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The breeding system of Watsonia knysnana (Iridaceae): An assessment of pollinator effectiveness

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Ongoing debate about specialisation vs generalisation in plant–pollinator interactions highlights the reliability of pollination syndrome traits as predictors of the primary pollinator of a species. The South African Watsonia knysnana (Iridaceae) is a case in point as its tubular corolla is consistent with ornithophilous floral traits to attract sunbirds (specialist nectarivore passerines) but the range of colours exhibited covers syndromes that would predict both birds and insects. From exclusion experiments we identified sunbirds as the most effective pollinators of W. knysnana with honeybees playing a minor role, if any. In addition, the nectar properties (concentration and volume) conform to plants pollinated mainly by specialist nectarivorous birds.

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1. Introduction

For many years pollination biologists have debated the degree of specialisation in plant–pollinator relationships (Waser et al., 1996; Ollerton, 1996, 1998). This is due mainly to the widespread idea that interactions between plant and animal pollinators tend to be specialised (Darwin, 1862; Stebbins, 1970). Specialisation includes the concept of "pollination syndromes" (van der Pijl, 1961). These are suites of floral traits (morphology, colour, nectar or odour) that represent adaptations to attract specific pollinators to particular flowers and optimise successful pollen transfer. In theory, these floral traits also exclude non-specific visitors that would feed on the floral reward without achieving pollination (van der Pijl, 1961).

Nevertheless, Ollerton (1998) warned against the assumption that pollinator identity is invariably predictable from an analysis of the pollination syndromes, based on findings by him and other pollination ecologists (e.g. Herrera, 1996; Waser et al., 1996) that highlighted an interesting paradox: flowers showing specialised floral traits are frequently visited by a wide taxonomic range of pollinators variable in time. According to Waser et al. (1996), this paradox can be explained if only a small proportion of the visitors are effective pollinators (Schemske and Horvitz, 1984), if the visitors are functionally similar and impose the same selective pressure (Waser, 1998), or if selection has operated only at certain times in the past (Ollerton, 1996). Besides, some studies have shown interspecific competition to access the same reward (nectar) produced by a plant, such as a pollinator displaced by another with physical aggressions (Tropek et al., 2013; Ollerton and Nutterman, 2013; Padyšáková et al., 2017).

Not all floral visitors play the same roles in the fitness of the plant (Padyšáková et al., 2013; King et al., 2013) and sometimes the main pollinator predicted by pollination syndromes is not the most efficient (Coetzee and Giliomee, 1985; de Merxem et al., 2009). This can also vary between seasons and populations (Herrera, 1988; Brown et al., 2011). The efficiency of pollinators depends on many factors, including the frequency of visits, but a visitation does not necessarily imply successful pollination (Johnson and Steiner, 2000; Fenster et al., 2004). The success of pollen transfer between flowers of the same species is determined by the amount of pollen transported and the composition of the pollen load (Sugden, 1986). Surprisingly, Castellanos et al. (2003) have shown that hummingbirds and bumblebees have similar per-visit pollen transfer efficiencies when visiting Penstemon strictus Bentham (Plantaginaceae), a bee–syndrome plant. This demonstrates that in some instances individual floral traits may function to attract different taxa and allow them to be equally efficient pollinators.

Although the reliability of pollination syndromes in predicting the main pollinator has been questioned over the past few years (Waser et al., 1996; Herrera, 1996; Ollerton, 1998; Johnson and Steiner, 2000; Ollerton et al., 2009), some pollination syndromes are well established and studied, e.g. bat pollination, long-proboscs fly pollination, moth pollination, wasp pollination, and their validity refutes the ongoing syndrome debate (Fenster et al., 2004), and support for the syndromes concept is recognised (Rosas-Guerrero et al., 2014).

In this study we investigate an example of the bird pollination or “ornithophily” syndrome, which is characterised by robust, often red- and mostly odourless flowers that are tubular in form, and produce large volumes of dilute nectar. These floral traits are directly linked to...
attract and reward specialised nectar feeding birds (Faegri and van der Pijl, 1979; Johnson and Nicolson, 2008). The pollination biology of southern South Africa Iridaceae has been relatively intensively studied, and the family is one of the best understood in the region (Goldblatt and Manning, 2006; Geerts and Pauw, 2009). The genus Watsonia Mill. is a notable exception, with only a few published studies being done (Geerts and Pauw, 2009; Goldblatt et al., 1999). Several species of Watsonia have orange or red flowers with a long cylindrical upper perianth, usually associated with bird pollination syndromes. Watsonia knysnana L. Bolus, however, has tubular flowers that are only rarely scarlet in colour and are more usually pale pink to purple, (Goldblatt, 1989), colours normally associated with insect pollination (Keveran and Baker, 1983; Barth, 1985).

