

# Large pollen loads of a South African asclepiad do not interfere with the foraging behaviour or efficiency of pollinating honey bees

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**Abstract** The pollen of asclepiads (Asclepiadoideae, Apocynaceae) and most orchids (Orchidaceae) are packaged as large aggregations known as pollinaria that are removed as entire units by pollinators. In some instances, individual pollinators may accumulate large loads of these pollinaria. We found that the primary pollinator of *Cynanchum ellipticum* (Apocynaceae – Asclepiadoideae), the honey bee *Apis mellifera*, accumulate very large agglomerations of pollinaria on their mouthparts when foraging on this species. We tested whether large pollinarium loads negatively affected the foraging behaviour and foraging efficiency of honey bees by slowing foraging speeds or causing honey bees to visit fewer flowers and found no evidence to suggest that large pollinarium loads altered foraging behaviour. *Cynanchum ellipticum* displayed consistently high levels of pollination success and pollen transfer efficiency (PTE). This may be a consequence of efficiently loading large numbers of pollinaria onto pollinators even when primary points of attachment on pollinators are already occupied and doing so in a manner that does not impact the foraging behaviour of pollinating insects.

**Key words** Pollen loads, Asclepiadoideae, *Cynanchum ellipticum*, foraging efficiency, pollinaria, pollen transfer efficiency.

## Introduction

Pollinators accumulate pollen on different parts of the body during foraging bouts. Excess pollen may be groomed off or used as reward (Proctor et al. 1996). The pollenkitt and other adhesive properties of pollen results in

pollen accumulating and forming layers of pollen that may compact on different parts of the pollinator's body (Morris et al. 1995; Harder and Wilson 1998). Pollen may be physically massed by some insects that specifically collect pollen as food (e.g. corbiculate bees, Michener 2000) or large pollen loads may be loaded incidentally onto pollinators when foraging on plant species with aggregate pollen (e.g. the pollinaria of orchids and asclepiads; Morse 1981, Johnson and Liltved 1997). In such species pollen accumulates to an extent where the pollen loads may become large enough to physically interfere with the movement of pollinators (Morse 1981; Johnson and Liltved, 1997).

The pollinaria of orchids and asclepiads are attached to pollinating insects either by the action of a sticky pad in the Orchidaceae and Periplocoideae (Johnson and Edwards 2000; Verhoeven and Venter 2001) or in the Asclepiadoideae by a mechanical clip (Wyatt and Broyles 1994). In some flowers with highly ecologically specialized pollination systems (sensu Ollerton *et al.* 2007; e.g. many orchids and asclepiads) the morphology of the flower and pollinator often correspond closely, resulting in pollinaria being placed on specific parts of the pollinator. In a few orchid (Johnson and Steiner 1997, Johnson and Litved 1997, Peter and Johnson 2009) and asclepiad species (Morse 1981; Coombs et al. 2009) pollinaria may attach to other pollinaria already present on the pollinator and form large pollinaria masses during periods of high pollinator activity.

insect (Morse 1981; Johnson and Liltved 1997), and in some cases lead to the death of pollinators foraging on orchids (Johnson and Liltved 1997) and asclepiads (Romeo 1933; Coleman 1935; Coombs and Peter 2010). Morse (1981) documented reduced foraging speeds of bumblebees visiting the flowers of *Asclepias syriaca* as a consequence of pollinaria loads on the mouthparts and possibly because the bees' tarsi become trapped between the rigid anther wings and in some instances, break. Physical damage to insect pollinators was also reported by Shuttleworth and Johnson (2006, 2009a) who show that pompilid wasps visiting the flowers of *Pachycarpus asperifolius* and *P. appendiculatus* regularly broke off labial palps between the rigid anther wings of the flowers of these species (Shuttleworth and Johnson 2006, 2009a). This in turn may result in insects reducing their foraging on asclepiads or alternatively only visiting asclepiad flowers at times when the preferred food sources are not available.

