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Dispersal of semi-fleshy fruits to rock crevices by a rock-restricted rodent

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Seed dispersal allows successive generations of plants to be mobile in space and time. *Heeria argentea*'s unusual fruit and its ubiquity in extremely rocky habitats, suggests that this tree requires a specialist disperser. We therefore investigated the dispersal ecology of *H. argentea* and *Hartogiella schinoides*. We found *M. namaquensis* rapidly removed *H. argentea* and *H. schinoides* fruits, moving them short distances within and between rock outcrops, and consumed only the pericarps. Birds were observed consuming *H. schinoides,* but not *H. argentea* fruits, suggesting *M. namaquensis* is its sole, specialist disperser. Most *H. argentea* seeds (65%) with removed pericarps germinated successfully, while intact fruits did not. We show rock outcrops represent fire refugia, allowing *H. argentea* trees to grow to large sizes, with small stems and a co-occurring, wind-dispersed tree, *Widdringtonia nodiflora* found away from these sites. This rodent–tree mutualism is perhaps the clearest global example of directed dispersal and shows that these endemic trees are highly adapted for survival in the southwestern Cape habitat and are not tropical relicts.

Significance:

- The fruits of rock-restricted Cape trees are directly dispersed by rock rats to rock outcrops. This is the first description of rodent dispersal of fleshy fruits in South Africa.

- This species-specific interaction allows for rapid germination of seeds and protection from frequent fires for adults. This rodent–tree mutualism is perhaps the clearest global example of directed seed dispersal.

Introduction

Seed dispersal allows plants, via their seeds, to be mobile in space and time. The spatio-temporal locations at which seeds arrive have a major influence on the subsequent fitness of offspring, as location is a major determinant of seed and seedling survival. Many small patches of fire-avoiding forest exist in a wider sea of fire-prone shrublands and savanna across South Africa. In the southwestern Cape, these forests are restricted to growing in extremely rocky habitats, such as on cliffs and amongst rock outcrops and screes.[1]

The dynamics of these forests are different to that of the adjacent shrublands (known as fynbos) where post-fire recruitment from long-lived seed banks of non-fleshy fruits dominates.[2] For example, many Proteaceae as well as *Widdringtonia nodiflora* (mountain cypress; Cupressaceae) are serotinous trees with dry, wind-dispersed seeds that grow in the open shrublands. In contrast, forest tree fruits are typically soft and non-dormant. *Heeria argentea* (rockwood) and *Hartogiella schinoides* (spoonwood) (sensu Islam et al.[3]) are important constituents of these forests. *Heeria argentea* has pale, yellow-green, leathery-coated fruits up to 30 mm in diameter with a 3 mm thin, fleshy pericarp surrounding a single, soft, chlorophyllous seed (Figure 1a,b). Similarly, *H. schinoides* seeds are chlorophyllous but the fruit is smaller (diameter = 15 mm) and more visually distinct being a dark, red colour (Figure 1c,d).

Birds are unlikely dispersers of *H. argentea*, because the fruits are unattractive and unrewarding. Marloth[4] suggested that *Procavia capensis* (rock hyrax) is the primary disperser of *H. argentea*. Presumably his main evidence was their overlapping distributions, both being rock-restricted, and the unusual fruit. Although there are no data, others have cited this hypothesis.[5,6] We investigated the dispersal ecology of these fruiting species based on Marloth's hypothesis.

Methods

Data were collected in April and May 2016 at seven sites in the Limietberg Nature Reserve (33.620355°S, 19.106678°E) in the southwestern Cape, South Africa. *H. argentea* fruits were collected directly off trees in April 2016. The fruits ripen and fall to the ground over several months in the austral summer (personal observation). We placed 5–10 *H. argentea* fruits at depots for 3 days, with six depots per site (n_{total} = six sites; n_{total} = 330 fruits); four sites were in rock outcrops and two sites were in adjacent non-rocky proteoid shrublands. To locate moved fruits, each was attached to a reverse-wound bobbin with fast-setting non-toxic glue. At each depot (placed ± 50 m apart), we used a LTL Acorn 6210M remotely activated camera trap (Shenzen LTL Acorn Electronics Co., Shenzen, Guangdong, China) to monitor animal–fruit interactions. Cameras were set to record one photograph, immediately followed by a 30-s video. Each time an animal interacted with a novel fruit or entered/left the field of view it was considered a new event. For *H. schinoides,* we followed a similar, scaled-down experiment, placing out six depots at a single site with 10 fruits per depot. No camera traps were used in this experiment.

