The Role of Beetle Marks and Flower Colour on Visitation by Monkey Beetles (Hopliini) in the Greater Cape Floral Region, South Africa

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INTRODUCTION

Convergent evolution has resulted in the recurrent development of the same suites of floral characteristics among different plant taxa that are pollinated by the same guild of pollinators (Faegri and van der Pijl, 1979). The value of floral syndromes as predictive tools is still relatively poorly tested and in some instances cannot be substantiated (e.g. Hingston and McQuillan, 2000; Ollerton et al., 2003; Zhang et al., 2005; Valdivia and Niemeyer, 2006). Among families dominated by specialist pollination systems, however, such as Iridaceae in southern Africa, pollination syndromes are more often diagnostic and still form the basis from which much of our understanding of pollination systems is inferred (Goldblatt and Manning, 2006).

Beetles were among the earliest pollinators of angiosperms, and plants that rely on these insects for pollination have classically been characterized by dull-coloured, chamber- or urn-shaped flowers with a strong, often unpleasant scent (Faegri and van der Pijl, 1979). In typical cantharophilous species, scent production is often stressed over pigmentation (Dafni et al., 1990). A striking deviation from the classical beetle pollination syndrome is found in the eastern Mediterranean region, where species of Anemone and Ranunculus (Ranunculaceae), Papaver (Papaveraceae) and Tulipa (Liliaceae) are pollinated mainly by Amphicoma scarab beetles. These plants have undergone convergent evolution for bright red, bowl-shaped flowers with a dark centre (Dafni et al., 1990). A remarkably similar syndrome is found in plants of the Greater Cape Floral Region of South Africa, which are pollinated by another group of scarab beetles known as monkey beetles (Scarabaeidae: Rutelinae: Hopliini). Plants that rely on these insects for pollination typically produce odourless, brightly coloured, shallowly bowl-shaped flowers or inflorescences (Goldblatt et al., 1998). In addition, many of these species have conspicuous dark (sometimes pale) markings known as beetle marks at the base of the tepals or petals, which give the flowers (or inflorescences) a dark or contrarily coloured central zone or eye (Fig. 1). Beetle marks have evolved in taxa in numerous different genera, particularly in the Asteraceae and Iridaceae (Picker and Midgley, 1996; Goldblatt et al., 1998).

By using model flowers, Dafni et al. (1990) demonstrated that the Amphicoma scarab beetles that are the major pollinators of this system in the Mediterranean display a distinct preference for red flowers with dark centres over other coloured flowers without dark centres. A more generalized attraction for beetles by dark markings has also been demonstrated in England, where the addition of ink spots...
to flowers of *Brassica napus* (Brassicaceae) increased visitation by the pollen beetle *Meligethes aeneus* (Free and Williams, 1978). Futhermore, mordelid beetles prefer inflorescences of *Daucus carota* with dark central florets over ones without dark florets in its non-native range in eastern North America (Westmoreland and Muntan, 1996). Such an effect was, however, not found for *Daucus carota* in its native range in Europe (Lamborn and Ollerton, 2000). Overall, these studies indicate that dark markings are used as visual cues by several groups of beetle species.

Although the convergent evolution of beetle marks suggests that they are adaptive, their exact role in floral function remains incompletely understood. Hutchinson (1946) suggested that the beetle marks on the ray florets of *Gorteria diffusa* mimic herbivorous beetles and thus function as repellents to such beetles. In a test of Hutchinson’s hypothesis, Midgley (1993) found no evidence that artificial addition of beetle marks to unmarked inflorescences of another species of Asteraceae repelled herbivorous monkey beetles. Because monkey beetles often carry significant quantities of pollen on their hairy bodies, Midgley (1993) suggested that it is more likely that beetle marks play a role in attracting monkey beetles as potential pollinators rather than deterring them. This is also likely to apply to many other plant species with beetle marks in the Greater Cape Floral Region. Monkey beetles, which feed on the pollen and also use the flowers as mating sites, have been identified as effective pollinators of many species with beetle marks (Fig. 1B; Goldblatt et al., 1998).

