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RODENT POLLINATION IN THE AFRICAN LILY *MASSONIA DEPRESSA* (HYACINTHACEAE)[1]

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Field studies in the semiarid Succulent Karoo region of South Africa showed that flowers of *Massonia depressa* (Hyacinthaceae) are visited at night by at least four rodent species, including two gerbil species. Live-trapped rodents were found to carry *Massonia* pollen on their snouts; they also had large quantities of *Massonia* pollen in their feces as a result of grooming their fur. Visits by insects to the flowers were infrequent at one site and apparently absent at another site. Plants enclosed in large-mesh wire cages, which excluded rodents but not insects, set very few seeds relative to open controls. Our initial hypothesis of rodent-pollination in *M. depressa* was based on the striking similarity of its flowers to those of unrelated, rodent-pollinated *Protea* species. Convergent traits include dull-colored and very robust flowers situated at ground level, a strong yeasty odor, and secretion of copious amounts of sucrose-dominant nectar during the evening when rodents are active. Despite having a low sugar concentration (~20%), the nectar of *M. depressa* is almost 400 times as viscous as an equivalent sugar solution. The jelly-like constituent in the nectar may discourage robbing by insects, while also facilitating lapping by rodents. Our findings illustrate the utility of floral syndromes for generating testable predictions about pollination systems.

Key words: convergent evolution; floral syndrome; Hyacinthaceae; *Massonia depressa*; nectar; pollen; pollination; rodent; southern Africa.

Of the many varied interactions between plants and animals, one of the most unexpected is pollination of flowers by rodents. The phenomenon was first recorded in *Protea* shrubs (Proteaceae) in the 1970s (Wiens and Rourke, 1978), and, until now, was thought to be confined to shrubs belonging to three dicotyledon families: Proteaceae, Loasaceae, and Melastomataceae (Lumer, 1980; Wiens et al., 1983; Cocucci and Sérsic, 1998). Here we report the discovery of rodent pollination in a monocotyledon and the first record of pollination by gerbils.

The group of flower visitors known as ''nonflying mammals'' (to distinguish it from bats) is composed mainly of marsupials, primates, and rodents. Since the first study by Porsch (1934), nearly 100 plant species, mainly in the southern hemisphere, have been found to be visited by at least 59 species of nonflying mammal (Carthew and Goldingay, 1997, and references therein). In only a handful of studies, however, has it been shown that the flowers are actually pollinated by these animals and in even fewer instances has it been shown that they are the primary pollinators and therefore likely to have shaped the evolution of floral traits.

Evidence that a plant is adapted for pollination primarily by nonflying mammals ideally must include: (1) observations of nondestructive feeding on flowers; (2) finding pollen on fur or in the feces of the animals; (3) observed contact between body parts covered with pollen and the stigma; (4) infrequent insect or bird visitation; and (5) reduced fecundity when nonflying mammals are excluded from flowers. In addition, (6) nectar secretion, scent production, and floral anthesis would be expected to be synchronized with the activity periods of nonflying mammals in a plant that is adapted for pollination by these animals.

Plants adapted for pollination by nonflying mammals tend to have robust flowers with dull coloration, copious amounts of nectar, and exserted styles and stamens (Carthew and Goldingay, 1997). Within this broad ''syndrome'' of traits, however, there are important differences that reflect the morphology and foraging behavior of the three main nonflying mammal groups. For example, flowers pollinated by primates tend to be unscented and very large to accommodate these relatively heavy flower visitors (Nilsson et al., 1993; Kress et al., 1994); flowers pollinated by marsupials are usually situated in the canopy (Turner, 1982), whereas flowers pollinated by rodents tend to be situated at ground level (Wiens et al., 1983). Thus, it seems appropriate to consider pollination by rodents distinct from, yet functionally related to, pollination by other groups of nonflying mammals.