Although sunbirds have been observed feeding on the flowers of W. knysnana (Brown, personal observations), specialist nectarivores may visit non-ornithophilous flowers as well. Hummingbirds, for instance, are known to visit a wide range of flowers, regardless of floral morphology or colour (Snow and Snow, 1972; Waser and Price, 1981). In Africa, sunbirds can also feed on both morphologically adapted and non-adapted inflorescences (Pauw, 1998; Mann and Cheke, 2010; Jančák et al., 2012; Heystek et al., 2014), although they are not always the primary pollinator (Brown et al., 2009; Padyšáková et al., 2013) of the latter.

The breeding system of the W. knysnana is relevant in this context as the flowers combine ornithophilous morphology with entomophilous colouration. In view of the fact that the interactions between sunbirds and plants includes signs of both ecological specialisation and generalisation, we sought to determine the importance of bird pollinators to the reproduction of W. knysnana. We hypothesised that sunbirds would be the main pollinators, based on floral morphology, despite observations of a range of insects and specialist nectar feeding birds on W. knysnana (Brown & Whitehead, unpublished data). We conducted field observations to determine which taxa visit and feed on W. knysnana, and then assessed the effect of exclusion of birds and/or insects on fruit set and seed production. We also quantified the nectar volume and concentration in order to compare it with other sunbird pollinated species (Johnson and Nicolson, 2008).

2. Material and methods

2.1. Study site and study species

Two sites with natural populations of W. knysnana were used for this study, one along the Groot River pass (Western Cape) and another along the R102 near Coldstream (Eastern Cape) in the southern Tsitsikamma Mountains (33°57′41″S; 23°41′16″E and 33°58′19″S; 23°44′33″E). Both sites are located in the Fynbos biome, defined as an evergreen, hard-leaved shrubland occurring on nutrient-poor soils in the Western, Eastern and Northern Cape provinces of South Africa.

The study species, Watsonia knysnana, is a cormous geophyte 1.2–1.6 m high, growing in dry situations on well-drained rocky upper mountain slopes, as well as more grassy sites (Goldblatt, 1989; Manning, 2009; Manning and Goldblatt, 2012). The flowers are zygomorphic and organised in a 2-ranked spike inflorescence with the tepals joined into a narrow tube 30–45 mm long but with free tepal tips (Fig. 1A). Perianth colour varies from bright red or purple to pale pink (Fig. 1B), and the anthers and the pollen are violet. Nectar is produced and is secreted directly into the base of the floral tube. Flowering normally takes place in the beginning of summer, from October or November to January but flowering in 2017/2018 was slightly delayed, plants only started to bloom in December until the middle of February.

2.2. Observation sessions

Observations on floral visitors to W. knysnana were made on the two natural populations located along Coldstream Route between the 10 January and the 5 February 2018 at three different times of the day. 6 h00–8 h00, 11 h00–13 h00 and 15 h00–17 h00. Observations were made over 6 days per population when it was not raining. The first hour of each session was dedicated to bird observations with the use of binoculars at a distance of 10–15 m from the patch in order to minimise disturbance of the birds. The second hour was dedicated to observing insects, with the observers situated at 1 or 2 m close to the flowers to reduce insect disturbance.

The number of plants visited by each bird feeding on the flowers or insect visitors seen at the site was counted, and time spent at each plant was recorded. Floral visitors were identified to species as far as possible. The sunbirds were not ringed, so it was not possible to identify them individually. Each floral visit to the patch of W. knysnana was recorded as a separate visitation.

2.3. Flower morphology and nectar properties

Plants were randomly selected for morphological measurements, including flower length (measured from bract to point where perianth separates itself into tepals, curvature taken into account) and width (measured where perianth separates into tepals). These measurements were taken to show homogeneity in morphology between flowers randomly chosen for 24 h nectar and standing crop nectar measurements. Nectar characteristics (volume and concentration) were measured as standing crop from 116 flowers between the 18 January and the 6 February 2018 (“standing crop”). Nectar availability in open flowers, from which animal visitors were excluded for 24 h, was measured for 68 flowers (“24 h crop”), and was in most cases sampled in the morning. Flowers sampled were chosen arbitrarily from each inflorescence from portions with flowers at the developmental stage during which they are visited by birds (determined by visual observation). Volume of nectar was determined with 5 μl capillary tubes and concentration with a handheld refractometer (Bellingham and Stanley, Tunbridge Wells, UK). Measurements were conducted only along the Coldstream Route site as this population had more flowers available for sampling.

