

First observations of nectar-drinking lizards on the African mainland

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Background and aims – Pollination of flowers is performed mainly by insects, but also by vertebrates. In South Africa, beside birds, non-flying mammals contribute to pollination. During video surveillance of plants adapted to non-flying mammal pollination, surprisingly, lizards were observed at the flowers. The question was addressed whether the lizards consume nectar and whether they could be potential pollinators of these plants.

Methods – Flowering *Massonia grandiflora* in the Cederberg and *Eucomis regia* (both Asparagaceae) in Namaqualand of South Africa were monitored with camcorders and camera traps for potential flower visitors. The footage was analysed for the type of floral visitor, foraging behaviour, contact areas of the plants' reproductive organs on the animals as well as potential pollen transfer between animals and flowers.

Key results – The Cape cliff lizard *Hemicordylus capensis* (Cordylidae) visited the flowers of *M. grandiflora* and the Namaqua day gecko *Rhoptropella ocellata* (Gekkonidae) visited *E. regia* flowers, both licking nectar. Thereby, the lizards touched the reproductive organs of the flowers and got dusted with pollen (at least *H. capensis*) on the same area of their head.

Conclusions – Visitation and pollination of flowers by lizards is a rarely observed phenomenon, especially in continental ecosystems. These are the first observations of lizards drinking floral nectar on the African mainland. As the areas on the animals' head where pollen got deposited by the flowers' anthers overlapped with the areas that touched the flowers' stigma, it is very likely that the lizards contribute to pollination. However, the lizards' role and importance as pollinators of the small-mammal-pollinated plants have to be proven by further observations and experiments.

Key words – Cordylidae, *Eucomis regia*, flower visits, Gekkonidae, lizards, nectar, non-flying mammals pollinated plants, *Massonia grandiflora*, pollination, South Africa.

INTRODUCTION

One of the most fascinating interactions between animals and plants is the process of pollination. Animals that pollinate flowers are mainly insects (especially bees), but also vertebrates (Faegri & van der Pijl 1971). Whereas birds and bats are well known pollinators, non-flying mammals as pollinators are relatively rare and unknown (Carthew & Goldingay 1997, Wester et al. 2009). Especially in South Africa,

mice (order Rodentia) and elephant shrews (order Macroscelidea within superorder Afrotheria) were found to regularly visit and pollinate flowers of specific plants (Wiens & Rourke 1978, Wester et al. 2009, Wester 2010, 2011, 2015). The flowers of these plants show characters that have likely evolved as adaptations to these pollinating non-flying mammals (e.g. geoflory, visual inconspicuousness, bowl-shaped, robust flowers with easily accessible nectar and specific smell; see also Wiens et al. 1983, Wester et al. 2009, Wester

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Plant Ecology and Evolution is published by Meise Botanic Garden and the Royal Botanical Society of Belgium
ISSN: 2032-3913 (print) – 2032-3921 (online)

2010, Johnson & Pauw 2014). Two of these plant species, *Eucomis regia* (L.) L'Hér. and *Massonia grandiflora* Lindl. (Asparagaceae), have been found to be pollinated by different mouse species and elephant shrews (Wester et al. 2019, P. Wester unpubl. data).

During video surveillance of these plants in the Kamiesberg area (Namaqualand) and in the Cederberg area of South Africa, surprisingly, additional flower visits by lizards were recorded. Flower visiting, nectar drinking and pollination by lizards is a rare phenomenon and is largely restricted to islands (Olesen & Valido 2003). Here I present the first observations of nectar drinking lizards on the African mainland. I discuss the observations in terms of the lizards' role as pollinators and the animals' taxonomic affiliation in the context of the taxa already known as flower visitors.

