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The nightshift: Seed dispersal and consumption differences by rodents before and after dark

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ABSTRACT

Seed burial by dispersal vectors in fire-prone ecosystems is thought to increase seed survival rates by protecting them from fire and other seed consumers. In the fire-prone fynbos, seed burial is usually performed by ants. Historically, rodents in the fynbos were viewed purely as seed consumers; however, more recent evidence suggests that some species may also disperse seeds. This is done by scatter-hoarding the seeds in caches buried below the soil surface. Since seed dispersal and consumption by rodents usually takes place unobserved, it has been difficult to positively confirm which rodents disperse seeds and which ones only consume them. Here, the dispersal and consumptive behaviour of 2 rodents, *Rhabdomys pumilio* and *Gerbilliscus paeba*, are disentangled by using a combination of camera traps and the temporal compartmentalisation of seed fate patterns into day versus night in a depauperate, Cape strandveld rodent community. In this study, it is clearly demonstrated that the nocturnal hairy-footed gerbil (*G. paeba*) dispersed *Willdenowia incurvata* (Restionaceae) seeds. Although *G. paeba* also consumes seeds, they cached more seeds than they consumed during the period of observation. In contrast, the diurnal 4-striped mouse (*R. pumilio*) consumed but never cached seeds left out during the day. These results demonstrate that ecological roles of Cape rodents vary between species and that rodents in general cannot simply be regarded as seed consumers or dispersers as they have in the past.
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Seed dispersers define the ecological context in which animal-dispersed plants spend their lives (Howe and Smallwood, 1982; Beattie and Culver, 1983; Forget, 1992; Theimer, 2001; Hirsch et al., 2012b). This affects subsequent seed survival, seedling establishment, plant survival rates, and consequently, persistence and dynamics of populations (Vander Wall, 1990; Linder et al., 1998; Theimer, 2001; Rusch et al., 2013a). Furthermore, along with pollen transport, seed dispersal is the most important process promoting gene flow in plant populations, emphasising its importance in shaping plant communities (Van der Pijl, 1982; Jordano et al., 2007; de Waal et al., 2014).

Seed dispersal vectors also have the ability to shape plant traits. The presence of elaiosomes or wings are 2 seed traits commonly found in plants of the Cape Floristic Region (CFR) (Le Maitre and Midgley, 1992; Cowling et al., 1997). Several studies demonstrate that eliaosomes and wings enhance dispersal by ants (Bond and Breytenbach, 1985; Narbona et al., 2014) and wind (Matlack, 1987; Cody and McC, 1996; de Waal et al., 2014), respectively, suggesting that these dispersal vectors may have selected for the evolution of eliaosomes and wings. Seed traits of unrelated plants may converge because they share a similar dispersal vector. Such a suite of convergent traits are known as a seed dispersal syndrome (Forget et al., 1991). Elaiosomes are one of the most important traits associated with the ant dispersal syndrome, further suggesting that ants selected for the evolution of this trait (Pfeiffer et al., 2010). Similarly, many large-seeded fynbos shrubs belong to the guild of serotinous plants which appear to be adapted to post-fire wind dispersal as their winged seeds are released into the wind from fire-resistant cones only after fire has killed the parent plant.

In addition to ant and wind dispersal, rodent dispersal was recently recognised in the CFR (Midgley et al., 2002). While it appears as though relatively few plants in the CFR are rodent dispersed, it is important in temperate and tropical plant communities (Brewer, 2001; Theimer, 2001; Jansen et al., 2004; Hirsch et al., 2012b). The rodent dispersal syndrome is generally associated with large nut-seeded plant species in the CFR, which possess neither elaiosomes nor wing appendages (Rusch et al., 2013b). Rather, these seeds possess a thick hull, are large in size, and are released *en masse*. Rodents often store these seeds in times of plenty, enabling them to consume the seeds later when resources are less plentiful (Vander Wall, 1990; Haugaasen et al., 2010; Rusch et al., 2014).

Several studies in the CFR suggest that rodents disperse seeds, although the evidence is all inferential and not direct (but see White et al., in press). Consequently, no rodent species have been unequivocally identified as dispersers and it is still unclear which rodents consume seeds without dispersing them. The best studied putative disperser in the fynbos is the Cape Spiny Mouse (*Acomys subspinosus*) (Muridae), which is thought to scatter-hoard *Leucadendron* (Proteaceae) seeds in

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very small caches, typically containing only a single seed (Midgley et al., 2002; Rusch et al., 2013a). *A. subspinosus* was implicated as a disperser because it was one of the dominant rodents found in the community where the tagged, nut-like seeds were being buried. They were also observed burying seeds in captivity (Vlok, 1995; Midgley et al., 2002). Numerous nut-seeded plant species occur outside the habitats typically associated with *A. subspinosus*, and one study found that the hairy-footed gerbil (*G. paeba*) is a dominant rodent species found within the sandy habitats where the nut seeds of *Willdenowia incurvata* (Restionaceae) (*Thunb*) H.P. Linder were frequently buried (Midgley and Anderson, 2004). The 4-striped mouse (*Rhabdomys pumilio*) was recorded in both studies during the day, and the role that this rodent plays as a seed consumer or disperser is yet to be investigated (but see White et al., in press). Seed dispersal by a diurnal rodent, such as *R. pumilio*, may be less likely because seed caching and retrieval during the day is probably more risky than during the night.