The flowers of the South African lily *Massonia depressa* Houtt. (Hyacinthaceae) captured our attention because they have many features in common with rodent-pollinated proteas, such as being positioned at ground level and lacking the colorful petals that most plants use to attract insects or birds (Fig. 2). The flowers also share stiff anthers, a stigma–nectar distance of ~10 mm, a yeasty scent, and a winter flowering period with their *Protea* counterparts (Wiens et al., 1983). On the assumption that convergent evolution of floral traits among unrelated plants reflects adaptation to similar pollinators (Faegri and van der Pijl, 1979; Johnson and Steiner, 2000), we hypothesized that *M. depressa* is pollinated by rodents.

The specific aims of this study were: (1) to determine whether rodents act as vectors of *M. depressa* pollen; (2) to establish the relative importance of insects and rodents as pollinators of this species; (3) to determine the breeding system of *M. depressa;* and (4) to describe the floral morphology, as well as physical and chemical properties of the nectar.

MATERIALS AND METHODS

Rodent trapping and pollen loads—We carried out observations and live-trapped rodents at two sites in the semiarid Succulent Karoo region of South

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TABLE 1. Pollen loads of rodents captured at two sites with populations of *Massonia depressa*.

Site	Rodent species	No. of animals caught	No. of animals with *Massonia* pollen on snout	*Massonia* pollen load on snout $\bar{X} \pm$ SD (range)	No. of animals with *Massonia* pollen in feces	*Massonia* pollen load in feces
Nieuwoudtville	*Aethomys namaquensis*	4	3	17.7 ± 15.5 (5–35)	2	>1000 grains
	Acomys subspinosus	3	2[a]	70.0 ± 2.8 (68–72)	2	>1000 grains
Vanrhynsdorp	*Gerbillurus paeba*	4	2	51.5 ± 64 (6–97)	4	>1000 grains
	Desmodillus auricularis	1	0	—	1	20 grains
	Mus minutoides	1	0	—	0	—

[a] One animal escaped before its snout could be sampled.

Africa during July 1998 and 1999. One site was situated on a sandy plain near the town of Vanrhynsdorp (31°38′ S, 18°45′ E, elevation 170 m), while the other was situated in clay soils on a rocky ridge in the municipal nature reserve close to the town of Nieuwoudtville (31°20′ S, 19°08′ E, elevation 800 m). Large *M. depressa* populations (>1000 plants) occur among sparse, scrubby vegetation at both of these sites. The total time spent at the sites was ~40 h over 6 d, of which 25 h were in daylight and 15 h at night.

For ethical reasons we carried out only live-trapping of rodents, although it is known that grooming by rodents in live traps can significantly reduce the load of pollen on their fur (Wiens et al., 1983). Peanut butter and rolled oats were used to bait the traps. We laid out 100 traps in four lines with 5 m between each trap at the Vanrhynsdorp site on the nights of 21 and 22 July 1998 and 70 traps in five lines with 5 m between each trap at Nieuwoudtville on the nights of 23 and 24 July 1999.

Rodents were removed from traps in the early morning (0600) and temporarily placed in plastic bags. Photographs and measurements were taken in order to confirm their identity. The snouts of the rodents protruded through a small hole in the corner of the plastic bag and were swabbed with a small block of fuchsin gelatine (Beattie, 1971), which was then melted onto a slide and examined microscopically for the presence of pollen. Rodent feces were retrieved from the traps and flowers and crushed in a mixture of water and fuchsin gelatine. A sample of this mixture was mounted on a slide and examined microscopically for the presence of pollen.

Evidence of rodent activity at flowers has been previously obtained from footprints left on glass ''smoked plates'' (Cocucci and Sérsic, 1998). We used sheets of stiff white cardboard (270 × 150 mm), which were blackened with soot over a paraffin lamp and placed adjacent to 11 flowering plants of *M. depressa* at the Nieuwoudtville site on the night of 24 July 1999. Footprints on these plates were compared to those made by captive rodents.

As it is virtually impossible to observe rodents in the field at night (cf. Wiens et al., 1983), we recorded the foraging behavior of captured rodents. Three gerbils captured earlier in the evening at the Vanrhynsdorp site were released one at a time from 2400 to 0100 into a 100 cm long by 30 cm wide glass tank with a 10 cm deep layer of sand containing two flowering plants of *M. depressa*. We also added several freshly picked *Hibiscus* flowers to determine if the rodents visit flowers selectively.