The effect of beetle marks on visitation by monkey beetles in the south-western part of the Greater Cape Floral Region was tested by Johnson and Midgley (2001) using artificial model flowers with and without dark markings. Although their study revealed slightly higher visitation rates of monkey beetles on model flowers with dark centres, this effect was not significant. There are, however, more than 200 species of monkey beetles in the Greater Cape Floral Region (Péringuey, 1902; Steiner, 1998), and their assemblages can differ considerably between areas within this region (Colville et al., 2002). Johnson and Midgley’s (2001) study was carried out on the Cape Peninsula, which is not known for its high incidence of plants with beetle marks. It is likely, therefore, that the role of beetle marks may be more pronounced in other areas within the Greater Cape Floral Region, particularly those with high concentrations of beetle flowers or which are known regions of monkey beetle diversity.

Therefore the experiments of Johnson and Midgley (2001) were repeated here on the Bokkeveld Escarpment, which is a centre of monkey beetle diversity in the Greater Cape Floral Region (Péringuey, 1902; Colville et al., 2002), by using arrays of plain coloured model flowers and marked model flowers to test the effect of beetle marks on monkey beetle visitation rates. The model flowers were positioned in populations of three differently coloured species of Iridaceae that are known to be pollinated by monkey beetles: *Hesperantha vaginata*, *Romulea monadelpha* and *Sparaxis elegans* (Fig. 1). Because flower colour itself may also play an important role in attracting monkey beetles (Picker and Midgley, 1996; Johnson and Midgley, 2001; Colville et al., 2002), model flowers of different colours were used to test whether monkey beetles showed a preference for the colour of the matrix species.

**MATERIALS AND METHODS**

**Study area and matrix species**

The study was performed in 2002 in Northern Cape Province, South Africa, in nature reserves around Nieuwoudtville (31°22’S, 019°07’E) on the Bokkeveld Escarpment. The study area is situated on the border between Namaqualand and the Cape Floral Region, both of which form part of the Greater Cape Floral Region (Born et al., 2007), and is known as a centre of monkey beetle diversity (Péringuey, 1902; Colville et al., 2002). The experiment (see below) was performed in populations of three species of Iridaceae known to be pollinated by monkey beetles (Goldblatt et al., 1998). *Hesperantha vaginata* (Sweet) Goldblatt has bowl-shaped, yellow flowers with dark brown spots and a dark centre (Fig. 1A, B), and occurs on heavy clay soils derived from dolerite; *Romulea monadelpha* (Sweet) Baker has bowl-shaped, red...
flowers with a dark centre (Fig. 1C), and occurs on doleritic clays; and *Sparaxis elegans* (Sweet) Goldblatt has shallowly bowl-shaped, orange flowers with yellow spots on a black ring (Fig. 1D), and occurs on lighter clay soils derived from tillite. All species flower between early August and late September.

**Experimental set-up**

Experimental methodology largely followed that of Johnson and Midgley (2001). Cone-shaped model flowers of different colours were constructed from orange, red and yellow cardboard, with an external diameter of 5 cm and a central opening 2 cm in diameter. Model flowers were taped onto empty film canisters (3 cm in diameter and 5 cm high) that functioned as traps. Model flowers of each colour were marked with three types of patterns, developed to match commonly encountered natural floral marking patterns (see x-axis of Fig. 2) as follows: (1) unmarked model flowers were mounted on a translucent film canister, thus with a pale centre; (2) model flowers with six dark spots (7 mm diameter) at regular intervals at a distance of 5 mm from the edge of the central opening were mounted on a translucent film canister, thus with a pale centre; and (3) model flowers with six dark spots as in (2) above were mounted on a black film canister, thus with a dark centre. Black spots were painted with carbon mixed with a clear acrylic medium. The model flowers were mounted individually on wire stakes inserted in the ground and positioned 10 cm above ground level.