It is possible that large pollinarium loads may influence the number of flowers that pollinators visit per inflorescence while foraging for nectar. This may occur when pollinaria that are attached to the mouthparts reduce the amount of nectar that insects can extract from the flowers resulting in pollinators visiting fewer flowers per inflorescence. The resultant behaviour may therefore be similar to that seen in pollinating bees that visit fewer flowers per plant when inferior nectar rewards are encountered (Pleasants et al. 1979; Jersakova and Johnson 2006; Johnson et al. 2004). When bees probe fewer flowers per inflorescence, geitonogamous self-pollination and pollen discounting may be reduced (*sensu* Harder and Wilson, 1998). Bees may, however, employ different foraging strategies depending on the size of the nectar reward, number of flowers per plant and distance between foraging plants (Zimmerman 1981), thus it is possible that bees may visit more flowers per inflorescence to gain the same amount of reward.

The genus *Cynanchum* includes approximately 400 species of which about 100 are African (Liede 1993; Ollerton and Liede 2003). Despite

the large number of species, little is known about the pollination biology of species in this genus. To date, pollinator observations have only been made for 13 species (Ollerton and Liede 2003; Ollerton et al. 2010; Coombs 2010) representing 3% of the species in the genus. In this study, the pollination biology of *Cynanchum ellipticum* (Asclepiadoideae, Apocynaceae), a common asclepiad vine endemic to southern Africa (Liede 1993) was investigated. Our initial observations indicated that honey bees visiting this species can accumulate very large pollinarium loads (>200) on their mouth parts, allowing us to test the hypothesis that large pollinarium loads influence the foraging behaviour of pollinators. Specifically, we investigated whether large pollinarium loads negatively influence the foraging behaviour of honey bees by slowing foraging speeds or reducing the number of flowers visited per inflorescence. We also investigated other aspects of the pollination biology of *C. ellipticum* to determine the benefits to the plant of loading multiple pollinaria on pollinators.

## Methods

### Study species and study site

*Cynanchum ellipticum* (Harv.) RA Dyer (Fig. 1A) is a common perennial climber found along the South African coast and adjacent interior (Liede 1993). The species produces flowers almost continuously throughout the year (peaking from April to September). The flowers are arranged as a sciadioid (pseudo-umbel) which bear between 1–12 open flowers (Liede 1993). During peak flowering periods, large plants can produce substantial flower displays consisting of several hundred inflorescences, each inflorescence displaying several open flowers simultaneously. In our study population, most plants flowered synchronously with several flowering events occurring at different times throughout the year. A small number of individuals flowered unpredictably at times when most other plants were not in flower. Flowers produce nectar as a pollinator reward.

This study was carried out at three different sites in the Eastern Cape, South Africa. These were Grahamstown (33° 18' 20''S, 26° 31' 28''

E), Port Alfred (33° 36' 00"S, 26° 53' 00" E) and Kenton-on-Sea (33° 40' 50"S, 26° 40' 14"E). At each of these three locations *C. ellipticum* is a common climber growing on shrubby vegetation and on fences. The study populations consisted of plants growing on fences and natural vegetation throughout these three towns.

### **Pollinator observations and pollinarium loads**

Honey bees (*Apis mellifera*) are the main flower visitors (Coombs 2010) and we collected bees at all three study sites during 2007. Sampling was conducted primarily during the morning peak of insect activity (8:30 - 10:30) but continued throughout the day at Kenton-on-Sea and Port-Alfred. During 2007 we collected all flower visitors, however, due to the abundance of honey bees, we only collected flower visiting insects besides honey bees (primarily flies and smaller Hymenoptera) during 2008 and 2010 although the presence of honey bees was recorded. Nocturnal visitors were collected only in Grahamstown during 2009. One hour observation periods from dusk (19:00 - 20:00) were conducted on three evenings. All insects were captured, pinned, identified and for each specimen, the number of full pollinaria (pollinaria with both pollinia attached), ½ pollinaria (pollinaria with one pollinium removed) and corpuscula (pollinaria with both pollinia removed) were counted. The total number of pollinaria carried was then calculated as the sum of full pollinaria, ½ pollinaria and corpuscula.

