring the underlying evolutionary and ecological processes of adaptive success of insects on non-native plants, especially in ~~the~~ habitats where the dynamic transition of native plant and non-native plant abundance is taking place.

Delineating the calling pattern of *Oecanthus indicus* from native and non-native plant species

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Abstract

The study attempted to understand the effect of the host plants on the call parameters of native tree cricket, *Oecanthus indicus* (Order: Orthoptera, Sub-order: Ensifera, Family: Gryllidae) while calling from native (*Justicia adhatoda*) and non-native host plant species (*Lantana camara* and *Hyptis suaveolens*). The study was conducted at five locations across India. Calls of ~~*Oecanthus*~~ *indicus* were recorded on these host plants in the field and spectral and temporal parameters of calls were analyzed. Additionally, the calling site along with the microhabitat was noted. The results suggested that the peak frequency and syllable period varied across the host plant species. The peak frequency varied among the two non-native plant species while the difference in temporal pattern between the native and non-native host plants was observed only in the syllable period. The study also quantified the choice of microhabitat site of calling insects from the three~~-~~host species. The native *O. indicus* chose non-native *H. suaveolens* leaves extensively as a preferable site to baffle (37%). Differences in the call parameters and choice of host plant by insects may ultimately affect the preference and performance of insects. The study would aid in exploring the underlying evolutionary and ecological processes of adaptive success of insects on non-native plants, especially in ~~the~~ habitats where the dynamic transition of native plant and non-native plant abundance is taking place.

Introduction

The ecological role of insects in terms of facilitation of establishment, colonization, and naturalization of invasive plants through interactions such as herbivory, seed dispersal and pollination has been extensively studied (Pearse & Altermatt, 2013; Sunny et al., 2015). The dynamic alternation in the abundance of introduced non-native plant species and insect interactions are subjected to varied ecological and evolutionary ~~phenomenon~~ such as ecological fitting and evolutionary trap (Janzen, 1985; Schlaepfer et al., 2002). The ecological interactions between organisms could arise due to their matching ecological traits and environmental ~~factor~~ at play. Agosta & Klemens (2008), proposed that "phenotypic plasticity, correlated trait evolution and phylogenetic conservatism" act~~s~~ as means of ecological fitting. Non-native plants may render themselves as a suitable habitat initially due to their resemblance to habitats of insects. However, insects experience reduced fitness over time, referred to as evolutionary trap (Schlaepfer et al., 2002). Host preference and eventually the performance of insects on abundant non-native plants are greatly governed by the abovementioned processes/ ~~phenomenon~~. Host shift is shaped by the host preference of the insects when the native and exotic plants coexist and/or co-occur (Castells et al., 2014).

Oecanthus uses acoustic communication for species recognition and mate attraction (Metrani & Balakrishnan, 2005). Insects like *Oecanthus indicus* may prefer native or non-native plants as a site for feeding, mate attraction using acoustic signals, and mating. "Preference" is the ability of an insect to choose a host plant for food or oviposition. ''Performance'' is quantified based on the total number of eggs laid and their larval development (Sunny et al., 2015). The insect may tend to choose similar habitats despite experiencing reduced fitness or performance (Schlaepfer et al., 2002). Thus, host preference could be an important attribute that affects the reproductive fitness of an acoustically communicating insect. Several studies have reported the association of *Oecanthus* with a non-native plant, *H. suaveolens* (Mhatre et al., 2011; Deb et al., 2012; Bhattacharya et al., 2017). The association of *Oecanthus* species with non-native plants can provide an excellent system to investigate the effect of preference based on various call characteristics. *Oecanthus* was found to be calling abundantly from a wide variety of habitats comprising both native and non-native plants (Native- *Justicia adhatoda,* Non-native- *Lantana camara,* and *Hyptis suaveolens*), which were co-occurring ~~with each other~~ across the sampling locations.

The suitability of the habitat is an important parameter that can affect reproductive success in terms of male fitness and call quality. In terms of acoustically communicating crickets, spectral and temporal features are used by conspecific females to assess male call quality (Symes, 8). It has been observed that females prefer a male calling song with a higher chirp rate and longer chirp duration (Wagner, 1996). Chirp rates are known to be affected by diet and anthropogenic disturbances (Wagner & Hoback, 1999). Andrade & Mason (2000) found that male cricket *Ornebius aperta* that fed on a high-nutrient diet were healthier and transferred more spermatophores on average than low-diet males in Australia. The call parameters act as a determinant for females to assess sperm quality and nuptial gifts, resulting in fit progenies (Brown, 2011).