Germination trials were conducted on intact and handled *H. argentea* fruits (n = 40 of each) over 6 weeks at the University of Cape Town's glasshouse. Fruits were placed in individual trays on the surface of a potting soil medium and watered once a week. We used a chi-squared test in the R programming language[7] to compare overall germination of fruits.

Scale bar = 2 mm

Figure 1: Intact and cross-sectioned fruits of (a,b) *Heeria argentea* and (c,d) *Hartogiella schinoides*, showing the thin, fleshy pericarps and chlorophyllous endosperm/embryo.

We investigated fire impacts on *H. argentea* and *W. nodiflora* individuals 1 year post-fire. We measured the basal diameter (mm) of *H. argentea* and *W. nodiflora* adults in relation to distance within and from the outer edge of rock outcrops (defined here as a collection of rocks ≥ 2 m^2). We estimated the fire damage by rating the proportion of the canopy dead in *H. argentea* and *W. nodiflora*. All individuals were surveyed within a 0.6-ha area that included both shrublands and rock outcrops. Beta regression[8] in R[7] was used to determine the relationships between tree size, distance to rock outcrops and fire damage. Reported values are mean ± standard deviation.

Results

Rock outcrops

Within only 3 nights, 6.63±3.85 fruits per depot were removed (total = 66%; n=159/240). Of these 159 fruits, 31% were located and collected, and 40% were not retrieved, but were tracked to a minimum distance until the thread either snapped or was dislodged. The remaining 29% were considered lost, likely as a result of thread failure.

Of the 159 moved fruits that left a thread trail, we determined that 90% of these had been moved at least 0.3 m into rock outcrops 3.26±3.77 m from the initial depot. Of these dispersed fruits, 92% had more than 75% of the pericarp removed (Figure 2a,b). None of the chlorophyllous seeds were visibly damaged. Seeds with pericarps did not germinate (n=0/40) whereas seeds with removed pericarps did (n=26/40, 65%; X^2=31.5, d.f.=1, p<0.001; Figure 2c).

Despite observation of their droppings within 50 m of all sites, only one rock hyrax was recorded on camera at one depot and this individual did not interact with the fruits. Instead, *Micaelamys namaquensis* (Namaqua rock rat) was the most frequently viewed small mammal on camera trap observations (n=151) and was the only animal viewed removing fruits in the rock outcrop sites (n=100 events) (Supplementary video 1). No bird visitation was documented. Fruits were typically moved out of the camera field of view but at one site we observed a Namaqua rock rat

consuming the pericarp (Supplementary video 2). We also viewed the following carnivores on the camera trap observations: *Genetta tigrina* (Cape genet) and *Galerella pulverulenta* (Cape grey mongoose), neither of which interacted with fruits.

Dispersal of *H. schinoides* appeared to follow the same pattern. Within 3 days, 80% of fruits (n_{total} = 60) were removed and 58% of these were located (n=28), with 93% of those moved to rock outcrops and 68% had their full pericarp removed. We incidentally observed *Onychognathus morio* (red-wing starlings) feeding on *H. schinoides* fruits.

Shrublands

Fruits were rarely moved (2.25±2.31 per depot; 16% of n=90) at shrubland sites, with most located (n=11/14). Fruits occasionally showed the pericarp slightly consumed (n=11), with the pericarp never fully removed. All moved fruits were discarded in the open on the soil surface. Camera trap observations showed that the four small mammal species recorded usually ignored fruits (Supplementary video 3). These species included *Rhadbomys pumilio* (four-striped grass mouse) (n=92), *Otomys irroratus* (vlei rat) (n=46) and *Acomys subspinosus* (Cape spiny mouse) (n=14), as well as occasionally *Hystrix africaeaustralis* (Cape porcupine), with only *R. pumilio* occasionally interested in *H. argentea* fruits (removing n=10 fruits).