2.4. Pollinator effectiveness

To determine the effectiveness of various groups of pollinators, two exclusion experiments (see Brown et al., 2009, Brown et al., 2010a; Wilson et al., 2009 for details) were performed along both Groot River Pass (33°57′37″S; 23°31′44″E) and Coldstream Route (33°58′19″S; 23°44′33″E) sites. Before the buds opened, mosquito-netting exclusion bags were placed on 10 inflorescences to exclude all pollinators (“Bagged” condition), and plastic mesh (aperture diameter of 12.5 mm) bird exclusion cages were placed over an additional 10 inflorescences (“Caged” condition). After the flowering finished, fruit set and seed set were determined for both these groups, in addition to natural fruit (Fig. 1F) and seed set were taken from 10 unmanipulated control inflorescences (“Open” condition). Fruits were measured and those smaller than 5 mm were excluded from the count as they proved very difficult to open and assess seeds. Seeds that are potentially aborted can potentially differ visually from those that are fully viable, with viable seeds being plumper and larger in size compared to smaller and shrivelled-looking unviable seeds (Turner et al., 2012). Viable and non-viable seeds were discriminated visually: viable seeds are 0.5–1 mm thick and 2–4 mm long in size whereas non-viable seeds are flat and less than 2 mm long (Angoh et al., 2017).

2.5. Statistical analyses

All statistical analyses were executed with RStudio© version 1.1.383 (R Core Team, 2016). Homoscedasticity and normality was first tested before doing the statistical tests. The estimated time spent on the patch and the number of plants visited by insects and sunbirds were compared with a Mann–Whitney test.
The percentages of fruits set between the conditions Open, Caged and Bagged were compared with a Kruskal–Wallis test followed by a Pairwise post-hoc test (p-value adjustment method: holm). The length of fruit and the number of seeds (plus viable and non-viable) per fruit were also compared with the same tests between the conditions Open, Caged and Bagged.

The results of nectar properties (volume and concentration) in standing crop and 24 h crop were analysed with Mann–Whitney tests.

### 3. Results

#### 3.1. Estimation of pollinator effectiveness in the field

During the observation sessions, more insects were observed than sunbirds (Table 1). During 30 h total time spent in the field, four species of sunbirds were identified feeding on *W. knysnana*: Malachite sunbird (*Nectarinia famosa*, *n* = 9), Greater double-collared sunbird (*Cinnyris afer*, *n* = 3), Amethyst sunbird (*Chalcomitra amethystina*, *n* = 30) and Southern double-collared sunbird (*Cinnyris chalybeus*, *n* = 11).

Among insects, positive identifications were possible for honeybee (*Apis mellifera*, *n* = 278), carpenter bee (*Xylocopa flavorufa*, *n* = 8)

|             | Sunbirds | Insects | p-value |
|-------------|----------|---------|---------|
| n           |          | 53      | 329     |
| Number of species or taxa observed | 4        | 5       |         |
| Time (s) spent per individual on the patch | 96.17 ± 10.15 | 91.82 ± 5.13 | 0.09 |
| Number of plants visited | 7.32 ± 0.75 | 4.11 ± 0.19 | <0.0001 |

Symbols represent mean ± standard errors (except for *n* and Number of species or taxa observed).
and horsefly (*Philoliche* spp, *n* = 23). Unnamed species included a few individuals of beetles (*Coleoptera*, *n* = 5) and solitary bees (possibly *Megachile chrysorrea* or *Ceratina nasalis*, *n* = 15). Ants (probably *Streblognathus aethiopicus*) were abundant and present inside the flowers. The Green-banded swallowtail butterfly (*Papilio nireus lyaeus*) was occasionally observed feeding on inflorescences.

Individual sunbirds and insects spent the same amount of time foraging on *W. knysnana* (*Coldstream*). (Table 1, Mann–Whitney test: *W* = 10,014, *p*-value = .09) However, sunbirds visited a greater number of plants during this time than insects (Table 1, Mann–Whitney test: *W* = 11,806, *p*-value < .0001).

Some honeybees only fed on the bracts of flowers. They were also observed feeding on the anthers (Fig. 1G) and some of them went inside the tubular perianth to drink the nectar. In comparison, sunbirds were seen drinking nectar from flowers and therefore made contact with the reproductive parts of the flowers (anthers and stigma) (Fig. 1E).

