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The function of plants collected by bush Karoo rats (*Otomys unisulcatus*): Do dried up food plants represent stored food?

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ABSTRACT

Food storing to cope with food reduction during winter has been observed in many rodents in the northern hemisphere. Food storing could also be adaptive in semi-deserts of the southern hemisphere, which experience food-restricted dry seasons. We studied the function of dried food plants found at the stick lodges of bush Karoo rats in a semi-desert in South Africa. We performed 998 focal animal observations and monitored 12 lodges to record the fate of plant pieces carried back to the lodges. Collected plant species were eaten green (68 %), eaten as plantong (12 %), incorporated into the structure of the lodge (11 %), or their fate was unknown (9 %). Especially succulents carried back to the lodge dried out, forming what we refer to as plantong. This happened mainly in the food rich moist season. However, plantong was not stored from the moist to the dry season but was consumed within 6 ± 5 days. Bush Karoo rats readily ate plantong presented to them experimentally. We regard plantong as leftover from food freshly consumed at the lodge, but not as food collected in the moist season to be stored for later consumption during the dry season.

1. Introduction

Collecting and storing food is an important adaptation of many small mammals, especially rodents living in seasonal environments. Red squirrels (*Tamiasciurus hudsonicus*) and European hamsters (*Cricetus cricetus*) store and hoard food for the winter (Hurly and Robertson, 1990), when seasonal cold greatly reduces food availability (Van Vuuren and Armitage, 1991). Rodents mainly store nuts and seeds (Blendinger and Díaz-Vélez, 2010; Den Ouden et al., 2005) or grass dried as hay (Batzli and Pitelka, 1970; Murie and Elbroch, 2005). In arid regions of southern Africa, small mammals collect seeds which retain moisture over long periods, permitting longer storage (Huntley, 2023). Stored food enables small mammals to survive through the food-restricted season (Olenev and Grigorkina, 2014), when conditions are energetically and nutritionally demanding (Day et al., 1999).

Climatic seasonality influences the availability of food plants. Winter in the northern hemisphere is associated with long, harsh, and often snowy conditions when plants either die off or stop growing (Banks and Dickman, 2000; Korslund and Steen, 2006). In arid regions, lack of water and heat can lead to a halt in plant growth (Cowling et al., 1999). This might especially impact herbivorous animals. Semi-deserts are characterised by seasonally high plant productivity, which could theoretically allow small mammals the opportunity to store food plants for the forthcoming food-restricted dry season.

While seeds, grasses and herbs can be stored as hay, it is unclear whether succulent leaves can or are stored as food. There is ample information on the nutritional quality and its seasonal variation of grasses, herbs and foliage from a variety of dry areas (e.g., Feldt et al., 2017; Namukonde et al., 2023; Schlecht and Susenbeth, 2006; Stolter et al., 2022). Nutritional quality is linked to high protein and energy content. Energy can be derived from fat, protein and carbohydrates that are either soluble (sugars) or part of structural components, such as neutral detergent fibre (NDF) as parts of the plant cell wall. Animals can digest parts of NDF with the help of specialised digestive morphology and

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microbial fermentation. Apart from providing energy, proteins are essential for growth, maintenance, and reproduction (Speakman, 2008). Protein and other chemical contents are key in the nutritional ecology of animals and their availability is affected by season. Different plants differ in nutritional value, and one might expect animals to store food of high nutritional value (Ortmann et al., 2006; Schradin and Pillay, 2006). Little information is available about the availability and nutritional value of succulent plants used by herbivores (Dröscher et al., 2016).