Reproductive success and survival in crickets are also dependent on their calling sites. These sites help them in predator avoidance and influence their probability of securing mates (Mhatre et al., 2011). They also manipulate the plant leaves by making holes in the leaf and calling from them for sound amplification (Deb et al., 2012).

Studies have investigated the effects of host plants on insect performance in terms of oviposition success, larval development & performance, adult body mass, and fecundity (Keeler & Chew, 2008; Fortuna et al., 2013) while little is known about the effect of host plant and calling sites on the calling parameters of acoustically active species e studied the acoustic traits of tree cricket *Oecanthus indicus* across native and non-native host plant species. The objectives of the study were (i) to investigate variation in call parameters of *O. indicus* calling from native and non-native plants and (ii) the choice of calling sites of *O. indicus* from native and non-native plant species. We tested the hypothesis that there is no difference in the call parameters between *O. indicus* calling from native and non-native plants.

Materials & Methods

Study site and period

The sampling was carried out from 2013 to 2015 across five different locations in India viz. Amarkantak (22.6833° N, 81.7333° E); Dehradun (30.2333°N, 78.1667° E); Delhi (28.6° N, 77.18333° E); Dhanbad (23.7957° N, 86.4304° E) and Muzaffarpur (26.1209° N, 85.3647° E) (Fig.1). Sampling locations were selected based on the presence of *O. indicus* in dominant stands of native plant, *J. adhatoda* and non-native, *H. suaveolens* and *L. camara.* The temperatures ranged from 17.5°C to 33.5 °C while the relative humidity ranged from 55% to 98% across the sampling locations.

Study system

The tree crickets genus *Oecanthus* belongs to the sub-order Ensifera and family Gryllidae of the insect order Orthoptera. These crickets are small-sized, nocturnal, and semi-arboreal, widely distributed across the ecoregions of the world except the poles. Genus *Oecanthus* has four described species (*O. rufescens* Serville, *O. henryi* Chopard, *O. bilineatus* Chopard and *O. indicus* Saussure) on the Indian subcontinent (Metrani & Balakrishnan, 2005). While *O. henryi* has been associated with *H. suaveolens* (restricted to South India), *O. indicus* is a generalist, widely distributed and observed to be calling from both native and non-native plants. *O. rufescens* calls mostly from grasses and *O. bilineatus* has been observed calling from trees (personal observation).

H. suaveolens (Lamiaceae) is native to Tropical America but is now found across the globe and emerged as a pantropic weed (Sharma et al., 2009). It is one of the abundantly spread species of the Vindhyan highlands, India after *Lantana camara* (Sharma et al., 2009). A significantly large portion of the total geographic area of India i.e., approximately 40.20% (1,320,119 km^2) is predicted to be suitable for *Hyptis* (Padalia et al., 2014). So, the species has a likelihood of rapid spread and subsequently its interacting insect species.

Lantana is a member of the family Verbenaceae, it is native to Tropical America. It is naturalized in India and occurs as dense monospecific thickets. Owing to its rapid naturalization and invasion outside its native range, it is considered a weed of international significance (Sharma et al., 2005). Using extensive field sampling data and modeling, Mungi et al. (2020) have reported that 44% of the Indian forests are invaded by *L. camara.*

J. adhatoda is a native to India belonging to the family Acanthaceae. It is a perennial, evergreen, and highly branched shrub widespread throughout the tropical regions of Southeast Asia (Dhankar et al., 2011). *J. adhatoda* has been found to co-occur with the other two non-native plant species.

Acoustic sampling

O. indicus calls were recorded in the evening at the study locations. Insects were ~~psycho~~acoustically located and sound recordings were taken using a digital recorder (TASCAM DR-08, TEAC, America Inc., USA, 44.1 kHz, 16 bits, .wav format) from a distance of at least 25 cm. Ambient temperature and relative humidity were recorded using a pocket weather meter (Kestrel 4500). Calling sites along with the microhabitat was also noted.