Floral characteristics—Dimensions of ten flowers, each sampled from a different plant, were measured to the nearest 0.5 mm. Patterns of anthesis were determined by marking 33 plants and recording the number of open flowers at ~3-h intervals for 24 h.

Daily rhythms in the nectar properties of *M. depressa* were determined by sampling the standing crop of nectar from ten randomly selected flowers approximately every 2 h over a 24-h period at the Vanrhynsdorp site in 1998 and the Nieuwoudtville site in 1999. The nectar volume was measured with 100 μL capillaries (Drummond Scientific Company, Broomall, Pennsylvania, USA) and nectar concentration was determined with a 0–50% field refractometer (Bellingham and Stanley, Tunbridge Wells, UK). Samples of nectar from five flowers were spotted onto filter paper and air dried for later determination of constituent free sugars using standard high pressure liquid chromatography methods, as detailed by Van Wyk (1993).

Viscosity of the nectar was determined from the descent times of a 20-μL sample over a distance of 80 mm in a 100-μL capillary with 0.563 mm radius, using the formulas given by Heyneman (1983). The accuracy of this method was verified from timed descent of sugar solutions of known viscosity (Fasman, 1975).

Breeding system and exclusion of rodents from flowers—To determine the breeding system of *M. depressa*, we kept ten plants in a pollinator-excluded greenhouse at the University of Cape Town and randomly selected newly opened flowers for one of three treatments: unmanipulated to test for autogamy, pollinated by hand with self- pollen to determine whether plants are self-compatible, and pollinated by hand with pollen from a different plant. The number of flowers that developed fruits and the mass of the fruits were determined for each treatment.

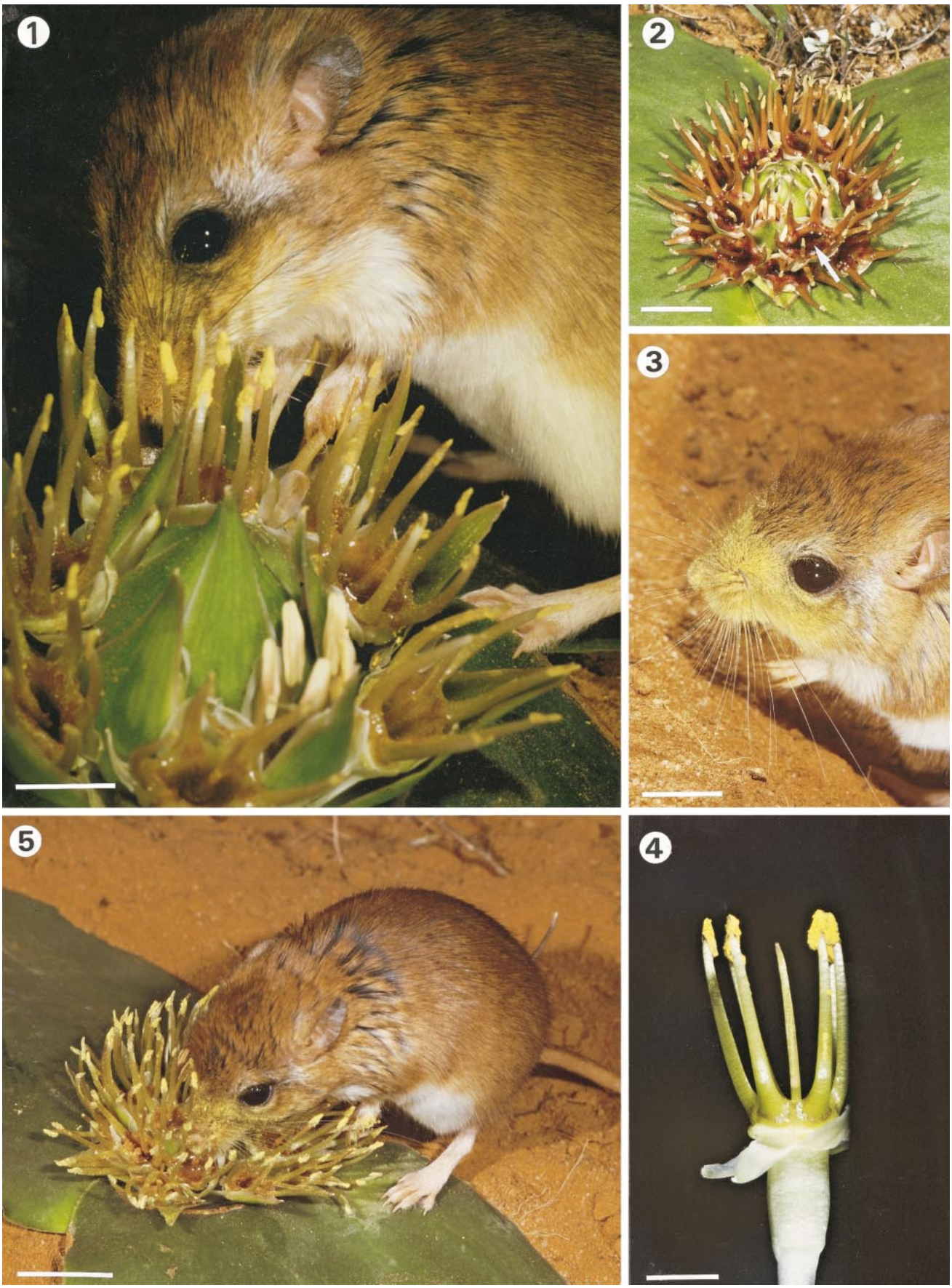
To determine whether rodents are important for seed production in *Massonia*, we selected 23 pairs of plants with the same number of flower buds at the lowland Vanrhynsdorp site and enclosed one member of each pair in a wire cage with a mesh diameter of 15 × 20 mm that excluded rodents but allowed insects free access to the flowers.