We focussed on the feeding and potential storage of plants by bush Karoo rats (*Otomys unisulcatus*) in the Succulent Karoo of South Africa (Figure S3 a). The Succulent Karoo is home to South Africa's smallest folivores, the bush Karoo rat and the closely related whistling rats (e.g., *Parotomys* sp.), with a body mass of only 100 g. These species feed primarily on leaves that are brought back to their burrows (Jackson et al., 2002). An important adaptation of the bush Karoo rat to its seasonally arid environment is the construction of stick lodges within shrubs (Figure S3 c) (Brown and Willan, 1991; Jackson et al., 2002; Schradin, 2005). The stick lodges provide protection against extreme weather conditions such as heat (temperatures above 40 °C) in summer and frost in winter (Brown and Willan, 1991; Du Plessis, 1989; Jackson et al., 2002; Vermeulen and Nel, 1988). Bush Karoo rats are central place foragers, foraging in a radius of 10–20 m around their lodges and carrying food back to the safety of their lodges (Vermeulen and Nel, 1988; Jenkins and Breck, 1989). They store food plants in stacks on and around the lodge, showing characteristics of larder hoarders and central place foragers (Vermeulen and Nel, 1988; Jenkins and Breck, 1989). At least some food plant species left around and, on the lodges, dry out and become "plantong", a term derived from the Afrikaans combination of plant and tong, meaning a strip of dried plant (Figure S3 b). The function of plantong for bush Karoo rats remains unknown: It could function as food, as building material, or have no function but simply represent non-used plant material brought to the lodge which decomposes there. While it is plausible that plantong represents a stored food source, empirical evidence for a species storing succulent leaves is not known. Alternatively, plantong could be part of the material used to build lodges, the wooden parts becoming part of the lodge while the leaves decompose.

Our aim was to determine the function of plantong collected by bush Karoo rats. Our objectives were to: (i) establish which plant species are carried back to the lodge; (ii) compare the nutritional value of food plants and plantong to other plant species; (iii) assess whether there is seasonality in plantong collection and consumption, (iv) ascertain the fate of plantong over time, i.e. whether it is eaten, becomes part of the lodge structure, or disappears, and (v) to test experimentally whether bush Karoo rats eat plantong.

2. Material and methods

2.1. Study site

The study was conducted at a field site of 4.5 ha next to the Succulent Karoo Research Station (SKRS) in Goegap Nature Reserve in the Northern Cape, South Africa. The area is semi-arid and dominated by Succulent Karoo vegetation, especially annual succulents and ephemeral herbs, as well as single standing *Tetraena retrofracta* and *Lycium cinereum* shrubs inside which bush Karoo rats build lodges (Jackson et al., 2002; Keller and Schradin, 2008). The study area receives an average of 160 mm of rainfall per year (Jackson et al., 2002; Schradin, 2005) with temperatures ranging from −5 °C in winter to 42 °C in summer (Schradin, 2005). The study took place from January 2022 until July 2023 and covered all seasons, with winter (June–August) and spring (September–November) being the cold moist seasons, and summer (December–February) and autumn (March–May) the hot dry seasons.

2.2. Trapping

Adult bush Karoo rats were trapped with foldable Sherman traps and locally produced Sherman-like metal traps. Traps were baited with a mixture of bran flakes and sunflower oil and placed in the shade around stick lodges. Trapping was done both in the morning and afternoon for 1.5 h. The bush Karoo rats are diurnal and therefore active in the early hours of the morning and late afternoon before the sun set. Traps were checked twice at an average interval of 30 min between checks in the morning and once in the afternoon. Six areas were trapped in the field site of which two were trapped simultaneously for 3 days by two people, before moving on to the next two areas. The sex of trapped individuals was ascertained by examination of the ano-genital distance (shorter in females than males), and their body mass was recorded with an electronic scale (accuracy 0.1 g). For identification of individuals, we attached metal ear tags with a unique code on each ear (National Band and Tag Co., Newport, KY, U.S.A.) (Schoepf and Schradin, 2012). To allow for identification of individuals during behavioural observations (see below), the rats were individually marked with non-toxic hair dye (Inecto Rapido, Pinetown, South Africa) of different colours (black, red, blonde) in different patterns onto the pelage of the rats. Rats were released at their site of capture or taken to a nearby laboratory at the research station located about 5 min away from the field site for experiments in captivity (see below).