MATERIAL AND METHODS

On the farm Windhoek (4 km north of Kamieskroon, Namaqualand, Northern Cape, South Africa; 30°10.288'S, 17°56.758'E, elevation 960 m a.s.l.) about 40 *Eucomis regia* plants occur on granite outcrops in shady places under bushes or between rocks. Near the Kliphuis campsite at the Pakhuis pass in the northern Cederberg area of the Western Cape in South Africa (32°8'19.34"S, 19°0'41.10"E; elevation 740 m a.s.l.) about 100 *Massonia grandiflora* plants grow in shady rock crevices of rocky outcrops. Four *E. regia* plants (in 2014) as well as 29 (in 2016) and three (in 2017) *M. grandiflora* plants were monitored for potential flower visitors in the field. Monitoring was carried out with video camcorders with internal infrared light sources (HDR-XR520, HDR-XR550, Sony, Tokyo, Japan), partly in combination with additional self-made infrared lights (with three 1 Ampère SMD 940 nm LEDs), and USB powerbank (20000 mAh Astro Pro, Anker, Shenzhen, China) connected to 12V/18Ah lead-acid batteries as power source. Camcorders and light sources were positioned about 50 to 100 cm away from the plants, running non-stop (6 to 13 h). Additionally, monitoring was performed with motion and infrared sensor camera traps (Nature View HD Max 119440, Bushnell, Kansas City, U.S.A.). The camera traps have 0.7-s shutter lag and were set on maximum sensitivity, 1-min video recording, 1-s interval and low IR illumination. Close-up lenses enabled 25 to 250 cm operating distances. Monitoring for *E. regia* took place over two days and two nights (23–25 Aug. 2014) with three camcorders and external IR lights, powerbank and batteries, totalling 86 hours of observations (33 hours during daytime and 53 hours at dawn/dark). Monitoring of *M. grandiflora* was carried out on six days in 2016 (30 Aug. – 5 Sept.) with two camcorders (with powerbank only; four plants, 52 hours) and 21 camera traps (25 plants, 2806 hours), recording 45% during daytime and 55% in the dark, and on four days in 2017 (4–10 Sept.) with three camcorders (three plants), resulting in 57 hours daytime footage.

The footage was later analysed for the type of floral visitor and visitor behaviour, time of foraging behaviour, number of flower visits, licking frequency (in-and-out flicking of tongue) during nectar feeding, contact areas of the plants' reproductive organs on animals as well as potential pollen transfer on animals.

The *Massonia* population is most similar to *M. grandiflora*, but differing from the original description (Lindley 1826) in having microstipulate leaves. As leaf morphology can vary within *Massonia* species, the name *M. grandiflora* is tentatively used until a revision of the whole genus might clarify the species status.

RESULTS

Hemicordylus capensis (A. Smith, 1838) (Cape cliff lizard, Cordylidae) visited three different *Massonia grandiflora* plants (one in 2016, two in 2017) on five days (two days in 2016, three days in 2017). All flower visits happened between 10:20 h and 16:35 h, with visitation frequency peaks between 10:20 h and 11:50 h, and again between 15:50 h and 16:35 h. The lizards (unknown how many individuals) sometimes tongue-flicked before approaching the *M. grandiflora* inflorescences, then targeting the flowers and inserting their head in the flowers (fig. 1A–C; electronic appendices 1–2, available as Supplemental online material). At least 55 flower visits (1–10 flower visits per plant) could be observed (14 flower visits of 13 flowers in 2016 and 41 flower visits of 36 flowers in 2017) in which the lizards clearly licked nectar with a licking frequency of 1.8 ± 0.3 Hz (range 1.1–2.2 Hz, $n = 32$), spending on average 8.4 ± 4.8 seconds (1.8–23.1, $n = 32$) per flower. Mostly (in about 90% of the flower visits), the lizards visited the flowers from above or a bit laterally, resulting in touching the anthers and probably the stigmas (the latter hardly to see in the videos, but one time clearly visible). Touching took place on and around the eyes, the side of the mouth, the chin and the whole distal part of the head. Sometimes, pollen transfer on the animals could be clearly seen, taking place on and around the eyes, the side of the mouth and its tip and the chin during touching the anthers or being visible after the flower visits. Due to the yellowish pattern on the lizards' head, probably not all pollen was not clearly visible. In about 10% of the flower visits, the lizards approached the flowers from the side, probably not (or to a lesser extent) touching the anthers and stigma. After the flower visits, often the lizards tongue-flicked, probably to remove the sticky nectar from the tongue. One time, a lizard shortly rubbed his snout at an *M. grandiflora* leaf, probably to get rid of the sticky nectar or pollen. In about 20 additional short flower visits it was not clearly visible whether the animals drank nectar or only tongue-flicked without finding nectar or caught insects. One time an ant was caught by a lizard on an *M. grandiflora* leaf.