### **The effect of large pollinarium loads on the foraging efficiency of honey bees**

To investigate the role of large pollinarium loads on the foraging efficiency of honey bees, we first quantified whether pollinaria accumulate on bees through the day and whether pollinaria are groomed off overnight. We then quantified whether large pollinarium loads affected the foraging behaviour of honey

bees in terms of the time spent visiting each flower and the number of flowers per inflorescence visited.

#### *Diurnal pollinarium loads*

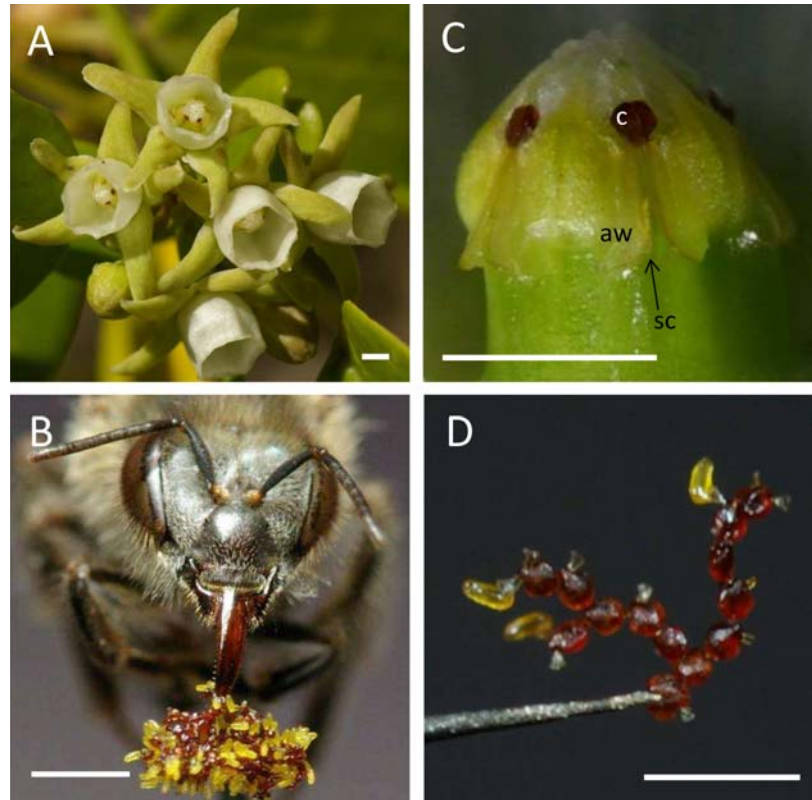
Diurnal pollinarium accumulation was monitored by collecting honey bees foraging on *C. ellipticum* over seven one-hour periods throughout the day. For each of these time intervals, between 3 and 8 plants were examined and up to three bees were collected from each plant per sampling interval. Sampling periods were spaced more closely in the morning when foraging activity is highest. Sampling was replicated on three different days except dawn sampling (two days). To determine whether bees carry pollinaria overnight, the first nine bees arriving at the plants at dawn (i.e. "first arrivals") were collected over a period of 10 minutes and examined for the presence of *C. ellipticum* pollinaria.

To determine whether there is a pattern of pollinarium accumulation throughout the day, a one-way ANOVA was used to test for differences in the mean pollinarium loads of *C. ellipticum* borne by bees at different times of the day. Data of total pollinarium loads for *C. ellipticum* at different times of the day were Box - Cox transformed to meet the assumptions of normality (Komolgorov-Smirnov and Liliefors) and homoscedascity (Levene's test).

#### *Weight of pollinarium loads carried by bees*

Bees carrying pollinaria were caught and immobilized by quickly cooling them in a freezer. They were then weighed on an electronic balance before and after the pollinaria were removed under a dissecting microscope using fine forceps, the difference representing the weight of the pollinarium load. The number of removed pollinaria was then counted. We investigated the proportion of the bees total weight that pollinaria masses constitute using univariate regression.