RESULTS

Rodent trapping and pollen loads—Captured rodents included two gerbil species (Family Muridae, subfamily Gerbillinae), *Gerbillurus paeba* (A. Smith) and *Desmodillus auricularis* (A. Smith), and three murid species (Family Muridae, subfamily Murinae), *Aethomys namaquensis* (A. Smith), *Acomys subspinosus* (Waterhouse), and *Mus minutoides* A. Smith (Table 1). These are all species that are known to be mainly nocturnal foragers. Microscopic examination of gelatine blocks dabbed onto the rodents' snouts showed that 7 of the 13 rodents carried *Massonia* pollen on their snouts, despite being able to groom for several hours in the traps. Feces from nine rodents representing four of the five species contained *Massonia* pollen in very large quantities (>1000 grains per dropping), suggesting that pollen is groomed off the fur and ingested. Other evidence of rodent visitation included *Massonia* pollen found in five of six rodent droppings found next to the flowers and rodent footprints (identifiable as those of *A. namaquensis*) on 2 of the 11 smoked plates left next to flowers overnight.

Captive gerbils visited flowers of *M. depressa* within seconds of their introduction into the observation tank, but they ignored the *Hibiscus* flowers. All of the nectar within each open flower was lapped up within 5 sec, and the snouts of the animals became liberally dusted with pollen (Fig. 3). Contact between the pollen-coated areas of the snout and the stigma occurred during feeding (Figs. 1, 5). Gerbils fed only on nectar and made no attempt to eat flower parts or pollen directly. After feeding, the gerbils spent long periods grooming pollen from their fur.

Soon after its release back into the field at the Nieuwoudtville site in 1999, we observed an individual Namaqua rock mouse (*Aethomys namaquensis*) feeding on the flowers of several plants of *M. depressa* at 0700.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Floral morphology and patterns of anthesis—The flowers of *M. depressa* are situated at ground level and lack any bright pigmentation (Fig. 2). The nectar is situated in a bowl-shaped chamber formed by the fused bases of the anthers (Figs. 2, 4). The chamber is ~5.6 mm in depth (SD = 1.3, $N = 10$), and its entrance measures ~9.1 mm (SD = 1.4, $N = 10$) by 5.9 mm (SD = 1.1, $N = 10$). The anthers are ~18.3 mm in height (SD = 2.8, $N = 10$), while the stigma is ~15.9 mm in height (SD = 5.6, $N = 10$). The diameter of the inflorescence is ~28.8 mm (SD = 8.8, $N = 10$).