Plant distribution and fire damage

Heeria argentea trees were distributed on the margin or within rock outcrops (64%), and 36% were found away from rock outcrops. Large adult *H. argentea* trees were typically found far within rock outcrops (-2.65±2.89 m) and lacked any fire damage. Small *H. argentea* trees were mostly found away from rock outcrops (7.83±8.94 m) and often received full top-kill from fire damage (53% of n=139 trees)(see Figure 3). *W. nodiflora* was never found within rocky refugia and always experienced full top-kill from fire damage. Both basal diameter (estimate ± s.d. = -0.04±0.01, z=-3.57, p<0.001) and distance relative to rock outcrops (0.06±0.01, z=4.58, p<0.001) were significant predictors of fire damage in *H. argentea* (pseudo R^2 = 0.46).
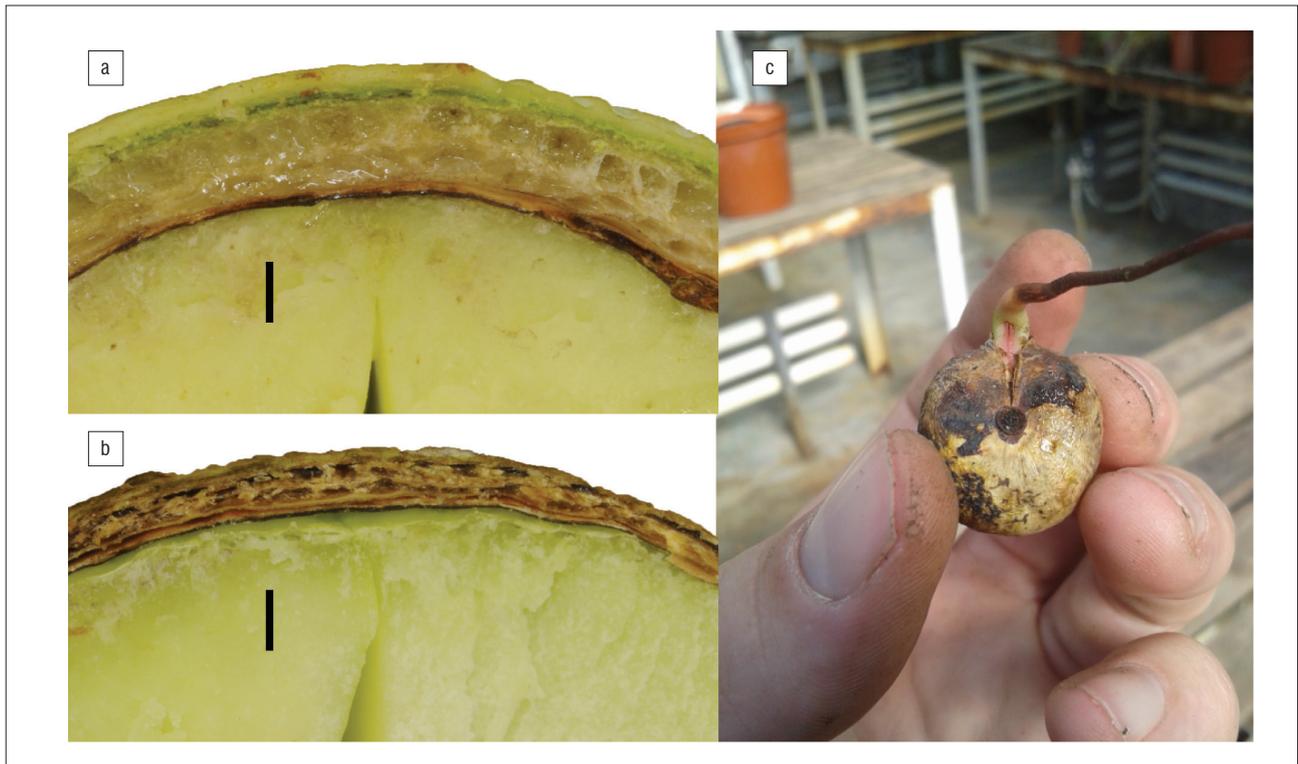
(a,b) Scale bar = 1 mm