Acoustic analyses

Spectral and temporal patterns of the sound recordings of *O. indicus*, such as peak frequency, chirp duration, chirp period, syllable duration, and syllable period were analyzed. Peak Frequency (PF) is the frequency with the highest amplitude. Syllable represents the sound produced by complete stridulatory movement (during the closing stroke of the wings), syllable duration (SD) being the time period from the beginning to the end of a syllable. Syllable period (SP) is the time period from the beginning of a syllable to the beginning of the next. Chirp represents the sound produced by ~~the partial movement~~ of the wing and is the first-order assemblage of syllables. Chirp duration (CD) is the time period from the beginning to the end of a chirp. Chirp period (CP) is the time period from the beginning of a chirp to the beginning of the next one (Metrani & Balakrishnan, 2005).

RAVEN Pro 1.4 (Cornell Lab of Ornithology, Ithaca, NY, USA) and Spectra Plus 5 (Pioneer Hill Software, Poulsbo, WA, USA) were used for temporal and spectral analysis.

Statistical analyses

Non-parametric statistics were performed as the data was not ~~normal~~. Kruskal-Wallis ANOVA was used to determine differences between the call parameters. The coefficient of ~~V~~ariation (CV) for call parameters on each host plant was calculated to compare the degree of variation between datasets. Post- hoc test was carried out to examine the differences in plant species. All the statistical tests and analyses were conducted using STATISTICA (StatSoft Inc., Version 12) and Sigma Plot.

Results

Effect of host plant on acoustic parameters

A total of 50 calls of *O. indicus* were recorded calling on native *J. adhatoda* and non-native *L. camara* and *H. suaveolens* plant species. The peak frequency (kHz) of *O. indicus* calling on *J. adhatoda* (2.34 ± 0.17 kHz, CV= 7.42%) was similar to *O. indicus* calling from *L. camara* (2.43 ± 0.17 kHz, CV= 7.35%). The peak frequency of *O. indicus* calling from *H. suaveolens* was lesser as compared to the other two host plants (2.26 ± 0.19 kHz, CV=8.19%) (Table 1). Despite having low CV values, peak frequency of *O. indicus* individuals calling from *L. camara* was significantly different from individuals calling from *H. suaveolens* (Kruskal- Wallis, H (2, N=50) = 7.24, p= 0.027) (Fig. 2) (Table 2).

The syllable period ranged from 29.62 - 42. 91 ms between the three host plant species. However, the syllable period of *O. indicus* calling from native *J. adhatoda (*42.91± 23.31 ms) was significantly different from non-native *L. camara* (29.62± 9.17) (Kruskal- Wallis, H (2, N=50) = 6.36, p= 0.041) (Fig. 2) (Table 2). Syllable duration was found to be between 17.25 - 17.95 ms on all plant species. There was no significant difference in the syllable duration between individuals calling from *L. camara* (17.25± 3.54 ms), *H. suaveolens* (17.45± 1.46 ms), and *J. adhatoda* (17.95 ± 2.29 ms) (Kruskal- Wallis, H (2, N=50) = 0.54, p= 0.76) (Fig. 2) (Table 2).

The chirp duration of *O. indicus* individuals calling from *L. camara* (0.77±0.42 s), *H. suaveolens* (0.75±0.26 s), and *J. adhatoda* (0.66±0.35 s) were not significantly different (Kruskal- Wallis, H (2, N=50) = 2.07, p= 0.36) (Table 2). The chirp period of *O. indicus* individuals ranged from 0.95±0.33 s on *J. adhatoda* to 1.23±0.37s on *H. suaveolens* respectively (Table 1). There was no significant difference in the chirp period of *O. indicus* calling from the three plant species (Kruskal- Wallis, H (2, N=50) = 5.79, p= 0.06) (Table 2).

The use of calling sites from native host plant vs non-native host plants

O. indicus was found to be calling from four sites on native and non-native species viz. top of the leaf, leaf margin, using the leaf as a baffle, and between two leaves (Fig. 3). Leaf margin was found to be the most frequently used site by *O. indicus* on *L. camara* (60%) and *J. adhatoda* ([illegible]%) (Fig. 3). Using leaf as baffle was predominantly seen on *H. suaveolens* (36.84%) and then on *J. adhatoda* (20%). *O. indicus* also called from the top of the leaf on *H. suaveolens* (42.10%) (Fig. 3)

