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ABSTRACT

Rodents are important pollinators and seed predators of fynbos Proteaceae, but their role as florivores has received little attention. Chacma baboons (*Papio hamadryas ursinus*) are known to feed on Proteaceae inflorescences, however, their effect on plant reproduction has not been quantified. We recorded the extent of damage by rodents and baboons to inflorescences of the dominant shrub, *Protea neriifolia*, in 20 × 20 m plots in the Jonkershoek Nature Reserve near Stellenbosch. Damage was distributed patchily across the landscape. Rodents damaged up to 23% of the inflorescences per plot by feeding on styles and nectar. We observed the striped mouse (*Rhabdomys pumilio*) climbing up plants to feed on inflorescences. Up to 14% of inflorescences in some plots were destroyed by rodents gnawing through inflorescence stems. Baboons damaged or destroyed 12% to 29% of inflorescences at three study sites, but did not forage at all in the three remaining study sites. Among plant individuals affected by baboons or rodents, a mean proportion of 0.49 ± 0.31 (SD) of individuals' inflorescences were damaged or destroyed. Florivory by rodents and baboons can thus reduce the fecundity of *P. neriifolia* significantly. *Protea* inflorescences may be an important seasonal food source for certain rodents. In an evolutionary context, rodent florivory may have been an important selective force that caused certain Proteaceae species to shift to rodent pollination. Further work is needed to determine which rodent species feed on *Protea* inflorescences and whether rodent florivory is widespread in fynbos.

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1. Introduction

Florivory, the consumption of flowers prior to seed coat formation, is an important biotic interaction, but it has received relatively little attention in its own right (McCall and Irwin, 2006). Florivory should be distinguished from leaf and shoot herbivory, since the effects on plants can differ (McCall and Irwin, 2006). Plant fitness may be reduced by florivory in a number of ways. Flower damage or loss can directly affect plant fecundity by reducing both seed set (female fitness) and pollen export (male fitness). Flower loss also represents a loss of invested resources, which is especially costly for plants that reabsorb nutrients from old flowers in resource-limited environments (Ashman, 1994). Florivory can indirectly reduce plant fitness too, by altering floral display or reward, thus decreasing the attractiveness of plants to pollinators (Krupnick et al., 1999). Florivory can act as selective force on flower traits, e.g. plants may evolve less conspicuous floral displays to reduce florivory (De Waal et al., 2012).

Herbivory is often considered to be less prevalent in the fynbos vegetation of the Cape Floristic Region than in other biomes and is thus not well studied. Fynbos typically occurs on nutrient poor soils; hence fynbos foliage is usually low in nutrients. The leaves of many fynbos plants are also well-defended against herbivory by sclerophylly, pubescence

and/or high phenolic content (Anderson et al., 2014). It has been suggested that plant parts such as flowers and seeds, which are potentially less defended and more nutritious, will support a greater abundance and diversity of insect herbivores than leaves in fynbos (Cottrell, 1985). Not much is known about insect herbivory in fynbos in general, hence there is insufficient evidence to test Cottrell's hypothesis. Inflorescences and infructescences of *Protea* (Proteaceae) are attacked by a diversity of insect borers (Roets et al., 2006) and high levels of leaf herbivory by chewing insects has also been recorded in certain *Protea* species (Wright and Giliomee, 1992). The abundance and diversity of herbivorous mammals in fynbos are relatively low, likely as a result of the low forage quality (Pauw and Johnson, 1999). However, even small amounts of herbivore damage may have significant effects on fynbos plants, since plants are slow growing and nutrients are not easily replaced in a low-nutrient system (Anderson et al., 2014).

The Proteaceae family is a characteristic and often dominant component of fynbos vegetation (Rebello, 2001). Fynbos Proteaceae are ecologically and commercially important, well-studied and considered to be a model for biodiversity research and conservation (Schurr et al., 2012). Proteaceae interact with various animals, including rodents and chacma baboons (*Papio hamadryas ursinus*).