For each colour, two replicate model flowers of each marking pattern type were randomly assigned to positions in rectangular plots (2 × 3 model flowers) with 10 cm between model flowers. Each plot was paired with another plot at 5 m distance that had model flowers of a different colour. Yellow and orange model flowers were positioned in matrices of either yellow *Hesperantha vaginata* flowers or orange *Sparaxis elegans* flowers, and orange and red model flowers were positioned in a matrix of red *Romulea monadelpha* flowers. Pink or blue model flowers were not used because the guild of monkey beetles that visit flowers with these colours are poorly represented at Nieuwoudtville (Colville et al., 2002). The paired plots were replicated five or eight times on the same site or on the same date, and paired plots were >40 m apart. Each of these experiments was repeated at the same site on five days (25, 27 and 28 August, and 6 and 7 September, 2002) for the *H. vaginata* matrix, on four days (24, 25, 27 and 28 August, 2002) for the *R. monadelpha* matrix, and at six sites (two sites per date; 24, 26 and 27 September, 2002) for the *S. elegans* matrix. These different dates and locations are hereafter referred to as repetitions. A total of 31, 20 and 30 paired plots were used for the *H. vaginata*, *R. monadelpha* and *S. elegans* matrices, respectively. A total of 972 model flowers were used, of which three had to be discarded because of wind damage.

All experiments were conducted on sunny days when monkey beetles are most likely to be active (Goldblatt et al., 1998). The traps (model flowers) were set up during the early morning before the flowers opened, and were collected at the end of the same day after the flowers had closed. For *R. monadelpha* traps were in the
field between $\pm 1100$ and 1645 h; for *H. vaginata* between $\pm 1130$ and 1700 h; and for *S. elegans* between $\pm 1000$ and 1630 h.

The central film canisters of the model flowers were filled with water to prevent escape of visiting monkey beetles. Model flowers were checked at least every 1–2 h to prevent the monkey beetles from drowning. Trapped beetles were released at some distance away (>600 m) from the study site to reduce the chance of re-trapping the same individuals.

For each model flower, the number of each species of trapped monkey beetles was tallied. Beetles were identified by comparison with a reference collection identified by H. Dombrow (Worms, Germany) and J. Colville (University of Cape Town, South Africa).

**Analysis**

The count data on the number of monkey beetles per model flower followed a negative-binomial distribution. The data were therefore analysed with a series of generalized linear models with the negative-binomial distribution implemented in the statistical software Genstat (Lawes Agricultural Trust, IACR, Rothamsted, UK). Data for each of the three matrix species, *H. vaginata*, *S. elegans* and *R. monadelpha*, were first analysed separately to test for effects of ‘colour’ (yellow and orange for *H. vaginata* and *S. elegans*, and orange and red for *R. monadelpha*), ‘dark spots’ and ‘dark centre’, and the interactions of ‘colour’ with ‘dark spots’ and ‘dark centre’. ‘Dark centre’ was first fitted in the model to compare the plain model flowers and those with dark spots and a translucent centre with the model flowers with dark spots and a dark centre. Then ‘dark spots’ was fitted to compare plain model flowers with those with dark spots and a translucent centre. The conclusions remained the same when ‘dark spots’ was fitted before ‘dark centre’. Variation due to ‘replication’ (i.e. date for *H. vaginata* and *R. monadelpha*, and date and location for *S. elegans*), ‘paired plots’ and ‘plots’ was controlled for by including these factors in the model. To test for differences in the effect of marking patterns on monkey beetle visitation between the matrix species, data on all three matrix species were analysed together for the orange model flowers, which were used for all matrix species.

For each factor, ratios of changes in mean deviance (quasi $F$-values) were calculated after adding the factor to the model. Quasi $F$-values approximately follow the $F$-distribution (Payne et al., 2005), enabling us correctly to test differences between colours against variation among plots, and differences between marking patterns (i.e. effects of dark spots and dark centres) against their interactions with ‘replication’. The canonical link function, log ratio, of the negative binomial distribution was used and the aggregation factor was set to one. However, in the analyses of the data of the *S. elegans* matrix and the analysis of all three matrix species together, the model could not be fitted because some of the fitted values predicted by the model were out of the valid range for the applied model. For these analyses, the log-link function was used.