The primary aim of this study is to investigate the interaction between the rodent community of the strandveld and seeds of *W. incurvata* using remote camera footage and seed tracking. Preliminary, unpublished data suggested that *R. pumilio* and *G. paeba* are the dominant rodent species recorded during the day and night, respectively, and this study aims to test this observation. Considering the higher daytime predation risks, it is hypothesised that only *G. paeba* will be found adopting seed-caching behaviour and consequently seeds will only be dispersed at night. In contrast, it is expected that *R. pumilio* will only consume seeds and that seeds left out during the day will not be buried. Secondarily, this study aims to provide an ecological description of strandveld rodent behaviour including the burial depth of cached seeds, the distance seeds are moved, and how many seeds are cached together. Furthermore, if seed dispersal occurs at night, it is hypothesised that *W. incurvata* may have evolved a nocturnal seed release strategy to minimise the exposure to diurnal seed predators.

1. Materials and methods

1.1. Study location and system

Jakkalsfontein Private Nature Reserve is situated on the West Coast of Southern Africa between the Dwars Rivers North and South, 60 km north west of Cape Town and 15 km south east of Yzerfontein (33°25′S 18°15′E). The reserve is an 1800 ha protected area previously used as coastal farmland until 2001. A diversity of vegetation types have been classified on the reserve and these include dune thicket, sandplain fynbos (Low et al., 1998), Saldanha flats strandveld, Langebaan dunes strandveld, Hopefield strand fynbos, Atlantis sand fynbos, Cape seashore vegetation, Cape lowland freshwater wetlands, and Cape inland salt pans (Rebelo et al., 2006). The reserve experiences a typical Mediterranean climate, with rainfall (253 mm per annum) falling predominantly in winter.

The study was conducted on an Atlantis and Hopefield sand fynbos section of the reserve. These fire-prone vegetation types are both classified as endangered and vulnerable, respectively, (Mucina and Rutherford, 2006). *W. incurvata*, the focal plant of this study, is one of the dominant native species of these vegetation types (Low et al., 1998).

1.2. Study species

W. incurvata (Restionaceae) (vernacular name: Sonkwasriet) is an endemic CFR plant, widely distributed within the Western and Northern Cape of South Africa, and represents a typical element of the strandveld. Female plants produce a nut which has a hard surface and a pitted wall. These seeds are 7–9 mm long, 5–6 mm in diameter, and brown in colour, with elliptical shape, and possess neither an elaiosome nor wing appendage. The seeds also have a thick, hard hull, and are produced in large quantities during the early summer months (October/November) (Linder et al., 1998). These traits suggest that *W. incurvata* may be dispersed by rodents (Midgley and Anderson, 2004). The hairy-footed gerbil *Gerbilliscus paeba* (A. Smith 1836, previously Gerbilluris paeba - see Knight et al., 2013; Monadjem et al., 2015) is a small, noctural Murid rodent with a wide distribution in the arid parts of the south western Cape (Davis, 1974). Stutterheim and Skinner (1973) observed that laboratory-held *G. paeba* females bury food stuffs into single larders, usually in the corners of enclosures, while males buried food stuffs in numerous places inside an enclosure. Diet has been recorded as seed dominant in the Kalahari and foliage dominant in the Karoo, but overall diet also includes arthropods (Nel, 1978; Kerley, 1989). *R. pumilio* (Muridae) is a small, diurnal murid rodent (Schradin and Pillay, 2004). *R. pumilio* occupies a variety of habitats in southern Africa including grasslands, marsh, forests, semi deserts, and deserts. Diet includes vegetation and arthropods; however, seeds are the preferred diet when available (Smithers, 1986).

1.3. Study site

A stand of *W. incurvata* inside Jakkalsfontein Private Nature Reserve was chosen as the study site. This area was approximately 8 ha and dominated by mature *W. incurvata* bushes with clear sandy areas between them. This site was selected as it was not invaded and *W. incurvata* was common, but not dense enough to make seed tracking difficult. Inside this site, 4 transects were laid down in straight lines approximately 200 m in length and spaced approximately 100 m apart.

2. Determining the rodent community

To determine whether different rodents were active during different times of the day, 34 Sherman traps were placed into the field in the 4 different transects. Ten traps were placed in the first transect, due to its slightly longer length, while the other 3 transects each had 8 traps. Traps were spaced 20 m apart and placed under *W. incurvata* bushes where rodent tracks were evident. Trapping was conducted for 2 sessions of 7 consecutive days and 7 consecutive nights during April/May 2015. Trapping was conducted under ethical approval by the Research and Ethics Committee (REC): Animal Care and Use of Stellenbosch University, protocol number SU-ACUD15-00021 and with permission by Cape Nature, permit number 0056-AAA008-00056. Nocturnal trapping commenced when traps were set at sunset and ended at sunrise when traps were checked for a final time. Diurnal trapping commenced at sunrise and ended at sunset when traps were checked for a final time. Traps were baited with peanut butter and a trail of oats leading into the traps which contained a slice of apple inside for moisture to hydrate trapped rodents. Traps were checked every 3–4 h and occupants of traps were recorded to species level along with time of capture. The individual was released immediately and the trap was left shut until the next session commenced. Captures may not be independent as the same rodent could have been captured more than once. The differences between nocturnal and diurnal captures were analysed using a Pearson chi-squared test in SPSS statistics (version 23).

3. Nocturnal versus diurnal seed fate

To determine whether the fate of seeds differed between night and day, 2 depots of 10 tagged *W. incurvata* seeds were laid out inside each of the 4 transects spaced 40 m apart on the soil surface for 7 consecutive days and nights in April/May 2015 following rodent trapping. To track seeds, fluorescent yellow Dacron tags (10 cm long) were attached to a sanded down portion of the *W. incurvata* seed using non-toxic and odourless Pratley's Putty (described in Rusch et al., 2013a). This allowed the seed to be tracked using a UV torch during the night. Tags were barcoded using a coding system so that transect, depot number, and time of field placement could be associated with the seeds. The

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