2.3. Behavioural observations

998 behavioural observations were conducted by several field assistants and researchers on 121 lodges, representing 164 different bush Karoo rats to ascertain which plant species the bush Karoo rats fed on, which ones were carried back to the lodge, and which ones became plantong. Bush Karoo rats were habituated to the presence of observers which allowed us to conduct focal animal observations at their lodges. Observations were done approximately 5 m away from the lodge in the early morning at sunrise and in the late afternoon before sunset sitting on a chair directly in front of the bush karoo rat lodges. Before observations started, all food plant species carried back by the rats to the lodge were recorded. The food plant pieces were categorised as fresh (plant pieces collected on the same day), green (plant pieces that looked older but not dry), or dry plantong (plant pieces completely dry). Behavioural observations involved focal animal sampling for 30 min using the naked eye or with the help of binoculars. All behaviours were recorded every minute per individual rat. Recorded behaviours included whether the individual carried sticks or food plants, and whether it was feeding, which plant species was eaten and the category of plant: fresh, green, or plantong.

From these data, we collected information about the plant species at the lodge, and whether they were fresh, green, and plantong. We ranked them on how commonly they were observed to generate frequency scores. This allowed us to generate the ratio of food plants to non-food plants recorded at lodges. Furthermore, we used data collected during nest observations to analyse what plant species were consumed on site, stored as plantong, or carried for lodge building.

2.4. Plant species abundance around lodges

Plant surveys were done around 12 randomly selected and occupied bush Karoo rat lodges. Surveys were done in September 2022, December 2022, March 2023, and June 2023. A square area of 10 m × 10 m with the lodge at the centre was marked using 4 iron rods. Within the square, all plant species, and the percentage of the area they covered were recorded. Plants were categorised as succulents when they head thickened, fleshy leaves for storing water, and we differentiated between annual succulents and perennial wood building succulent shrubs. Non-succulent plants were categorised as either annual herbs (including wildflowers), grass, or perennial shrub, depending on growth form.

Plants were identified using the "Namaqualand Wildflower Guide" (leRoux et al., 1997) and with the help of a local botanist.

2.4.1. Marking of plant pieces

To assess the fate of fresh plant pieces found at the lodges (presumed to have been carried there by the rats), we marked 12 pieces of fresh plant pieces at each of the 12 lodges that were used to ascertain the abundance of plant species. If any lodge was abandoned by the bush Karoo rats before data collection was finished, a new lodge was selected for the study, increasing the number of lodges used to 24. Lodges were divided into two groups of six each, with one group being checked on the same day, and the other six on the next day. Lodges were monitored for five days a week from July 2022 until August 2023.

Plant pieces were marked using non-toxic food dye which was applied using a 250 ml spray bottle. A pilot study in captivity showed that food dye did not influence plant selection and consumption. When a piece of marked plant pieces disappeared, we marked a new fresh piece of the same species that was closest to the position of the plant piece that disappeared, such that each lodge always had 12 marked plant pieces, unless there were less than 12 pieces at a lodge (often in summer and autumn). Fresh plant pieces were chosen because they allowed us to follow their fate from the day they were brought to the lodge until they were consumed green, as plantong, became part of the lodge or disappeared.

The condition of all marked plant pieces was recorded three times a week as follows: 1) was it present or had it disappeared; 2) the state of the plant pieces (fresh, green or dry = plantong); 3) the position of plant pieces in relation to the lodge (base, middle or top); and 4) the final fate of the plant, such as eaten green (bite marks and disappeared within a 1–3 days from being marked), eaten as plantong (dry plant piece with bite marks that then disappeared), became lodge building material (plant pieces stacked within the lodges; as a result, often becoming covered and thus not visible over time anymore), unknown (plant pieces that were marked and its final fate was unknown).