**Fig. 1** The small flowers (2-4mm) of *C. ellipticum* are arranged in a sciadoid inflorescence (A). The primary pollinators of *C. ellipticum* are native honey bees (*Apis mellifera*) that can accumulate large numbers of pollinaria on their mouth parts (B). A gynostegium (structure formed by the fusion of the androecium and gynoecium in the Asclepiadoideae) of *C. ellipticum* showing position of anther wings (aw) covering a narrow stigmatic chamber (sc) into which pollinia are inserted to effect pollination. The proboscides of pollinating honey bees are drawn between the rigid anther wings and as a consequence remove the corpusculum (c) and associated paired pollinia (hidden behind the anther wings). Subsequently, corpuscula may attach to other pollinaria already in place on the pollinators forming large chains of pollinaria (D). Scale bars: A, C & D = 1mm; B = 3mm.



#### *Influence of pollinarium loads on the foraging times and percentage of flowers visited*

To determine the impact of large pollen loads on the time that bees spent foraging per flower, we tracked the foraging bouts of individual honey bees using an electronic data logger. Bees were subsequently caught and the number of full pollinaria, half pollinaria and corpuscula each bee carried was counted. Foraging bees were selected haphazardly and their foraging bouts tracked until individuals had visited a maximum of 10 flowers. Sampling periods were confined to one hour sessions in either the morning (starting 10:30) or afternoon (14: 30) and up to 10 individual bees were caught in any single sampling period. From these data, we calculated the average time that each bee spent visiting flowers and investigated the relationship between the average time bees spent visiting flowers and the total pollinarium load carried using Spearman's rank correlation as data were not normally distributed.

On two days during March 2009 we tracked the foraging bouts of individual bees between 8:00 and 11:00am to determine whether bees carrying large pollinarium loads visit fewer flowers per inflorescence. Each bee was

tracked until it had visited between one and three inflorescences and care was taken that each inflorescence had at least two open flowers (range of flowers per inflorescence for this population: 1-12). The number of flowers that each bee visited and the number of flowers on the inflorescence were recorded. Each bee was then caught and the pollinarium load counted. We used univariate regression analysis to examine the relationship between the proportion of flowers visited per inflorescence (arcsine square root transformed) and the total pollinaria load of each bee.

#### **Pollinarium removal, deposition and pollen transfer efficiency**

To quantify average levels of pollen removal, deposition and pollen transfer efficiency we sampled flowers from all three sites during 2007. Flowers were sampled by randomly picking three flowers per plant from between 30 and 50 individuals. In 2008 this was repeated for one date at Port Alfred and three dates in Grahamstown. During the same year, at Kenton-on-Sea, pollination success was tracked throughout the year (May 2008 until March 2009). In all populations, flowers were

sampled at midday following periods of good weather. Pollinarium removal and pollinium deposition was scored for all sampled flowers and these data were used to calculate the pollen transfer efficiency (PTE) for the population. Pollen transfer efficiency in asclepiads is calculated by dividing the average number of deposited pollinia by twice the average number of pollinaria removed per sample (there are two pollinia per pollinarium; also see Coombs et al. 2009; Coombs et al. 2011) and represents an estimate of the fraction of removed pollinaria deposited on conspecific stigmas (Johnson et al. 2005).

### Nectar rewards

The nectar volume produced by *C. ellipticum* flowers is minute and accumulates in a small corona cup (ca. 2mm wide). Flowers were bagged to accumulate nectar over a period of ca. 36 hrs before the measurements of volume and concentration were made. Nectar was not removed from flowers prior to bagging. Depending on the volume of nectar that each flower accumulated we collected all the nectar from between two to five flowers per inflorescence and divided the final volume by the number of flowers to obtain an average nectar volume per flower. Nectar volumes and concentration for *C. ellipticum* were measured only in the Grahamstown population. All nectar concentration measurements were made using an Atago 0 to 50% sucrose refractometer.