Rhoptropella ocellata (Boulenger, 1885) (formerly *Phelsuma ocellata*, Namaqua day gecko, Gekkonidae) visited *E. regia* inflorescences four times during one day (between 10:55 h and 11:10 h). At least 13 flower visits (2–5 flowers per plant) at two plants could be observed. The gecko(s) (unknown how many individuals) sometimes tongue-flicked in front of the inflorescence/flower, but always went purposefully to the flowers and inserted its head deep into the flowers (the head more or less perpendicular to the vertically arranged flower) where it also tongue-flicked (fig. 1EF; electronic appendices 3–4, Supplemental online material). Licking frequency (when licking nectar) was 1.6 ± 0.3 Hz (range 1.3–2.0 Hz, $n = 7$). The animals spent on average 8.5 seconds per flower ± 6.9 (1.8–20.0, $n = 11$). They stayed on average



Figure 1 – Nectar drinking lizards in South Africa: A, *Hemicordylus capensis* (Cape cliff lizard) visiting a *Massonia grandiflora* inflorescence near the Pakhuis pass (Cederberg); B, licking nectar, touching the anthers and getting dusted with pollen at its snout; C, another *H. capensis* licking nectar with its with its tongue and touching the stigma of a flower (near the tip of the snout). D, three *Eucomis regia* ssp. *pillansii* (Pineapple Lily) near Kamieskroon (Namaqualand) with the left inflorescence being visited by *Rhoptropella ocellata* (Namaqua day gecko); E, the same individual lapping nectar at another plant (in the middle), thereby touching the anthers. All photos are still images from video footage by P. Wester.

half as long at the lower flowers (5.3 seconds on average, up to 8 seconds; older flowers with probably no/little nectar) as they did at the upper level flowers (10.3 seconds on average, up to 20 seconds, flowers with large amounts of nectar) and they licked on average half as many times as on the lower flowers (22 times, 8–29) as they did at the upper ones (11 times, 6–14). *Rhoptropella ocellata* visited the lower flowers mostly with one or two front feet on the inflorescence or a neighbouring leaf, but crawled up the inflorescence to reach the upper flowers. During the flower visits, the lizards touched (at least sometimes) the anthers (around the eyes and further distal) and at least one time the stigma (on the dorsal part of the head). Due to the animals' dot pattern (white on black ground), pollen deposited on the head was difficult to recognise (probably two times on the snout end and one time on the side of the head).

Several lizards passed *M. grandiflora* plants without showing any interest in the flowers: *Agama atra* Daudin, 1802 (Southern rock agama) two times in 2016 and three times in 2017, *Trachylepis homalocephala* (Wiegmann, 1828) (Red-sided skink) one time in 2016 and one time in 2017 as well as *Trachylepis variegata* (Peters, 1870) (Variegated skink) three times in 2016.

DISCUSSION

This study undoubtedly shows that two species of lizards purposefully visited the flowers of non-flying mammal-pollinated plants in South Africa. Whereas *Rhoptropella ocellata* was observed only on one day at *E. regia* flowers (but observation time was only two days), *Hemicordylus capensis* could be detected at *M. grandiflora* flowers on five days during two years. This is remarkable as in general even the main pollinator species do not necessarily visit flowers so regularly (Wester et al. 2019, P. Wester unpubl. data; for other species e.g. Wester et al. 2009, Wester 2010, 2015), indicating that the lizards' behaviour is not an exception.

It was clearly noticeable that the lizards were lapping nectar, especially in *H. capensis* at the more easily visible flowers of *M. grandiflora*, and only rarely (or never in *R. ocellata*) were looking for insects. The animals inserted their head into the flowers and tongue-flicked inside the flowers for a while, indicating nectar-licking (rather than short visits for insect catching). In *E. regia*, the lizards remained for a longer time in the upper (nectar-containing) flowers of the inflorescence with more licking events than in the lower flowers. Most likely this is because the plant has an acropetal sequence of blooming, from the bottom of the inflorescence upwards, and the upper flowers contain more nectar than the lower (older) flowers and also only these upper-level flowers were visited by elephant shrews (P. Wester unpubl. data). Tongue-flicking was also observed in front of the inflorescence/flower and can be interpreted as sampling chemicals for vomerolfactory analysis for detecting food (Cooper 2007). The lizards might be attracted to the odour of the *E. regia* and *M. grandiflora* flowers, just like the main flower visitors, small mammals (Wester et al. 2019, P. Wester unpubl. data).