Discussion

The study attempted to understand the interactions between insects and non-native plants through changes in the call parameters of an acoustically communicating insect species. The results of the study showed that the peak frequency of *O. indicus* calling from *L. camara* was different from that of non-native *H. suaveolens* and the syllable period of *O. indicus* calling from *L. camara* was different from that of native *J. adhatoda.* Temporal patterns such as chirp duration, chirp period, and syllable duration did not show any difference between individuals calling from native and non-native plants. This could be attributed to morphological constraints of the song-producing structures or stridulatory structures affecting their ability to manipulate finer call characters [illegible]hatre et al., 2011; Orci et al., 2016). Studies have investigated the effect of diet on the reproductive fitness and growth performance of orthopterans (Magara et al., 2019). The host plant quality has been reported to affect the performance and reproductive strategies of individual insects as well as the interaction between the insects (Awmack & Leather, 2002). The metanotal gland feeding, a nuptial gift given by singing males to females is largely dependent on the male diet (Smith et al., 2017). Comparative quantification of nuptial gifts by *O. indicus* feeding on native and non-native plants could further provide insights into the role of non-natives as evolutionary traps. The results illustrated that there was a difference in call parameters in terms of peak frequency and syllable period of the *O. indicus* on *L. camara* as compared to the other native and non-native plants. Studies have reported that females of *Oecanthus* species prefer large males and not necessarily males calling at lower peak frequency (Deb et al., 2020). Performance studies in terms of larval growth and development are also needed to investigate the reproductive fitness of *Oecanthus* on native and non-native plants. This will provide valuable information on the specialist and generalist feeding habits of the species.

The calling site of *O. indicus* varied as it chose non-native *H. suaveolens* leaves extensively as a site to baffle (36.84%) as compared to other plant species (Fig. 3). The study showed that the cricket species exhibited baffling behaviour more on leaves of *H. suaveolens. Oecanthus* use baffle as a strategy to amplify signals for effective long-distance communication. It is a reproductive strategy where the males, often the smaller and low-amplitude callers have resorted to this strategy to acquire mates (Deb et al., 2020). This is suggestive of a preferential host shift for reproductive success. Shift to novel hosts can have implications on various traits of the insects. Cocroft (2007) opined that the host plant environment as a means of production, transmission, and propagation of signals is very crucial for sexual communication, mate recognition, and attraction. Host shifts may drive natural selection through divergence and signal evolution of acoustically communicating insects and are often associated with ecological speciation in plant-feeding insects (McNett & Cocroft, 2007).

Conclusions

The study revealed significant differences in the peak frequency of *O. indicus* calling from the two non-native plant species- *L. camara* and *H. suaveolens* while the syllable period varied significantly between the calls from the native plant species- *J. adhatoda* and non-native plant species- *L. camara*. In terms of the calling sites, calling through the holes in the plant leaves i.e., baffling was extensively observed in *H. suaveolens.* The top of the leaf was the second preferred calling site by *O. indicus.* Empirical studies investigating the calling parameters of *Oecanthus* from various calling sites on native and non-native plants are needed to further shed light on the possibility of host shift of *Oecanthus* on non-native plants. Future work evaluating the diet preference, mating success, and reproductive output of *Oecanthus* species on native and non-native plants will help provide insights into the preference and performance of insects found closely associated with non-native plant species.

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Table 1(on next page)

Call parameters of *O. indicus* calling from different plant species. Peak frequency (PF), Syllable period (SP), Syllable duration (SD), Chirp duration (CD), and Chirp period (CP) (n=50).

Values in parentheses denote standard deviation. The coefficient of variation is expressed in %.

Table 1: Call parameters of *O. indicus* calling from different plant species. Peak frequency (PF), Syllable period (SP), Syllable duration (SD), Chirp duration (CD), and Chirp period (CP) (n=50). Values in parentheses denote standard deviation. The coefficient of variation is expressed in %.

Call parameter	***L. camara***	***H. suaveolens***	***J. adhatoda***
PF (KHz)	2.43(0.17); 7.35 %	2.26(0.19); 8.19 %	2.34(0.17); 7.42 %
SP (ms)	29.62(9.17); 30.95%	34.65(10.75); 31.04 %	42.91(23.31); 54.33 %
SD (ms)	17.25(3.54); 20.54 %	17.45(1.46); 8.38 %	17.95(2.29); 12.76 %
CD (s)	0.77(0.42); 55.11 %	0.75(0.26); 35.17 %	0.66(0.35); 53.49 %
CP (s)	1.02(0.42); 40.92 %	1.23(0.37); 30.39 %	0.95(0.33); 34.60 %

Table 2(on next page)

Results of Kruskal-Wallis ANOVA test of call parameters (dependent variables) between host plant species (grouping variable) and post-hoc comparisons (z’ values are quoted).