2.5. Nutritional value of plant species

We compared the nutritional value of (1) food plants versus non-food plants for bush Karoo rats, and (2) plant species that became plantong versus species that did not. For this we used data from 61 plant samples (averaging at 6.46g; leaves and flowers) of 35 plant species collected in 2017 within the field site (Table S1). Samples were dried at room temperature, weighed daily until they reached a stable weight, and were then analysed at the University of Hamburg, Germany. Samples were analysed using standard methods (Ortmann et al., 2006; Rothman et al., 2012). The dry raw material was ground in a Retsch mill to a homogenous powder. The ground plant material was dried again at room temperature overnight prior to chemical analyses to obtain accurate and reliable measurements of their chemical composition. Nitrogen was measured using the Kjeldahl method. The nitrogen concentrations were multiplied by 6.25 to obtain a measure of crude protein as part of the estimation of the energy content (see below). Soluble carbohydrates (sugars) were extracted with 50 % methanol. Concentrations of sugars were determined as the equivalent of galactose after hydrolysation of 50 % methanol extract. Samples were analysed for neutral (NDF) and acid (ADF) detergent fibres, with NDF representing all the insoluble fibre (cellulose, hemicellulose, and lignin) and ADF, representing the fibre fraction containing cellulose and lignin. Lipid content was determined by extraction using petroleum ether, followed by evaporation of the solvent. We measured condensed tannins as equivalents of quebracho tannin (Oates et al., 1977), and we assessed polyphenols following Folin-Ciocalteu (Stolter et al., 2009). We analysed alkaloids qualitatively via triple assays with Mayer's, Dragendorf's, and Wagner's reagents (Cromwell, 1956). A sample was considered to contain alkaloids if all three reagents indicated the presence of alkaloids.

2.5.1. Calculation of energy content

We estimated the total available energy content of the plants derived from crude protein, total non-structural carbohydrates (TNC) and NDF. Concentrations of total non-structural carbohydrates (TNC) were calculated as %TNC = 100 % - %crude protein - %NDF - %lipids - %ash (Conklin-Brittain et al., 2006). Most lipids in green plant parts are waxes that are part of the cuticula of plants to reduce water loss. These waxes are not digestible for herbivorous mammals and are not assumed to contribute to their energy uptake. We used energetic values of 4.2 kcal/g for crude protein and for TNC (National Research Council, 2003). NDF consists of a non-digestible fraction and a mixture of components that are associated with the cell wall but can be digested by fermentation. Energy from the digestible portion of fibre (NDF) is available via fatty acids produced by anaerobic microbes during hindgut fermentation. Since these microbes use some of the energy for their own growth, the energy available from 1 g of the digestible portion of NDF is about 3 kcal/g (Conklin-Brittain et al., 2006). We assumed that NDF digestibility by the bush Karoo rat is equivalent to fibre digestibility by the similar sized *Neotoma lepida* (Woodrats), small rodent herbivores with a body mass of about 150 g. The mean fibre (NDF) content in our sample was 25.28 %. Woodrats of 150 g were able to digest about 40 % of the NDF in a diet containing 25 % NDF (Justice and Smith, 1992; their figure 3). Thus, the energy provided by 1 g of NDF is estimated as 3 kcal/g * 0.40 (the digestibility of NDF) = 1.2 kcal/g. In summary, we estimated the physiological fuel value of 100 g dry plant material as 4.2 kcal * % crude protein +4.2 kcal * %TNC +1.2 kcal * %NDF.

2.6. Experimental plantong presentation

Plant preparation. Fresh plant pieces were collected within the compound of the Succulent Karoo Research Station without any impact on the field site. The plant pieces were collected from the three most abundant food plant species on our field site, all being succulents: *Galenia sarcophylla, Mesembryanthemum guerichianum,* and *Mesembryanthemum (Psilocaulon) subnodosum*. The plant pieces were cut into pieces of 1.5 g (fresh material) which is similar to the sizes selected and carried by the bush Karoo rat in the field. Half of the plant pieces were frozen, and the other half dried as plantong in a plastic box with holes placed in the sun to create a greenhouse effect. We initially preferred freezing the plant pieces rather than using fresh material since we did not expect to have access to fresh plant material for the trials in the dry season. To test whether freezing had an effect, we also presented fresh plant pieces during trials in the moist season (see below).