## Results

### Pollinator observations and pollinarium loads

The flowers of *Cynanchum ellipticum* (Fig. 1A) were visited by a wide variety of Hymenoptera, Diptera and Lepidoptera (Coombs 2010). However, honey bees (*Apis mellifera*) carried by far the most pollinaria and accumulated large pollen loads with one bee in the Grahamstown population carrying 224 pollinaria on its mouth parts (Table 1, Fig 1B). Bees were the most common flower visitor caught in

Grahamstown in all study years. Although fewer bees were caught while visiting *C. ellipticum* in Kenton-on-Sea and Port Alfred, bees were nevertheless the primary pollinators at these sites and also accumulated large numbers of pollinaria on the mouth parts (Table 1). One bee caught on 16 May 2008 in Port Alfred bore a load of 73 pollinaria.

Other visitors to the flower that occasionally bore pollinaria include butterflies (*Dira clytus eurina* (Satyrinae, Nymphalidae), flies (Tachinidae, Calliphoridae, Muscidae and Syrphidae), as well as smaller solitary bees such as *Allodape pernix*, *Allodapula melanopus* and *A. variegata* (Xylocopinae, Apidae) (Coombs 2010).

The stigmatic chamber of *C. ellipticum* is small and flowers typically only received one pollinium per stigmatic chamber (Fig. 1C). The mechanism of pollinaria attachment to pollinators in *C. ellipticum* is typical for asclepiads but is particularly efficient in forming long continuous chains (Fig. 1D). Pollinarium chains may be easily constructed by hand using a small insect pin to simulate the proboscis of the pollinator. The pollinarium load may be further consolidated as the pollinia become cemented together by nectar.

### The effect of large pollinarium loads on the honey bee foraging efficiency

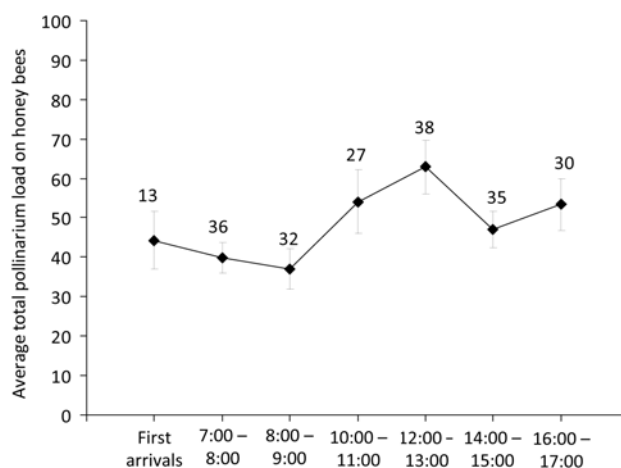
#### *Diurnal pollinarium accumulation and removal of pollinaria through grooming*

In Grahamstown, the average pollinarium load carried by honey bees ranged between 37 (SE = 5.1) and 62.9 (SE = 6.8) on different sampling intervals (Fig. 2). There was no significant effect of the time of day on the size of pollinarium loads ( $F_{(6,207)} = 1.95, p = 0.074$ ).

The average pollinarium load of bees caught at first light arriving at the flowers was 44.3 (SE = 7.4; n = 13 bees). Due to the large pollinarium loads present on honey bees

**Table 1** Summary of the average number of full pollinaria, 1/2 pollinaria and corpuscula borne by honey bees visiting the flowers of *C. ellipticum* at three different study sites.

Order	Family	Site	Species	No. of individuals sampled	No. of individuals pollinaria (percentage)	Full pollinaria (mean $\pm$ 1 SE)	1/2 pollinaria (mean $\pm$ 1 SE)	Corpuscula (mean $\pm$ 1 SE)	Total (mean $\pm$ 1 SE)
Hymenoptera	Apidae	Grahamstown	<i>Apis mellifera</i>	26	25 (96)	13.35 $\pm$ 1.83	19.96 $\pm$ 3.39	29.88 $\pm$ 4.23	63.19 $\pm$ 9.08
	Apidae	Kenton-on-Sea	<i>Apis mellifera</i>	11	8 (73)	4.45 $\pm$ 1.20	6.36 $\pm$ 1.95	9.18 $\pm$ 2.56	20 $\pm$ 5.24
	Apidae	Port Alfred	<i>Apis mellifera</i>	3	1 (33)	8.33 $\pm$ 8.3	4.0 $\pm$ 4.00	10.33 $\pm$ 10.33	22.67 $\pm$ 22.67



**Fig. 2** Changes in the average total number ( $\pm$  1 SE) of pollinaria carried by honey bees visiting *C. ellipticum* at different times of the day (values above bars indicate sample sizes).

foraging at dawn, it is unlikely that honey bees groom pollinaria off overnight.