Rodents play a number of important ecological roles in fynbos. Most species in fynbos are wholly or partially herbivorous (Skinner and Chimimba, 2005). Rodents have strong interactions with Proteaceae in particular, acting as seed predators (Bond and Breytenbach, 1985), but

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also dispersing the seeds of certain *Leucadendron* species (Midgley and Anderson, 2005). Moreover, rodents pollinate several *Protea* species (Wiens et al., 1983; Biccard and Midgley, 2009; Melidonis and Peter, 2015; Zoeller et al., 2016) and three *Leucospermum* species (Johnson and Pauw, 2014; Johnson, 2015). As many as 35 species of *Protea* and *Leucospermum* are thought to be rodent-pollinated (Rebello and Breytenbach, 1987). Inflorescences of rodent-pollinated plants are typically robust and present nectar rewards in an accessible manner to prevent damage by rodents (e.g. Wester et al., 2009; Johnson and Pauw, 2014). Inflorescences of some rodent-pollinated *Protea* are also robust enough to withstand foraging by larger mammals such as mongooses (Steenhuisen et al., 2015). Rodent-pollinated *Protea* may often be gnawed by rodents, but usually inflorescences are not destroyed, however, *Protea nana* (nomenclature of Proteaceae species in this article follows Rebello (2001)) loses many inflorescences to rodent gnawing (Biccard and Midgley, 2009). The styles and fleshy involucral bracts of geoflorous rodent-pollinated species such as *P. subulifolia*, *P. amplexicaulis* and *P. decurrens* are also sometimes consumed by rodents (Wiens et al., 1983; Zoeller et al., 2016). Rodents are not known to feed on the inflorescences of bird-pollinated *Protea*. The only literature records we know of are by Wiens et al. (1983) who noted occasional light chewing of *Protea laurifolia* bracts by rodents and Rebello and Breytenbach (1987) who mention the presence of rodent faeces in *Protea repens* inflorescences.

Chacma baboons are opportunistic omnivores (Skinner and Chimimba, 2005) that include the flowers of at least 36 fynbos species in their diet, notably from the Amaryllidaceae, Ericaceae and Proteaceae families (Hall, 1962; Davidge, 1978). Baboons on the Cape Peninsula may spend as much as half of their time in summer feeding on Proteaceae inflorescences, especially *Leucospermum conocarpodendron*, as well as *L. hypophyllocarpodendron* subsp. *hypophyllocarpodendron* and *Mimetes fimbriifolius* (Davidge, 1978), while *Protea lepidocarpodendron* is a main food item from April to June (Hall, 1962). Inflorescences of *Protea scolymocephala* (Hall, 1962), *P. humiflora* and *P. repens* (Wiens et al., 1983) are also consumed by baboons. Entire inflorescences are broken from *Protea* and *Leucospermum* plants, and sometimes baboons tear open inflorescences and lick out the insides, most likely feeding on the nectar (Hall, 1962). Baboons also destroy the inflorescence buds of cultivated *Protea* when searching for insect borers (Malan, 2012).

Despite the potential importance of florivory by rodents and baboons, their effect on plant reproduction has not been quantified. In this study we aimed to determine the extent of damage by rodents and baboons to the inflorescences of *Protea neriifolia* R. Br., a widespread bird-pollinated species.

2. Materials and methods

2.1. Study area

We conducted our study in the Jonkershoek Nature Reserve near Stellenbosch. Study plots were established at six different sites in 5-year old Boland granite fynbos (Rebello et al., 2006), at altitudes of 380–467 m. Site numbers 1, 2 and 3 were on the valley's southwest-facing slopes, where the granite-derived soil supported dense stands of *Protea neriifolia* and *Protea coronata*. Site numbers 4, 5 and 6 were on the drier north-facing slopes, where the soil was sandier and the sparser vegetation was dominated by *Protea neriifolia* and *Protea repens*. At each study site, two 20 × 20 m plots were established, as part of a larger study on bird pollination. Birds and baboons, but not rodents, were excluded from one of the plots at each site by a 20 × 20 × 2.2 m cage of plastic netting (mesh-size 2 × 2 cm), while the other plot consisted of unmanipulated open vegetation. Rodents moved freely into bird enclosure plots, evidenced by numerous rodent runways underneath the netting. Coordinates of study sites: Site 1: 33°59'18.60"S, 18°58'20.87"E; Site 2: 33°59'24.92"S, 18°58'26.97"E; Site 3: 33°59'28.39"S, 18°58'44.04"E; Site 4: 33°59'31.69"S, 18°58'2.97"E; Site 5: 33°59'32.30"S, 18°57'57.48"E; Site 6: 33°59'32.65"S, 18°57'47.74"E.