### 3.1.1. Pollinator effectiveness

#### 3.1.1.1. Fruit set and length. Pollinator exclusion significantly reduces fruit set of *W. knysnana* (*Kruskal–Wallis* test, chi-squared = 18.887, df = 2, *p*-value < .0001). Open inflorescences set significantly more fruits than both Bagged and Caged inflorescences (Fig. 2: Pairwise Wilcoxon test, *p*-value < .0001). There was no difference in seed set between Caged and Bagged inflorescences (Fig. 2: Pairwise Wilcoxon test, *p*-value = .12).

Fruit length is significantly different in each condition (Fig. 3: *Kruskal–Wallis* test, chi-squared = 91.599, df = 2, *p*-value < .0001). Open inflorescences produce longer fruit than both Caged (Pairwise Wilcoxon test, *p*-value < .0001) and Bagged inflorescences (Pairwise Wilcoxon test, *p*-value = .00026) (Fig. 3), with Bagged plants producing the smallest fruit.

#### 3.1.1.2. Effective seed production. Seed production is reduced by pollinator exclusion (*Kruskal–Wallis* test, chi-squared = 50.553, df = 2, *p*-value < .0001). The inflorescences in the control condition (Open) set significantly more seeds per fruit than Caged and Bagged inflorescences (Fig. 4: Pairwise Wilcoxon test, *p*-value < .0001). Excluding all pollinators (Bagged) has the same effect on seed production as does the exclusion of birds only (Caged) (Fig. 4: Pairwise Wilcoxon test, *p*-value = .83).

The exclusion of pollinators reduces the number of viable seeds per fruit (Fig. 5A: *Kruskal–Wallis* test, chi-squared = 91.437, df = 2, *p*-value < .0001; Fig. 5B: *Kruskal–Wallis* test, chi-squared = 71.759, df = 2, *p*-value < .0001). Open inflorescences set significantly more viable seeds than Bagged and Caged inflorescences (Fig. 5A: Pairwise Wilcoxon test,
There is no significant difference between Caged and Bagged fruits (Fig. 5A: Pairwise Wilcoxon test, p-value = .28).

Non-viable seeds are more abundant in fruits when all pollinators are excluded (Bagged flowers) than when birds are ruled out (Caged flowers) (Fig. 5B: Pairwise Wilcoxon test, p-value = .03), and even more when compared with the control condition (Open flowers, Pairwise Wilcoxon test, p-value < .0001) (Fig. 5B). Caged inflorescences set less viable seeds than Open inflorescences (Fig. 5B: Pairwise Wilcoxon test, p-value < .0001).

3.1.2. Flower morphology and nectar properties

*Watsonia knysnana* has a narrow perianth tube about 41 mm long (Table 2).

Nectar volume per flower differs significantly between Open and Bagged inflorescences (Table 2: Mann–Whitney test, W = 3829.5, p-value < .0001): the mean nectar available after being bagged for 24 h is 6.99 μl, which is significantly higher than the standing crop in Open flowers (we infer that open flowers accessible to birds had been visited) (0.88 μl).

Nectar concentration is relatively dilute, averaging 19–21% w/w (Pyke and Waser, 1981) and is not significantly different between Open and Bagged inflorescences (Table 2: Mann–Whitney test, W = 1702, p-value = .10).

4. Discussion

Although insects, especially honeybees and Tabanids, were the most common visitors observed on *W. knysnana* (Table 1), our study shows that sunbirds are the most effective pollinators of *W. knysnana*, confirming our prediction based on floral traits.

Sunbirds visit a greater number of flowers within a patch over the same period than insects (Table 1). Because the anthers of *W. knysnana* are exserted from the perianth, the pollen loads are brushed onto the crown feathers and the bill of the sunbird during a visit when the bird probes the corolla tube for nectar (Fig. 1E, personal observation). Geerts and Pauw (2009) separated sunbirds into two groups, those with a long narrow curved bill (e.g. Malachite sunbird) and those with a short narrow curved bill (e.g. Southern double collared sunbird), and showed that the plant species that they pollinate differed significantly in floral tube length. *Watsonia knysnana* is visited by sunbirds belonging to both groups (Table 1). Geerts and Pauw (2009) also show that short bill sunbirds often robbed the nectar from long tube flowers (35 mm...
and more) by piercing the corolla. We noted such robbing holes on *Watsonia knysnana* flowers but did not record actual robbing events during our observations (although Carpenter bees have been recorded feeding on *Watsonia knysnana* in this way too – Brown unpubl. observations) and all recorded visits by sunbirds appeared to be legitimate feeding visits. It is possible that the long corolla of *Watsonia knysnana* (Table 2) prevents short bill sunbirds from reaching all the nectar in some or all cases although access to nectar is not determined simply by bill length as the bird's tongue extends some way beyond the bill (Geerts and Pauw, 2009). One possibility we did not investigate, was whether moth visitations occurred at night.