Peak frequency (PF), Syllable period (SP), Syllable duration (SD), Chirp duration (CD) and Chirp period (CP) (n=50). Bold letters denote statistical significance at p<0.05.

Table 2: Results of Kruskal-Wallis ANOVA test of call parameters (dependent variables) between host plant species (grouping variable) and post-hoc comparisons (z' values are quoted). Peak frequency (PF), Syllable period (SP), Syllable duration (SD), Chirp duration (CD) and Chirp period (CP) (n=50). Bold letters denote statistical significance at p<0.05.

Call parameters	**Host sp.** / **Host**	***L. camara***	***H. suaveolens***	***J. adhatoda***
PF (~~K~~Hz) (H=7.24, p=**0.027)**	*L. camara*	-	-	-
	H. suaveolens	**2.69**	-	-
	J. adhatoda	1.20	1.31	-
SP (ms) (H=6.36, p=**0.041)**	*L. camara*	-	-	-
	H. suaveolens	1.37	-	-
	J. adhatoda	**2.51**	1.18	
SD (ms) (H=0.54, p=0.76)	*L. camara*	-	-	-
	H. suaveolens	0.01	-	-
	J. adhatoda	0.65	0.65	
CD (s) (H=2.07, p=0.36)	*L.camara*	-	-	-
	H. suaveolens	0.62	-	-
	J. adhatoda	0.88	1.44	-
CP(s) (H=5.79, p=0.06)	*L. camara*	-	-	-
	H. suaveolens	1.85	-	-
	J. adhatoda	0.54	2.24	

Figure 1

Map showing the study sites in India.

Figure 2

Box-whisker plots showing the temporal and spectral parameters i.e. (a) ~~P~~eak frequency, (b) ~~S~~yllable period, (c) syllable duration, (d) ~~C~~hirp period, and (e) chirp duration of the three host plant species.

The bar denotes median, box shows the quartile range (25% - 75%), and whisker denotes the non-outlier range.

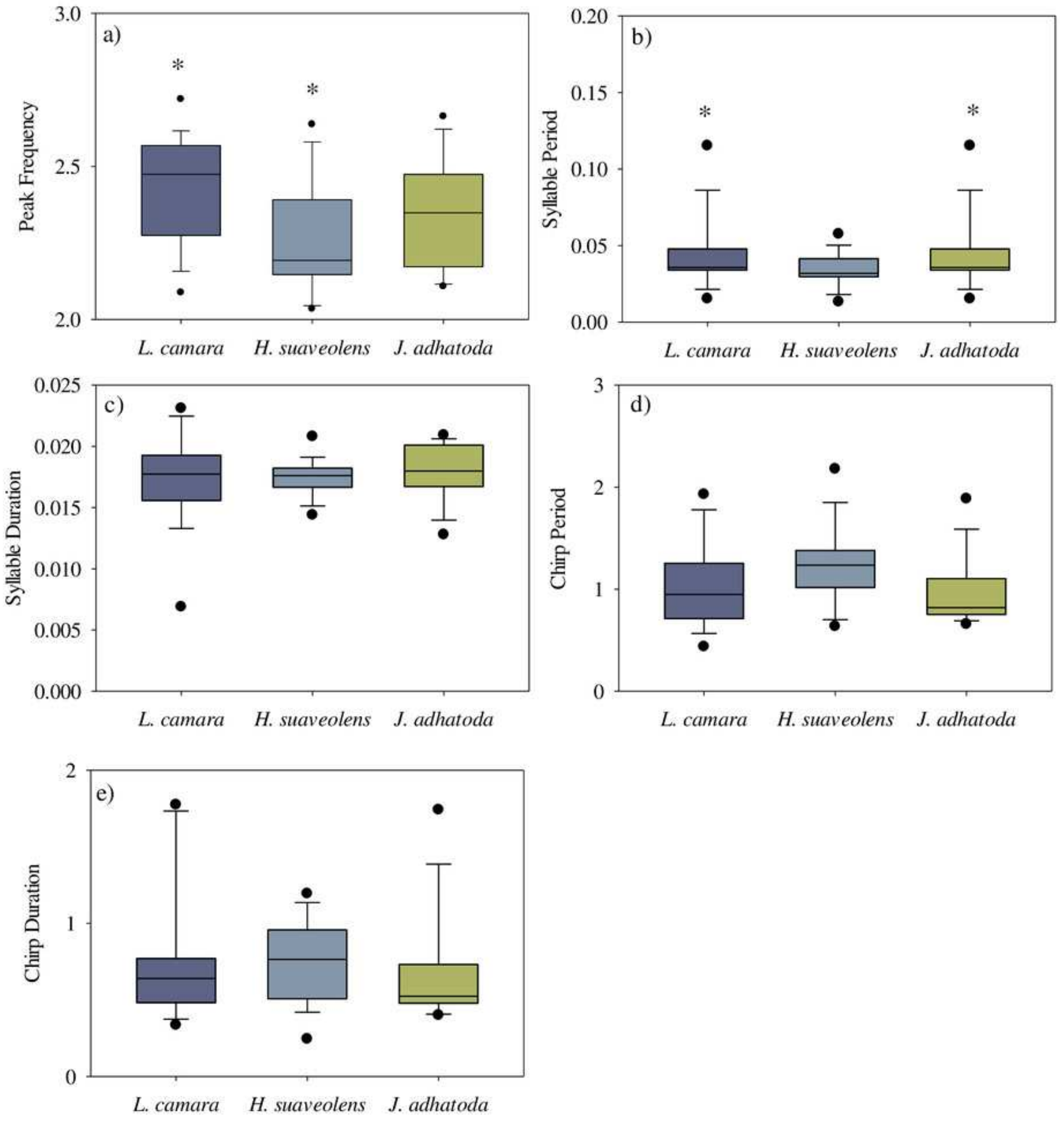
a)
Peak Frequency
3.0
2.5
2.0
b)
Syllable Period
0.20
0.15
0.10
0.05
0.00
c)
Syllable Duration
0.025
0.020
0.015
0.010
0.005
0.000
d)
Chirp Period
3
2
1
0
e)
Chirp Duration
2
1
0
*
L. camara
H. suaveolens
J. adhatoda