Experimental procedure. A total of 72 individuals were used for the study. We conducted experiments with three different treatments (Table 1). Bush Karoo rats were trapped early in the morning. Four individuals were captured per day and tested individually. All experiments started at 9:00 a.m. in a field laboratory at room temperature. Experiments lasted 3 h.

Table 1
Details of feeding experiments conducted with captive Bush Karoo rats. Plant species that were used for experiments were Mesembryanthemum guerichianum, Mesembryanthemum (Psilocaulon) subnodosom, and Galenia sarcophylla.

Experiment	Sample size	Period of experiment	Plant pieces condition
1	24 24	Moist season (September–October 2022) Dry season (March 2023)	Frozen and dried plant pieces of three species (6 pieces in total)
2	24	Moist season (November 2022)	Fresh and dried plant pieces of three species (6 pieces in total)
3	24	Start of dry season (January 2023)	Fresh, dried, and frozen plant pieces of three species (9 pieces in total)

During the 3 h experiments, the bush Karoo rats were housed individually in tanks measuring 45x35 × 30 cm, furnished with wood shavings and provided with different food plant pieces, depending on the type of experiment (Table 1). The food plants were presented on a plastic tray at one side of the cage. Before the experiment, all plant pieces (fresh, green, and plantong) were weighed to 1.5 g mass each. After the experiment, the remains of the plant pieces (if any) were weighed to calculate how much was eaten by the bush Karoo rats. Plant pieces (previously frozen and fresh) placed outside but next to the cages were also weighed to account for loss of mass due to evaporation. The behaviour of the rats was video recorded using a Canon web camera during the 3-h feeding trial. The camera footage was later analysed using BORIS software to record the order (choice) in which the rats consumed different plant pieces (Friard and Gamba, 2016). To record choice, a score of 1 represented the plant eaten first, 6 represented the last plant pieces eaten and 7 represented food plants that were not eaten (Experiment 1 and 2). To record choice in experiment 3, we used a score of 1 to represent the plant eaten first, 9 to represent the last plant pieces eaten and 10 to represent food plants that were not eaten. Water was provided *ad libitum* during the experiments. At the end of the experiment, the bush Karoo rats were given bait consisting of a mixture of all-bran flakes, salt, and oil, provided *ad libitum* for 60 min to compensate for any lost foraging opportunities. The bush Karoo rats were then released to their lodges.

2.7. Statistical analysis

Statistical analyses were conducted in R (version 4.3.1) and SPSS with the model significance set at 0.05 (R Core Team, 2022). For our first objective, which was descriptive, we listed all plant species found at the lodges and ranked them according to how often they were observed. To analyse whether season influenced the abundance of food plants and plantong species within a 10 × 10 m area around occupied bush Karoo rat lodges, we used an ANOVA with a post-hoc test to compare seasons in pairwise combinations. Whether a plant species was used as food plants was known from our behavioural observations. Plant species around the lodges were categorised into four groups based on their use: collected for food, also collected for plantong, not used as plantong, and not collected as a food plant. To test whether bush Karoo rats were more likely to carry food than non-food plants to their lodge, we used a Wilcoxon matched pairs signed ranked test to analyse the percent each food plant represented of all plants carried back to each lodge against the percent the same food plants represented by all plants occurring around the lodge, with each lodge having one data point for each of the four seasons.

For our second objective about the nutritional value of plantong, we used unpaired t-tests to compare each chemical content between food- and non-food plants, and between plantong and non-plantong. We also used Spearman correlations to assess the strength and direction of the relationship between chemical content and abundance of plants collected for food and non-food species. For alkaloids we used a chi-squared or Fisher's exact test comparing plant species in which these values were positive (1) vs negative (0).