#### *Weight of pollinarium loads*

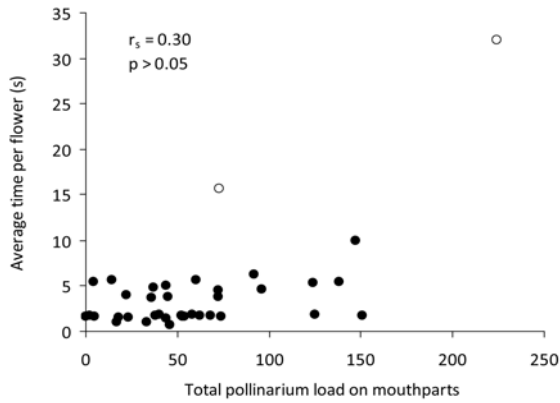
As pollinarium loads increased in size, they constituted a larger percentage of the total weight of bees ( $r^2 = 0.72$ ,  $n = 30$ ,  $p < 0.0001$ ). Within the range of pollen loads recorded (4 – 134 pollinaria), pollinarium loads never exceeded more than 2.5% of the body mass of a bee. Even very large pollinarium loads of 250 pollinaria (maximum recorded = 224) would not exceed 5% of the body mass of a bee.

#### *Influence of pollinarium loads on bee foraging*

There was a positive correlation between the time spent visiting flowers and the total pollinarium load (Spearman's rank correlation coefficient,  $r_s = 0.39$ ,  $n = 38$ ,  $p < 0.05$ ; Fig. 3). Two of these bees carried a pollinarium loads large enough to be considered statistical outliers (determined using Cook's distance). The correlation is not significant when these two are omitted ( $r_s = 0.30$ ,  $n = 36$ ,  $p > 0.05$ ).

We found no correlation between the numbers of pollinaria that bees carried on the mouth parts and either the absolute number of flowers visited ( $r^2 = 0.015$ ,  $p = 0.54$ , data not shown) or the percentage of flowers that bees visited per inflorescence ( $r^2 = 0.001$ ,  $p = 0.88$ , Fig. 4). Bees typically visited between two to four open flowers per inflorescence





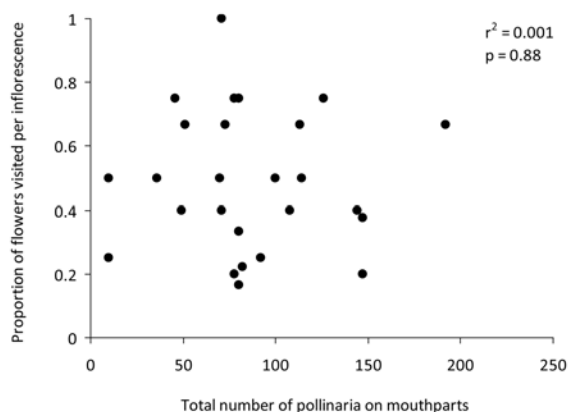
**Fig. 3** There is no correlation between the time that honey bees spent visiting each flower and the total pollinarium load of bees when two outliers (open circles) are excluded.

(median = 2 flowers visited,  $n = 27$ ) and rarely visited all open flowers regardless of the number of pollinaria they were carrying.

### Pollinarium removal, pollinia deposition and pollen transfer efficiency

Pollinarium removal and pollinium deposition rates were high at all three study sites. On most sampling dates during 2007 and 2008 the percentage of flowers with pollinaria removed exceeded 40%. Pollen deposition was lower than pollinarium removal on all sampling dates (Table 2).