Figure 2: Cross-section of *Heeria argentea* fruits that are (a) intact and (b) with the pericarp removed showing the fleshy layer that Namaqua rock rats consume. (c) A germinated seed with the radicle breaking through a fruit without the leathery pericarp.
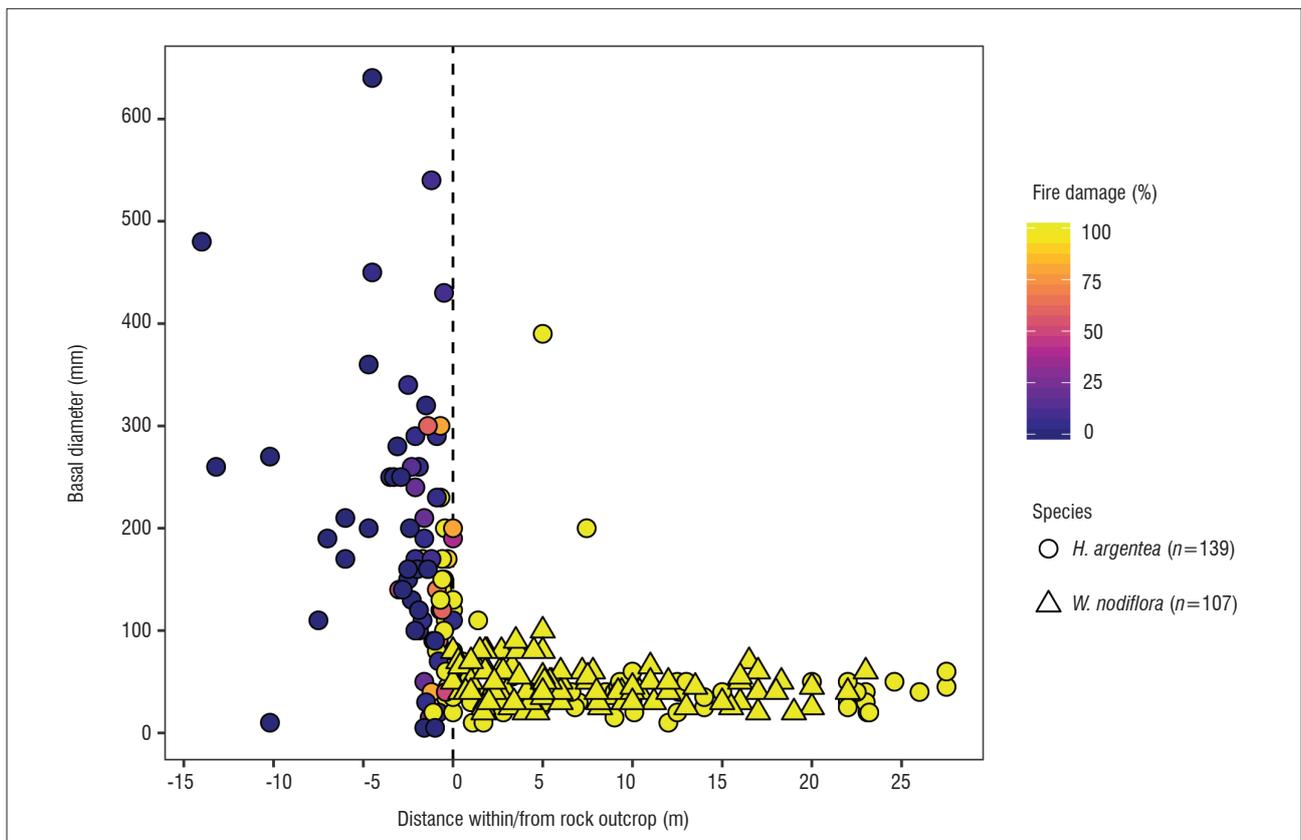
Figure 3: The proportion of canopy damage from a recent fire to *Heeria argentea* and *Widdringtonia nodiflora* trees of different sizes within (negative) and from (positive) rock outcrops.