Figure 2.

Figure 3

Calling site~~s~~ proportions of *O indicus* on native and non-native plants.

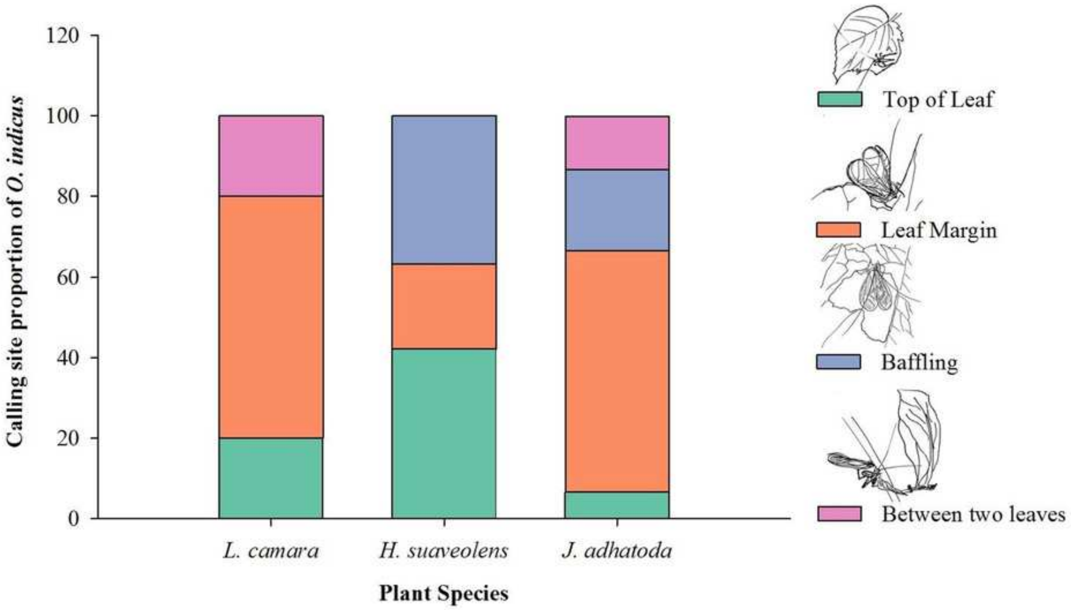
120
100
80
60
40
20
0
Calling site proportion of O. indicus
L. camara
H. suaveolens
J. adhatoda
Plant Species
Top of Leaf
Leaf Margin
Baffling
Between two leaves

Figure 3.