We recorded 88 open flowers (2.7 flowers per plant) on the 33 marked plants when observations commenced at 0700, which increased to 118 open flowers (3.57 flowers per plant) by 0700 the following day. Floral anthesis occurred mainly during the afternoon; of the 30 flowers that opened during the observation period, 16 (53%) opened in the 3-h period between 1300 and 1600. The flower opening patterns were significantly nonrandom (Table 2).

TABLE 2. Pattern of flower opening in *M. depressa* based on a sample of 30 flowers that opened in the course of 24 h. The number of flowers that opened per time period differs significantly from values expected if opening is random ($\chi^2 = 11.3$, P = 0.01).

	No. of flowers that opened per time period			
	0700–1230	1230–1600	1600–0030	0030–0700
Observed	5	16	6	3
Expected	7	4	11	8

Nectar properties—Large volumes of nectar (up to 182 μL) were found in individual *Massonia* flowers during the night. The average nectar volume declined throughout the day, reaching a minimum in the late afternoon, but was rapidly secreted in the early evening, reaching a maximum around midnight (Fig. 6). We recorded relatively large nectar volumes and dilute nectar concentrations at the montane Nieuwoudtville site (Fig. 6). This might be attributable to the relatively sheltered position of the plants among rocks at this site. The mean (±SD) nectar volume per flower at the Nieuwoudtville site at 1500 was 17.68 ± 26.0 μL ($N = 23$), but increased to 79.39 ± 49.2 μL ($N = 11$) by 2400. The content of simple sugars in the nectar of sampled flowers at the Nieuwoudtville site, calculated from the refractive index and corrected for density (Dafni, 1992), increased from 3.16 ± 4.7 mg at 1500 to 14.22 ± 8.8 mg at 2400. The sugars consisted of sucrose (42%), glucose (23%), fructose (32%), and xylose (3%).

The viscosity of *Massonia* nectar, calculated from capillary descent times (Heyneman, 1983), was found to be almost 400 times that of a solution of the equivalent sugar concentration (Fasman, 1975) (0.6544 ± 0.115 Pa.s for *Massonia* nectar, $N = 6$, vs. 0.00165 Pa.s for 16% sucrose solution at 20°C).

Breeding system and exclusion of rodents from flowers—Production of seeds by *Massonia* plants clearly requires visits by pollinators, as no fruit set occurred in flowers from which pollinators were excluded ($N = 29$). The average fruit set was 38.5% in self-pollinated flowers ($N = 26$) vs. 82.4% in cross-pollinated flowers ($N = 34$). This difference is highly significant ($\chi^2 = 10.5$ with Yates correction, $P = 0.001$). In addition, the average mass of fruits formed as a result of self-pollination (0.19 g, SD = 0.17, $N = 10$) was significantly less than those formed as a result of cross-pollination (0.29 g, SD = 0.12, $N = 28$) ($t = 2.18$, $P = 0.035$, two-tailed).

Exclusion of rodents from flowers at the Vanrhynsdorp site resulted in a significant decline in the number of plants that set fruit, as well as the number of fruits and seeds per plant (Table 3). Only 4.3% of plants in the rodent-excluded group set fruit vs. 30.4% in the control group, and an average of only 1.95 seeds were produced in rodent-excluded plants vs. 20.0 seeds in the control plants (Table 3). Honey bees were observed to collect pollen from flowers of *M. depressa* on approximately ten occasions at the Vanrhynsdorp site, but no insect visitors were observed at the Nieuwoudtville site. No visits by sunbirds were recorded at either site. Sunbirds ignored flowering plants of *M. depressa* while foraging on flowers of *Microloma sagittata* (Asclepiadaceae) just a few meters away.