Discussion

The rapid rate of fruit removal and pericarp consumption showed that the fruits of both *H. argentea* and *H. schinoides* are highly attractive and rewarding to Namaqua rock rats. Our findings thus lead to the rejection of Marloth's[4] original hypothesis. As the seeds have no dormancy, germination is not stimulated by fire, or its products, unlike most seeds in fire-prone ecosystems.[2] *H. argentea* is thus dependent on rock rats for dispersal and rapid initiation of germination. Avoiding predation by carnivores may explain why Namaqua rock rats take fruits to narrow and concealed crevices before consuming the pericarp layer.

The fruit dispersal patterns of *H. schinoides* also suggest Namaqua rock rat dispersal. Their fruits are smaller and dark red in colour – likely an adaptation for bird frugivory. We observed bird frugivory on *H. schinoides* fruits, but never observed birds feeding on *H. argentea*. The fruit of *Heeria* is likely too large for the gape of most local frugivorous birds and, as the seed is soft, pecking, biting or ingestion could destroy it. Further, birds would not likely disperse the seeds into crevices. As Namaqua rock rats also feed on *H. schinoides,* they are likely generalist frugivores.

The significance of dispersal to rock outcrops is not immediately apparent, as these may be poor sites for initial seedling growth. The large seed, and consequent large energy stores, of *H. argentea* may facilitate some growth in deep shade (Figure 4). Large *H. argentea* trees were mostly found within rocky refugia where they experienced almost no fire damage. In contrast, small stems were found away from fire refugia and generally experienced full canopy death. This difference suggests that individuals in less rock-protected sites are condemned to small size and likely reduced reproductive capacity as a result of frequent top-kill and consequent basal resprouting after repeated burning. Wind dispersal of *W. nodiflora* seeds appears to prevent arrival in rocky refugia because no individuals were observed within rock outcrops. Unlike *H. argentea*, all *W. nodiflora* trees experienced full top-kill during the recent fire (Figure 3).

Aspects of the *H. argentea*–Namaqua rock rat interaction are unusual. Firstly, rodent dispersal of fleshy fruits is a novel dispersal mechanism in the Cape. Rodents may be dispersers of non-fleshy, dry seeds typically by scatter-hoarding.[9,10] Namaqua rock rat dispersal of *H. argentea* differs from most other small mammal dispersal. In other rodent frugivory cases, the fruits may be partially damaged.[11-14] Globally, rodent frugivory, in which the seed is not ingested and left undamaged, has only been documented in a few studies.[13,15] Exotic rodents have been documented to disperse seeds while only consuming the pericarp.[13] By consuming only the pericarp, Namaqua rock rats still achieve a reward while leaving the seed intact. Secondly, this is an example of directed dispersal in which fruits disproportionately arrive at non-random, fire-protected destinations that are highly favourable sites for survival.[16]