Pollination success varied at different times in the flowering season for the population at Kenton-on-Sea (Fig. 5). Pollinarium removal and deposition ranged between 22.6 and 79.6% and 7.5% to 76.4%, respectively, resulting in relatively high PTE (range = 5% - 48%; Fig.



**Fig. 4** There is no correlation between the proportion of flowers that honey bees visited per inflorescence and the total pollinarium load carried by each honey bee.

5). The average PTE across all dates at Kenton-on-Sea was 35.7%, which is high given that the maximum value that this species may achieve is 50%, a limitation imposed by the stigmatic chamber only accommodating one pollinium (i.e. flowers may export 10 pollinaria but can only receive five; Fig. 1C).

### Nectar measurements

The average nectar concentration of flowers from Grahamstown was 31.16% sucrose equivalents (SE = 4.60,  $n = 19$  flowers, 12 plants) and the average volume was 0.83  $\mu\text{l}$  (SE = 0.50,  $n = 38$  flowers, 5 plants).

### Discussion

A diverse suite of insects visit *C. ellipticum*, although at our study sites honey bees (*Apis mellifera*) were the primary pollinators. Honey bees visiting *C. ellipticum* accumulate large pollinarium loads on their mouth parts, but the typical masses of pollinarium loads observed ( $< 150$ ) have little detectable impact on their foraging behaviour. However, a few honey bees carrying exceptionally large pollinarium loads did spend longer periods visiting individual flowers. This was surprising as we expected flower handling times to increase as a consequence of the large pollinarium loads frustrating the foraging behaviour of honey bees, as has been reported for bumblebees and hawkmoths foraging on asclepiads and orchids respectively (Morse 1981; Johnson and Liltved 1997).

Pollinarium accumulation has been reported previously in the Asclepiadoideae (Frost 1965; Morse 1981; Coombs et al. 2009; Weimer et al. 2011), but is particularly conspicuous in *Cynanchum ellipticum*. There may be several advantages to such pollinarium chaining in *C. ellipticum*. Firstly, adaptations promoting the linkage of individual pollinaria to other pollinaria may increase the amount of pollen removed by pollinators by increasing the number of attachment sites to pollinators. Secondly, larger pollen loads on pollinators may increase the chances of subsequent

**Table 2** Percentage of *C. ellipticum* flowers with pollinaria removed, pollinia deposited as well as Pollen Transfer Efficiency (PTE) on different sampling dates at three different sites.

Location	Date	Number of plants (no. of flowers)	Percentage of flowers with pollinaria removed	Percentage of flowers with pollinia deposited	PTE (%)
Grahamstown	02 April 2007	19 (57)	52.6	49.1	39.7
Grahamstown	17 March 2008	22 (64)	62.5	46.0	28.0
Grahamstown	29 March 2008	30 (87)	82.8	71.3	40.5
Grahamstown	14 April 2008	31 (92)	87.0	79.3	42.4
Port Alfred	11 April 2007	42 (126)	27.8	15.1	25.5
Port Alfred	16 May 2008	32 (96)	41.7	31.3	32.1
Kenton-on-Sea	04 April 2007	48 (144)	45.1	25.7	18.1

pollinarium attachment to pollinators, which could explain the large pollinarium loads carried by honey bees as well as the high levels of pollinarium removal, deposition and PTE found in our study. The adaptive significance of pollinarium chaining in asclepiads remains unknown. While pollinarium chaining may function to increase the number of pollinaria carried by pollinators in this species the absence of pollinarium chaining in most asclepiad genera and indeed in other species of *Cynanchum* indicates that there may be many constraints to the evolution of this trait.