Pollen transfer onto the lizard's head could be clearly seen in *H. capensis*. As the animals touched the anthers and the stigma in those regions of the head that were contaminat-

ed with pollen, pollen transfer to the flower's stigma is very likely. However, their role and importance as pollinators have to be proven by more observations and experiments evaluating pollen transfer to the stigma and examining seed set after pollination. Still, it is likely that lizards are additional pollinators of plants that are adapted to small mammals. In other plant species that are known to be pollinated by lizards, the lizards seem to be only additional pollinators as the plants are adapted to other animal groups, mostly birds, and any evidence that lizards act as selective pressure shaping floral traits is still lacking (Nyhagen et al. 2001; but see Hansen et al. 2006, Hansen & Müller 2009, Olesen et al. 2012).

Nonetheless, the observation of *H. capensis* and *R. ocellata* as nectar consumers is very remarkable as lizards eat mainly invertebrates (mostly arthropods), but also plant material, especially fruits, seeds and leaves (Schwenk 2000). Only to a lesser extent they consume nectar. Whereas their role as seed dispersers has been known for a long time, the knowledge about flower visits and pollination by lizards only emerged relatively recently (Elvers 1977, Olesen & Valido 2003). Interestingly, flower visiting, nectar-drinking and pollinating lizards are mainly confined to islands in the regions of Africa, America and Australia/Oceania (Olesen & Valido 2003). The present observations are the first of flower visits and nectar-feeding of lizards on the African mainland.

Rhoptropella ocellata is confined to Namaqualand (Bates et al. 2014) and known to feed only on small insects and spiders (Alexander & Marais 2007), but species of the closely related genus *Phelsuma* (Gekkonidae; Rocha et al. 2010) are known as flower visitors and pollinators on islands (Hansen & Müller 2009, Le Péchon et al. 2013).

Apart from geckos (Gekkonidae), six further lizard families contain species that are known as nectar consumers or pollinators: Diplodactylidae (New Zealand geckos; Whitaker 1987), Scincidae (skinks; Sazima et al. 2009), Lacertidae (true lizards; Pérez-Mellado & Casas 1997), Teiidae (autarchoglossan lizards; Dearing & Schall 1992), Dactyloidae (Anoles; Perry & Lazell 1997) and Tropiduridae (neotropical ground lizards; Gomes et al. 2013). With *H. capensis* an eighth lizard family, the Cordylidae (Girdled lizards) can be added to this list. *Hemicordylus capensis*, being endemic to South Africa where it is largely restricted to the Western Cape (Bates et al. 2014), has been stated to be insectivorous (Branch 1998) but was also observed to eat fruits (Lanse van Rensburg & Mouton 2009).

SUPPLEMENTARY DATA

Supplementary data are available at *Plant Ecology and Evolution*, Supplementary Data Site (<https://www.ingentaconnect.com/content/boel/plecevo/supp-data>) and consist of the following: (1) and (2) video footage (MP4) showing *Hemicordylus capensis* (Cape cliff lizard) visiting *Massonia grandiflora* near the Pakhuis pass (Cederberg) licking nectar with its tongue, mostly touching the anthers of the flowers, getting dusted with pollen at its snout and touching the stigma; (3) and (4) video footage (MP4) showing *Rhoptropella ocellata* (Namaqua day gecko) visiting *Eucomis regia* ssp. *pillansii* near Kamieskroon (Namaqualand) lapping nectar and touching the anthers of the flowers. High quality MP4

files are available at Zenodo (<https://doi.org/10.5281/zenodo.2273934>).

ACKNOWLEDGEMENTS

Thanks go to Natascha Karvang, Tim Niedzwetzki and Patricia Thüs (Heinrich-Heine-University, Düsseldorf, Germany) for help with field work, Le Fras Mouton (University of Stellenbosch, South Africa) for lizard identification advice, Dennis Hansen for valuable comments on an earlier version of the paper, Stuart Hall (University of Stellenbosch) and Wolfgang Wetschnig (Karl-Franzens-Universität Graz, Austria) for locality information, Stella and Ernest Schulze (Kamieskroon) for logistic support, Corneels Genis (Kamieskroon) for the permission to work on his property as well as the A.F.W. Schimper-Stiftung (Hohenheim, Germany), the Heinrich Hertz-Stiftung (Düsseldorf, Germany) and Klaus Lunau (Heinrich-Heine-University, Düsseldorf, Germany) for support.

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Manuscript received 12 May 2018; accepted in revised version 9 Nov. 2018.

Communicating Editor: Renate Wesselingh.