**RESULTS**

In total, 688 monkey beetles belonging to eight species were trapped during the experiment (Table 1). In the *H. vaginata* matrix, the model flowers were visited by three monkey beetle species, of which *Clania glenlyonensis* was by far the most frequent (94·6 %). In the *R. monadelpha* matrix, the model flowers were visited by four monkey beetle species, of which *C. glenlyonensis* again predominated (91·1 %). In these two matrix species, *H. vaginata* and *S. elegans*, beetles showed a clear preference for flowers with dark spots and a translucent centre, while *R. monadelpha* beetles frequented flowers with dark spots and dark centres.

**Table 1. Numbers of different monkey beetle species visiting model flowers in populations of the monkey-beetle-pollinated species Hesperantha vaginata, Romulea monadelpha and Sparaxis elegans**

| Monkey beetle species               | *H. vaginata* | *R. monadelpha* | *S. elegans* |
|-------------------------------------|---------------|-----------------|--------------|
| **Aniscochelus hilaris** Burmeister, 1844 | 1             | 0               | 144          |
| **Aniscochelus inornatus** Burmeister, 1844 | 0             | 0               | 68           |
| **Clania glenlyonensis** Dombrow, 1997 | 243           | 41              | 0            |
| Female                              | 11            | 2               | 0            |
| Male                                | 232           | 39              | 0            |
| **Clania macgregorii** Dombrow, 1997 | 13            | 2               | 0            |
| **Heterochelus bicolar** Dombrow, 2001 | 0             | 1               | 2            |
| Female                              | 0             | 1               | 0            |
| Male                                | 0             | 0               | 2            |
| **Heterochelus pickeri** Dombrow, 1997 | 0             | 1               | 2            |
| Female                              | 0             | 0               | 2            |
| Male                                | 0             | 0               | 0            |
| **Lepithrix freudei** Schein, 1959   | 0             | 0               | 80           |
| **Pachycnema calvini** Schein, 1959  | 0             | 0               | 90           |
| Female*                             | 0             | 0               | 49           |
| Male*                               | 0             | 0               | 41           |
| Total                               | 257           | 45              | 386          |

For dimorphic species, the numbers of female and male beetles are given in italics.

* Females of *P. calvini* might have been mixed up with the morphologically similar females of *P. multiguttata* Thunberg, 1888.
therefore, a single beetle species accounted for the great majority of all visits. In the *S. elegans* matrix, the model flowers were visited by six monkey beetle species, of which *Anisochelus hiliaris* was the most frequent (37.4%), followed by *Pachynema calviniana* (23.3%), *Lepithrix freudei* (20.7%) and *Anisochelus inornatus* (17.6%). In *S. elegans*, therefore, four beetle species together accounted for 99.0% of all visits.

Four of the eight observed monkey beetles in the experiment were dimorphic, allowing us to distinguish easily between females and males (Table 1). Male monkey beetles were the most frequent visitors (82.8%) but this was mainly accounted for by a single species, *C. glenlyonensis* (Table 1).

Monkey beetle visitation rates differed significantly between dates for the *H. vaginata* and *R. monadelpha* matrices and between locations and dates for *S. elegans* (significant ‘reppetition’ effects in Table 2). There was also significant variation among paired plots within the replications for the *H. vaginata* and *S. elegans* matrices, which indicates spatial variation in visitation rate at each location.

Colour of the model flowers had no significant effect on the number of monkey beetles within the *H. vaginata* matrix (149 and 108 beetles in total on yellow and orange model flowers, respectively) and *R. monadelpha* matrix (26 and 19 beetles in total on orange and red model flowers, respectively) but yellow model flowers (284 beetles in total) were visited more frequently than orange model flowers on *S. elegans* matrices and between locations and dates for *L. freudei* (20.7%) and *A. inornatus* (17.6%). In *S. elegans*, therefore, four beetle species together accounted for 99.0% of all visits.