DISCUSSION

Evidence for rodent pollination—The hypothesis of rodent pollination in *M. depressa* was supported by several lines of evidence. *Massonia* pollen was found on the snouts and in the feces of most of the captured rodents. Insect visits to flowers of *M. depressa* were infrequent at one site and absent at the other. Exclusion of rodents, but not insects, resulted in a sharp drop in seed production. Rodent footprints were left on smoked plates left next to flowers. Captive rodents eagerly fed on nectar and transferred pollen between flowers in a nondestructive manner.

Two of the rodent species found to carry pollen of *M. depressa* have been previously recorded as vectors of the pollen of *Protea* species (Wiens et al., 1983), but the capture of gerbils with *M. depressa* pollen loads was unexpected and is apparently the first example of pollination by these animals. Wiens et al. (1983) captured five individuals of the gerbil *Tatera afra* with very small amounts of pollen originating from *Protea laurifolia*, but there was no evidence that the gerbils effected pollination of the flowers of this species, which is morphologically adapted for pollination by birds.

Massonia pollen was present in very large amounts in the feces of the captured rodents, and, in some cases, made up the bulk of the solid matter. This pollen was presumably ingested only after grooming, as captive rodents made no attempt to feed directly on pollen in the anthers. Previous studies have shown that rodents can extract protein from *Protea* pollen (van Tets, 1997). By flowering in the middle of winter, when food resources are scarce, flowers of *M. depressa*, like their *Protea* counterparts, may become a valuable source of energy and protein for rodents. Nevertheless, nectar and pollen are prob-

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Figs. 1–5. Flowers of *Massonia depressa* and nectar-feeding visits by the rodent *Gerbillurus paeba* (hairy-footed gerbil). **1.** *Gerbillurus* pushes its head among the anthers to reach the nectar. Bar = 10 mm. **2.** Inflorescence of *Massonia* showing the drab color of the flowers. Jelly-like nectar (arrow) is secreted in the early evening immediately prior to rodent activity. Bar = 15 mm. **3.** *Massonia* pollen deposited thickly on the snout of a gerbil following a feeding bout. Bar = 10 mm. **4.** Morphology of a single *Massonia* flower showing the highly reduced petals and sturdy anthers and stigma. Bar = 5 mm. **5.** The ground-level position of *Massonia* flowers facilitates nectar-feeding by rodents. Bar = 20 mm.

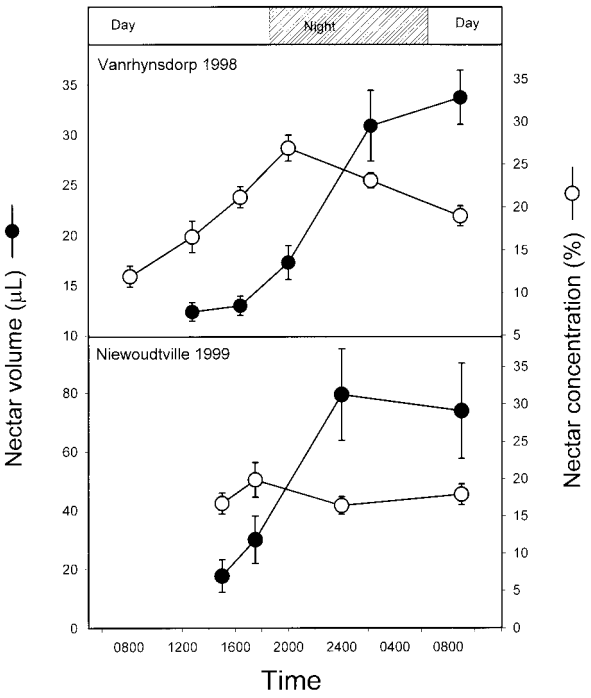

Fig. 6. Daily periodicity in average nectar volume and concentration per flower for *Massonia depressa* at two sites in South Africa. Bars represent ± 1 SE.

ably such a minor and spatially restricted element of the diet of rodents that morphological and behavioral adaptations for flower feeding are highly unlikely (Wiens et al., 1983).