The weight of maximum pollinarium load that was recorded in this study was only 1.62mg. It has been demonstrated previously that honey bees can carry pollen loads of other plants totalling 15 mg (Fukuda et al. 1969 cited in Wolf et al. 1989; Winston 1987 cited in Feuerbacher et al. 2003) and nectar loads of up to 40 mg (von Frisch 1965, cited in Wolf et al. 1989). The foraging times of bees with pollinarium loads up to *ca.* 150 pollinaria were of similar duration to that of lightly loaded bees. The small weight that pollinarium loads add to a honey bee is insufficient to affect foraging behaviour either through weighing bees down or physically hampering their handling of flowers while probing for nectar. This is supported by Schmid-Hempel (1986) who showed honey bees could forage while bearing several small weights each weighing 7 mg. By comparison, even exceptionally large pollinarium loads of *C. ellipticum* would only weigh approximately 2 mg extrapolated from the maximum pollinarium load of 224 pollinaria. Larger pollinarium loads may either be groomed off or excessively large chains may be limited by breaking under its own weight. Grooming behaviour was observed on several

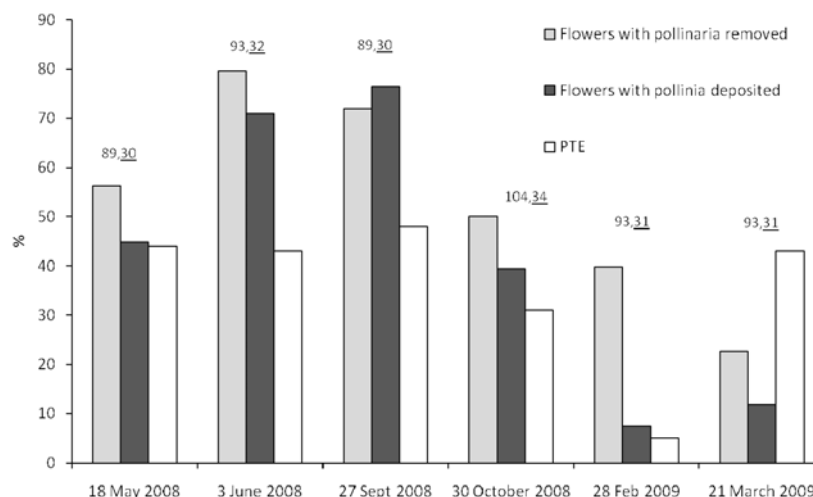
occasions, although the frequency of this behaviour was not quantified.

Estimates of pollen removal, deposition and PTE in *C. ellipticum* were high and, for PTE, frequently approached the maximum values, indicating that loading pollinators with long chains of pollinaria may have fitness benefits for the plants in the absence of any impacts on pollinator behaviour. Rates of pollinarium removal, deposition and PTE varied stochastically throughout flowering season, similar to that seen in the invasive species *Araujia sericifera* (Coombs and Peter 2010) but not in an orchid (Peter and Johnson 2009). Pollination success may also vary between different sites in some asclepiad species (Shuttleworth and Johnson 2006). While the PTE of *C. ellipticum* was high in comparison to many other species (cf. Harder and Johnson 2008), higher levels of pollination success have also been reported in other *Cynanchum* species. For instance, Wolff et al. (2008) report PTE of 73.7 % in *Cynanchum harlingii* in Ecuador.

The pollinaria of many asclepiads and orchids undergo re-configuration once removed from the flower as a mechanism to limit geitonogamous self-pollination (Peter and Johnson 2006). There is no evidence of a reconfiguration mechanism in *C. ellipticum* and this fact, combined with the high levels of PTE, indicates that this species may be at risk of geitonogamous self-pollination or rely on an as yet undiscovered mechanism to prevent self-pollination. Harder and Barret (1995) demonstrated that geitonogamous self-pollination increases with increased floral display sizes and highlighted the inherent tradeoffs between increased pollinator attraction and increased self-pollination in



**Fig. 5** Changes in the percentage of flowers with pollinaria removed, flowers with pollinaria deposited and pollen transfer efficiency (PTE, see methods for explanation) in flowers of *C. ellipticum* sampled on different dates at Kenton-on-Sea. Numbers above bars represent number of flowers and plants (underlined) sampled.



such rewarding hermaphrodite species. While male fitness may benefit from continued pollinaria removal that results from pollinarium chaining in this species, it remains to be seen how this pollinarium massing impacts female function in *C. ellipticum*.

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