pollinators. This pollination system might contribute to the maintenance of obligate protective mutualism with ants in this genus.

#### doi:10.1016/j.sajb.2013.02.113

## Remarkable adaptations for rodent pollination in *Leucospermum* arenarium

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Nonflying mammals, particularly rodents, have long been considered important pollinators for many Proteaceae species in South Africa. However, rodent pollination remains unexplored in the genus Leucospermum. We focused on Leucospermum arenarium, an endangered, semi-geoflorous Sandveld shrub which until now was thought to be insect pollinated. In this study we aimed to: (1) determine the role of rodents as pollinators; (2) explore the impact of grooming on pollen transfer efficiency; (3) describe the suite of floral traits associated with the evolution of rodent pollination; (4) test the adaptive significance of geoflory. Pollen swabs and fecal samples from captured rodents revealed that Hairy-footed Gerbils Gerbillurus paeba carried large pollen loads of L. arenarium. However, their efficiency as pollinators is strongly impacted by grooming as shown by experiments with captive rodents indicating that pollen deposition decreased exponentially as grooming time increases. This represents the first ever empirical study on the effects of pollinator grooming on pollen loss despite the fact that nearly all pollinators exhibit some form of grooming. Additionally, we have found evidence that floral nectaries have evolutionarily migrated from the base of the nectar tube (where they are located in other Leucospermum species) to the tips of the petals where the nectar is held in an external cup-structure formed by post-anthesis perianth segments, a unique adaptation for rodent pollination in the genus. Inflorescences were also subjected to three treatments in the field: (1) exclusion of all pollinators to test for autonomous selfpollination; (2) exclusion of rodents and other large pollinators; and (3) inflorescences raised above ground level to test the effect of geoflory. Results from these experiments and the controls will soon be available. In all, this study provides an in-depth look into an extremely specialized pollination syndrome as well as a general analysis of traits that promote rodent pollination.

doi:10.1016/j.sajb.2013.02.114

### Different ways to attract the same pollinator: The evolution of floral scent in *Satyrium* (Orchidaceae)

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The diversification of angiosperm flowers has often been attributed to pollinator-mediated selection. Evidence for this is provided by the observation that 1) suites of floral traits co-vary with functional pollinator groups, and 2) shifts in pollinators and floral traits are correlated throughout the evolutionary history of many angiosperm clades. While this has been established for floral traits that can be readily measured, such as floral rewards and trait dimensions, phylogenetic analyses of floral scent in combination with pollinator data are lacking. This is surprising, given that scent plays a central role in pollinator attraction, and is thus likely to undergo strong pollinatormediated selection. GC-MS analyses of scent blends of 35 species of the orchid genus Satyrium revealed a total of 288 different scent compounds produced. The majority of these were only found in one or few species. The most common compound was beta-Linalool, both in terms of relative composition and absolute emission. Scent varied according to both phylogenetic relationships and functional pollinator group. The evolution of bird pollination was repeatedly associated with a strong reduction in the number of scent compounds and emission rates. Species pollinated by moths produced the largest number of compounds and were characterized by the strongest emission rates. Moth-pollinated species varied in terms of the dominant scent compounds, with the majority of species either dominated by beta-Linalool, or by the relatively unknown methyl-nicotinate. The evolution of moth-pollination did not follow a predictable trajectory in terms of scent evolution. We conclude that, like other floral traits, broad similarity in floral bouquet co-varies with pollination systems. However, convergent adaptation to a functional pollinator group does not always coincide with convergent evolution of specific scent compounds. This may indicate either undetected hyper-specialization within functional pollinator groups, or adaptation to the same functional pollinator group via different adaptive pathways.

### doi:10.1016/j.sajb.2013.02.115

## Effects of visual and olfactory cues on carrion fly attraction, with special reference to the function of floral traits in stapeliads

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Stapeliads (subfamily Asclepiadoideae, family Apocynaceae) are a group of plants that mimic the scent of carrion, dung or urine, by emitting volatile compounds such as dimethyl disulfide, dimethyl trisulfide, indole and p-cresol, thereby falsely signalling the presence of food and brood sites as well as a place to find a mate, in order to attract carrion flies as pollinators. These basic odours vary vastly due to subtle changes in chemical composition or concentration contributing to the olfactory uniqueness of each species. Apart from this bizarre feature, stapeliads have unique visual cues in terms of colour, pattern and shape. While some work has been done on the chemical composition of scent emitted by stapeliads, there has been limited research into the effectiveness of scent and visual cues in attraction of the pollinators of these plants. Using model flowers to which scent compounds were added, I found that colour and pattern had little effect on attraction of carrion flies. However, carrion flies were found to prefer star-shaped flower models to disc-shaped ones. In terms of olfactory cues, on the whole, dimethyl disulfide and dimethyl trisulfide together were found to be more attractive to carrion flies than indole or p-cresol. These results highlight the importance of emission of oligosulphides and floral shape for attraction of carrion fly pollinators to stapeliad flowers.

doi:10.1016/j.sajb.2013.02.116

# The role of cone volatiles in the pollination ecology of *Encephalartos* Lehm.

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