The three classic examples of directed dispersal are somewhat controversial. Mistletoe seedlings can only establish on thin, sun-exposed branches with only specific bird species, such as *Dicaeum hirundinaceum* (mistletoebirds), considered able to disperse seeds to these sites. That generalist birds, marsupials[17], explosive seed release[18] and the wind[19] also effectively disperse mistletoe seeds weakens this argument. Myrmecochory (ant-dispersal) has been suggested as a mechanism for directed dispersal to ant nests (localised sites of high nutrients in nutrient-poor shrublands), but some evidence suggests otherwise.[20,21] Scatter-hoarding by rodents can be 'directed' to sites of low adult conspecifics.[22] However, the benefit of these sites is escape from seed predators. *H. argentea* fruit dispersal is possibly the clearest global example of directed dispersal – too short-distance, site-specific and beneficial to established plants (rather than seedlings), to be explained by escape of seed or seedling predators or by colonisation of prime sites by seedlings.[16]
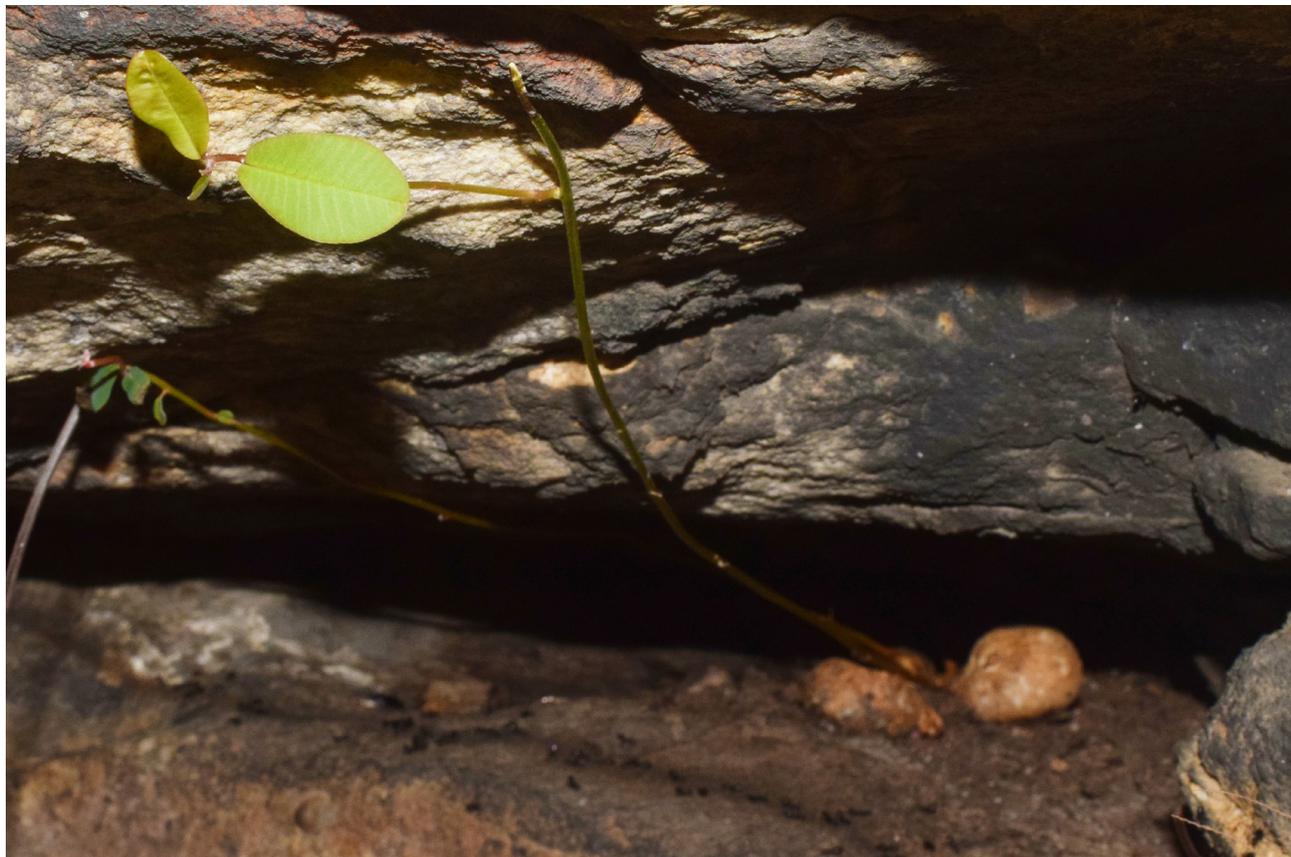
Figure 4:   A *Heeria argentea* seedling emerges from a dark, rocky crevice at Limietberg Nature Reserve.

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Authors' contributions

J.J.M. conceptualised the study. Both authors contributed to data collection and writing. J.D.M.W. did the data analyses.

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