For our third objective on seasonal differences in the collection and consumption of plantong, we analysed the number of different plantong species found at the lodges in spring (September to November), summer (December to February), autumn (March to May), and winter (June to August). We analysed the number of plantong assumed to be eaten in the four seasons using a General Linear Mixed Model (GLMM) with formula (II) below, utilizing the R package lme4, AIC/BIC, and plotted residuals.

I. Number of plantong pieces at lodge = season + number of green plant pieces at the lodge + lodge number as random factor.
II. Number of plantong pieces eaten = season + number of green plant pieces at the lodge + number of plantong pieces at the lodge + lodge number as random factor.

Our fourth objective was to assess what happens to collected plant pieces over time. For each plant species, we analysed the most common outcome (i.e. always eaten green) with the other outcomes combined compared to an outcome by chance (50:50) using a Fisher's exact test. For example, when we marked 100 *Mesembryanthemum* pieces and found 90 to be eaten green, 4 to be eaten dry, 2 to be part of lodge building and 4 to be unknown, the ratio of 90:10 was compared to the null ratio of 50:50.

For our last objective on whether bush Karoo rats ate plantong in captivity, in each of the experiments (Table 1), we ran a linear mixed model (LMM) using the R package *lme4* (R Core Team, 2022) to analyse factors that influenced consumption and choice of food plant pieces, in which we included condition (fresh, dry or frozen) we ran LMM, using the formulae below (III).

III. % Consumption = plant species + condition + season +ID (individual ID as random factor).
IV. Choice (ranks) = plant species + condition + season +ID (individual ID as random factor).

3. Results

What plant species are carried back to the lodge?

Twenty plant species were recorded in the 10 × 10m plots around the 12 focal lodges, and 15 of these were food plants (Supplementary Table S1). From our behavioural observations at 137 lodges on the entire field site of 4.5ha, we identified 31 plant species of which 20 were food plants (Supplementary Table S2). Before behavioural observations, a total of 2847 plant pieces were recorded at the lodges, of which 615 were fresh, 954 green and 1278 plantong. Bush Karoo rats carried 20 species back to the lodge. Of these 20 plant species, 19 species were food species, except for *Aptosimum spinescens* that was observed twice at a lodge but never consumed. Some of the plant species were used both as food and for lodge construction (*Tetraena retrofracta, Salsola zeyheri,* and *Mesembryanthemum (Psilocaulon) subnodosum*). Seventeen plant species were recorded as dry plantong.

3.1. Comparison of nutritional value of food and plantong compared to non-food plant species

Plants with different growth forms differed significantly in most chemicals (Supplementary Table S3). Succulents (annuals and shrubs combined) had higher water and ash content, but very low fibre concentrations, while grasses stood out due to their high fibre contents. Various chemical components showed strong correlations among each other (Table S4). Most notably, the water content was highly correlated with the ash content ($r = 0.828$, $P < 0.001$, $n = 31$).

Food plants had significantly higher ash content than non-food plants and lower concentrations of sugar and total non-structural carbohydrates as well as lower energy content than non-food items (Table S5). The remaining chemical components were not significantly different between food and non-food plants.

Plantong plants had only half as much sugar concentrations than non-plantong plants but significantly higher ash content (Table S6). A higher percentage of plantong plants (90 %) contained alkaloids than non-plantong plants (48 %). The remaining chemical components did not differ significantly between plantong and non-plantong (Table S6).

3.2. Is there seasonality in plantong collection and consumption?

During behavioural observations, bush Karoo rats collected most plant pieces in the winter and spring, both moist seasons, and fewer plant pieces were collected in the dry summer and autumn seasons (Fig. 1a). A linear mixed model (model I) indicated that season was a significant predictor of plantong pieces recorded at a lodge, with most plantong being recorded in winter (LME; estimate = −0.78, s.e. = 0.057,