On average, the most monkey beetles per model flower were found in the *S. elegans* matrix, followed by the *H. vaginata* matrix and the *R. monadelpha* matrix (Fig. 2; Table 2). This study is the first to demonstrate experimentally that beetle marks play a role in the attraction of pollinating beetles in the Greater Cape Floral Region. This finding contrasts with a previous similar study by Johnson and Midgley (2001) that found no significant effect of beetle marks on visitation of model flowers by monkey beetles in the southwestern part of the Greater Cape Floral Region, which has a less diverse monkey beetle fauna than the present study.

DISCUSSION

This study was the first to demonstrate experimentally that beetle marks play a role in the attraction of pollinating beetles in the Greater Cape Floral Region. This finding contrasts with a previous similar study by Johnson and Midgley (2001) that found no significant effect of beetle marks on visitation of model flowers by monkey beetles in the southwestern part of the Greater Cape Floral Region, which has a less diverse monkey beetle fauna than the present study.

**Table 2. Summary of generalized linear models based on a negative binomial distribution testing the effects of colour and presence of dark spots and dark centres of model flowers on the number of visiting monkey beetles in populations of *Hesperantha vaginata*, *Romulea monadelpha* and *Sparaxis elegans***

| Effect         | *H. vaginata* matrix | d.f. | Mean deviance | Quasi-*F* | *R. monadelpha* matrix | d.f. | Mean deviance | Quasi-*F* | *S. elegans* matrix | d.f. | Mean deviance | Quasi-*F* |
|----------------|----------------------|------|---------------|-----------|-------------------------|------|---------------|-----------|---------------------|------|---------------|-----------|
| Repetition     | 4                    | 8.3192 | 2.92*         |           | 3                     | 13-7611 | 13.43**       |           | 5                   | 52.4810 | 14.63***       |           |
| Paired plots   | 26                   | 2.8483 | 2.94**        |           | 16                    | 1-0244  | 1.40          |           | 24                  | 3.5884  | 3.06**        |           |
| Pairs          | 2                    | 2.9412 | 1.23          |           | 1                     | 0.7463  | 0.40          |           | 1                  | 27.9636 | 33.26**       |           |
| Colour         | 1                    | 1-5888 | 28.74**       |           | 1                     | 0.7322  | 5.77***       |           | 24                  | 1.7118  | 5.30***       |           |
| Plot           | 4                    | 0-0685 | 1.95**        |           | 3                    | 0-8518  | 2.53**        |           | 5                   | 0.8408  | 0.72          |           |
| Centre         | 1                    | 0.8994 | 0.93          |           | 3                    | 0.046   | 0.99          |           | 5                   | 0.8436  | 4.75**        |           |
| Pair X Centre  | 2                    | 1-2962 | 1.83          |           | 16                   | 0.3233  | 0.60          |           | 24                  | 0.6031  | 1.05          |           |
| Pair X Spots   | 2                    | 1.0663 | 2.53*         |           | 16                   | 0.5761  | 23.04**       |           | 24                  | 0.1775  | 0.48          |           |
| Colour X Spots | 1                    | 1-3541 | 1.91          |           | 1                    | 0-5443  | 1.01          |           | 1                   | 0.0172  | 0.03          |           |
| Plot X Centre  | 2                    | 0-7092 | 1.43          |           | 16                   | 0.5389  | 2.77***       |           | 24                  | 0.5734  | 1.71*         |           |
| Plot X Spots   | 2                    | 0-4210 | 0.85          |           | 16                   | 0.00003 | 0.00          |           | 24                  | 0.3718  | 1.11          |           |
| Residual       | 194                  | 0-4976 | 126           |           | 126                  | 0-1946  | 187           |           |                     | 0.3352  |              |           |

*P < 0.05, **P < 0.01, ***P < 0.001.
area. Even though the effect of dark centres in the study by
Johnson and Midgley (2001) was not statistically
significant, model flowers with dark centres were visited
more frequently than plain models in all the experiments
undertaken. The available evidence thus indicates that
flowers with dark centres are generally more attractive
to monkey beetles than flowers without dark centres. Further
research is required to demonstrate whether monkey
beetles have an innate preference for dark centres or
whether they have been conditioned to associate dark
centres with a reward.