2.2. Baboon damage to *Protea* inflorescences

We assessed all *Protea neriifolia* inflorescences in the open plots at Sites 4, 5 and 6 for baboon damage on 24 and 28 July 2014, after baboons passed through the area on 19 July 2014. *Protea* inflorescences are hermaphrodite. In addition, styles first serve a male function by acting as pollen presenters and thereafter serve the female function when stigmas become receptive. Inflorescences were scored as “damaged by baboons” if part of the inflorescence had been removed by the feeding baboons, but the remaining part of the inflorescence was intact and considered potentially capable of pollination and seed production. If all the flowers had been removed from an inflorescence or the inflorescence stem had been snapped by the baboons, the inflorescence was scored as “destroyed by baboons”. Inflorescences that were open and producing nectar at the time were scored “open”, while inflorescences that had finished flowering were scored “closed”. Inflorescences that were not yet open and flowering were scored as “bud”. We examined a random sample of 25% of *P. neriifolia* individuals (range 70 to 600) for baboon damage at Sites 1, 2 and 3 in October 2014. We also checked all six study sites regularly from March to October 2014 for indications of baboon activity such as digging, faeces, plant damage and overturned rocks.

2.3. Rodent damage to *Protea* inflorescences

We recorded rodent damage to *Protea neriifolia* inflorescences on 8 and 9 August 2014, at Sites 1, 4 and 5. Rodent gnawing at Site 2 was recorded in February 2015. All *P. neriifolia* individuals at Sites 4 and 5 were assessed (including those previously affected by baboons), and a random representative sample of individuals at the other sites (Site 1 Cage: n = 61, Site 2 Open: n = 123). All inflorescences on an individual were assessed. An inflorescence was scored as “damaged by rodents” when the central flowers of the inflorescence had been consumed by rodents. Rodent feeding of this kind hollowed out the centre of an inflorescence, with most styles gnawed off close to the base, and it left loose styles lying around the rim of the inflorescence and sticking out beyond the top of the involucral bracts (Fig. 1A, B). When the stems below inflorescences were completely gnawed off by rodents, with tell-tale gnawing marks, we scored it as “gnawed off by rodents” (Fig. 1C, D). Inflorescences that were in “bud”, “open” and “closed”, were scored as described above. Rodent damage could be distinguished from baboon damage, since rodents gnawed on inflorescences and stems while baboons plucked flowers and snapped stems. In addition, baboons could not enter caged plots. We recorded cones produced before 2014 at Sites 4 and 5 to determine the lifetime reproductive output of individuals.

3. Results

3.1. Baboon damage to *Protea neriifolia*

Chacma baboons damaged and destroyed substantial proportions of the total *Protea neriifolia* inflorescences on one side of the valley (Site 4: 12%, n = 150; Site 5: 28.6%, n = 189; Site 6: 18.4%, n = 103; sample sizes are inflorescence counts), but did not forage on the other side of the valley (Site 1: 0%, n = 91; Site 2: 0%, n = 223; Site 3: 0%, n = 314), as also determined by the lack of signs of baboon activity (described below). Baboons plucked flowers, i.e. styles and ovules, clean off the base of inflorescences, mostly leaving the involucral bracts. A number of inflorescences were partially damaged in this way (Site 4: 6.7%; Site 5: 9%; Site 6: 7.8%; sample sizes as above), but had some potentially functional flowers remaining (Table 1). Many inflorescences were completely destroyed, with all flowers lost or inflorescence stems snapped (Site 4: 5.3%; Site 5: 19.6%; Site 6: 10.7%; sample sizes as above) (Table 1). The way inflorescences were damaged suggests that baboons fed on nectar rather than flower parts, as also described

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