The wide-mesh cages that we used to exclude rodents from flowers would have also excluded birds and bats, but sunbirds were present only at the Nieuwoudtville site and ignored flowers of *M. depressa*, despite foraging on other plants in close proximity. Wiens et al. (1983) reported ''rare and inconsequential'' sunbird visits to rodent-pollinated *Protea* species, but flowers of *Cajophora coronata* (Loasaceae) in South America are frequently pollinated by at least five bird species, in addition to rodents (Cocucci and Sérsic, 1998). Pollination by bats has not been recorded in the western half of southern Africa and is most unlikely to occur in *M. depressa*, as there are no flower-visiting bats in the Succulent Karoo region. The Egyptian fruit bat (*Rousettus aegyptiacus)* has been recorded from some large caves in the Cape region, but it is not known to occur in the Succulent Karoo.

Nectar characteristics—The presence of the pentose sugar xylose in the nectar of *M. depressa*, albeit at a concentration of just 3%, is interesting because it has been previously reported as a common constituent of rodent-pollinated *Protea* species in South Africa (Van Wyk and Nicolson, 1995). The ecological significance of xylose, however, remains unclear. Birds and honey bees show strong aversion to xylose, but it is willingly consumed by the Namaqua rock mouse (*Aethomys namaquensis*; Johnson, Van Tets, and Nicolson, 1999). Also, in contrast to birds, Namaqua rock mice show up to 97% absorption of xylose and probably metabolize the sugar with the aid of intestinal bacteria (Johnson et al., 1999).

The jelly-like constituent in the nectar of *M. depressa* is probably a mucopolysaccharide (unpublished data). The remarkable viscosity of the nectar (almost 400 times greater than a solution of equivalent sugar concentration) may serve to prevent robbing by insects. Although the nectar is very exposed, it did not appear to be fed on by insects, which may reflect the difficulty they have of drawing viscous solutions through their tubular mouthparts (cf. Heyneman, 1983). An alternative, though not mutually exclusive, explanation is that rodents prefer to feed on viscous nectar because it is more easily lapped into their mouths with their tongues. Bat-pollinated *Musa* spp. (Musaceae) have jelly-like nectar, while their bird-pollinated congeners have watery nectar (Nur, 1976). Polysaccharide mucilage has been reported in the nectar of *Musa paradisiaca* L. var. *sapientum* Kuntze (Fahn and Benouaiche, 1979). There is no evidence that the nectar of rodent-pollinated proteas is particularly viscous, however Cocucci and Sérsic (1998) describe the nectar of a putatively rodent-pollinated South American plant, *Bromelia urbaniana* (Bromeliacae), as ''jelly-like.''

The rodent pollination floral syndrome—The flowers of *M. depressa* show striking convergence to rodent-pollinated proteas. Convergent traits include: dull-colored, robust flowers positioned close to the ground with exserted wiry anthers and a stigma–nectar distance of ~10 mm; a yeasty odor; copious amounts of easily accessible nectar secreted in the evening; and winter flowering. Other South African monocotyledons, such as *Androcymbium pulchrum* Schltr. & Krause, *Androcymbium eucomoides* (Jacq.) Willd. (Colchicaceae), and *Eucomis humilus* Bak. (Hyacinthaceae), have similar traits that fit the rodent pollination syndrome, suggesting that this mode of pollination may be more widespread than previously believed.

The concept of floral syndromes (Faegri and van der Pijl, 1979) has come under criticism for being typological and lacking the flexibility to accommodate the generalized nature of many pollination systems (cf. Waser et al., 1996). But here we have shown that convergent syndromes can be used successfully to develop predictive hypotheses about which animals have shaped the evolution of floral traits. We emphasise that all hypotheses based on floral syndromes must be tested through field observations and experiments.

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TABLE 3. The effects of excluding mammals on fruit and seed production by plants of *Massonia depressa*.

Measure of reproductive success	Control plants (N = 23)	Mammals excluded (N = 23)	Tests (one-tailed)	P
Plants that set fruit (%)	30.4	4.3	Fisher's exact	0.023
Fruits per plant, $\bar{X}$ ± SE	1.39 ± 0.61	0.47 ± 0.47	Mann-Whitney, Z = 2.19	0.014
Seeds per plant, $\bar{X}$ ± SE	20.0 ± 9.9	1.95 ± 1.95	Mann-Whitney Z = 2.26	0.012

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