The exclusion experiments support the hypothesis that sunbirds play a major role in pollination of *Watsonia knysnana* at Coldstream Route (Table 1). It is likely our inclusion cages prevented larger species like *Xylocopa flavofurca* or *Papilio nireus*, but observation rates were low for these species anyway, and all observations of *Xylocopa flavofurca* feeding involved nectar robbing, so likely the cage set data represents a bird exclusion scenario quite effectively. The absence or presence of insects does not significantly affect fruit set (Fig. 2), number of seeds per fruit (Fig. 4), or number of viable seeds per fruit (Fig 5A). However, Wilson et al. (2009) have demonstrated that site can influence pollinator success, raising the possibility that the relative role of bees in pollination of primary bird-pollinated plants can vary from one site to another. Additional exclusion experiments need to be conducted on other *Watsonia knysnana* populations to confirm the relative importance of bee-pollination in this species. Indeed, Wilson et al. (2009) show that in the bird pollinated *Aloe pruinose* Reynolds, bees contribute substantially towards reproductive output at some sites. Nevertheless, the inflorescences allowing bird visitation in *Watsonia knysnana* had the highest fruit set (Fig 2, about 70%), the longest fruits (Fig. 3) and the most viable seeds per fruit (Fig. 4, Fig. 5A), demonstrating that sunbirds are the most effective pollinators of *Watsonia knysnana* in the populations that we have studied.

Some seed set in Bagged inflorescences indicate that *Watsonia knysnana* may be able to self-pollinate, but fitness seems reduced compared to the Caged trials as the fruit are shorter (Fig. 3) and contain more non-viable seeds (Fig 5B). Tung (1987) has shown that when *Zama pumila* L. (Zamiaceae) is deprived of its main pollinators (beetles) it produces no viable seeds. Similarily, excluding sunbirds in the Caged and Bagged conditions reduces viable seed set in *Watsonia knysnana* (Fig 5A).

In several other southern African plants with ornithophilous floral traits insects have been shown to contribute less than sunbirds to seed set (*Brown et al., 2009, Brown et al., 2010b; 2011; Whitehead, 2018*) but unlike *Watsonia knysnana*, these plant species are not self-compatible. These results suggest that *Watsonia knysnana* may be a strong pollination specialist, and reinforce the proposition by Bond (1994) that facultative self-pollination is one of the compensatory mechanisms in plants with highly specialised pollination systems, allowing a population to survive and breed without its mutualist partners.

*Watsonia knysnana* produces a nectar that is similar in volume (about 7 μl in 24 h crop) and concentration (about 20% w/w) (Table 2) to that produced by other flowers pollinated by specialist nectar feeding birds (*Johnson and Nicolson, 2008; Pyke and Waser, 1981*), and relatively dilute compare to bee pollinated flowers (36% w/w) (Pyke and Waser, 1981). Although sugar type has not been studied in this present work, Johnson and Nicolson (2008) have shown that species pollinated by specialist nectarivores tend to produce sucrose rich nectar, whereas those pollinated by generalist nectarivores tend to have hexose rich nectar. Sunbirds are specialist passerine nectarivores and appear to be the main pollinators of several *Watsonia* species (Goldblatt et al., 1999). We can therefore suppose that *W. knysnana* is more likely to produce a sucrose dominant nectar even though different species of *Watsonia* produce either sucrose-dominant or hexose-dominant nectars (Goldblatt et al., 1999). The significant difference of nectar volume between the standing and the 24 h crop measurements (Table 2) indicates that there is a very high visitation rate in the two populations of *W. knysnana* in this present study.

### 5. Conclusion

Our observations confirm that *Watsonia knysnana* is specialised for bird pollination. Despite criticisms about the reliability of the pollination syndromes to predict the main pollinators (*Waser et al., 1996; Herrera, 1996; Ollerton, 1998; Ollerton et al., 2009; Johnson and Steiner, 2000*), they provide great utility in understanding the mechanisms of floral diversification and highlight the floral traits on which they exert selection pressures (Fenster et al., 2004). We accept our hypothesis that the main pollinator based on the ornithophilous traits exhibited by *Watsonia knysnana* is sunbirds. The reason why it exhibits colour polymorphism remains unclear, as sunbirds, honeybees and Tabanids were all observed feeding on white–pink–purple flowers of *Watsonia knysnana*.

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