Although the current experiments show that monkey
beetles prefer flowers with dark centres and dark spots,
the presence of dark spots alone (i.e. without an associated
dark centre) was positively associated with visitation rates
only in the R. monadelpha matrix. Other plant species
that are pollinated by monkey beetles, such as the
peacock irises in Moraea subgenus Vieuusseuxia (Steiner,
1998), have dark markings on the tepals but lack a dark
centre. Similar studies in areas with a high frequency of
these species should reveal whether the local monkey
beetles have a preference for dark spots in the absence of
an associated dark centre.

The preference of monkey beetles for flowers with dark
centres demonstrates that beetle marks do not function as
deterrents of herbivorous monkey beetles as was first
suggested by Hutchinson (1946) for Gorteria diffusa. The
frequent use of flowers as mating sites by monkey beetles
(Fig. 1B; Johnson and Midgley 2001) led Midgley (1993)
to propose that beetle marks are mimetic, attracting
beetles in search of a mating partner. The study by
Johnson and Midgley (2001), however, did not find that
model flowers with dead female or male monkey beetles
 glued to them attracted more visiting ones than plain
model flowers but their study was carried out in a region
of the south-western Cape that is relatively poor in
monkey beetle diversity.

Johnson and Midgley (2001) found a very strong prefer-
ence of monkey beetles on the Cape Peninsula for orange
over red, yellow and blue. The present study, however,
revealed only a slight preference for yellow over orange
model flowers in the matrix of S. elegans, and no colour pre-
fERENCE in the matrices of H. vaginata and R. monadelpha.
Whereas both H. vaginata and R. monadelpha are mainly
visited by the monkey beetle Clania glenlyonensis,
S. elegans was visited by a suite of other monkey beetle
species dominated by four different species (Table 1). It is
clear that species of monkey beetle may differ in their
colour preference, a conclusion that was also drawn by
Picker and Midgley (1996), who used colour preference
(among other features) to distinguish between three guilds
of monkey beetles. Their study, on the West Coast near
Darling, South Africa, did not include the species of
monkey beetles observed in the current study.

Sparaxis elegans has orange flowers, and the preference
for yellow over orange model flowers indicates that
monkey beetles in the Nieuwoudtville area are not condi-
tioned to associate the orange colour with pollen
reward. Similarly, Picker and Midgley (1996) found that
Lepithrix sp. preferred red traps although it was most
frequently seen on yellow flowers. This indicates that
monkey beetles may have an innate preference for certain
colours and are not conditioned by the colour of the
locally most frequent matrix species. This has significant
implications for the evolution of precise pollinator–plant
relationships by favouring strong convergence for specific
flower colours in certain guilds.

CONCLUSIONS

Our understanding of specialized beetle pollination has
improved in recent years, because a number of recent
studies have documented specialized beetle pollination of
species that do not have the classical beetle pollination syn-
drome (Dafni et al., 1990; Sakai and Inoue, 1999; Ollerton
et al., 2003; Peter and Johnson, 2006; Johnson et al., 2007).
The monkey beetle syndrome is another major exception to
to plants with the classical beetle pollination syndrome that
use floral scent as the primary attractant of pollinating
beetles, plants with the monkey beetle pollination syndrome
rely primarily on visual signals. The present study, together
with others (Picker and Midgley, 1996; Johnson and
Midgley, 2001; Colvillle et al., 2002), demonstrates that
some species of monkey beetle use colour as the primary
visual cue while others use beetle marks as the primary
visual cue. In addition, monkey beetles, in some regions
at least, prefer marked flowers to unmarked flowers, provi-
ing convincing evidence for an adaptive role of beetle
marks in increasing visitation rates and pollination success.

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