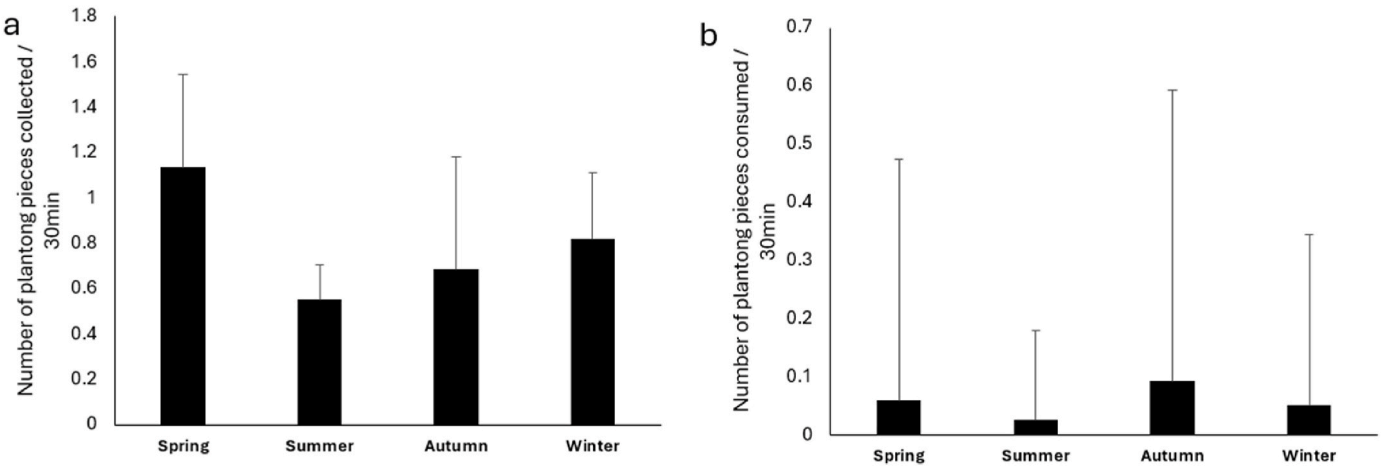

Fig. 1. Mean ± SD of (a) plant pieces collected during focal observations and (b) plantong pieces consumed during focal observations in the various seasons at the lodge during a total of 595 min observations.

CI: 0.32/1.2, $t_{1245.6} = -13.44$, P = <0.001) followed by spring (LME; estimate = −0.21, s.e. = 0.08, CI: 0.37/-0.05, $t_{1251} = -2.58$, P = <0.01) (Table S8). When there were more fresh green plant pieces at the lodge, then we also recorded more plantong pieces (p = 0.03, Table S8). The consumption of plantong was lowest in summer (LME; estimate = −0.07, s.e. = 0.028, CI: 0.12/-0.02, $t_{1211.4} = -2.56$, P = 0.01) and highest in autumn, though not significantly so (Fig. 1b; Table S9). The more plantong pieces were present at the lodge, the more we observed the rats to eat plantong (LME; estimate = 0.05, s.e. = 0.012, CI = 0.02/0.08, P = <0.001) (see Table S9).

3.2.1. *What happens to the plantong over time*

We investigated how the bush Karoo rat utilised the 12 different plant species that were marked at the 12 focal lodges. All 12 plant species were eaten green. Nine plant species were eaten as plantong, and nine plant species were used as lodge building material (Fig. 2).

Of all the plant pieces marked at the lodge over the study period, 68 % were eaten green while 12 % were eaten as plantong, 11 % were incorporated into the structure of the lodge and 9 % disappeared (assumed to have decomposed; Supplementary Table S10).

Over all 12 plant species were eaten green withing 4 ± 1 days. When they became plantong, then the plantong was eaten within 6 ± 4 days (maximum: 12 days).

3.3. *Do captive bush Karoo rats eat plantong?*

3.3.1. *Experiment 1. consumption and choice of dry vs frozen plant pieces in the dry and moist season*

Of the 48 bush Karoo rats tested, 39 individuals consumed plantong and frozen plant pieces, 6 consumed only frozen plant pieces, and 3 individuals did not eat anything. Significantly more frozen plant material than plantong was consumed (LME; $t_{248} = 11.39$, P = 0.001; Fig. 3,

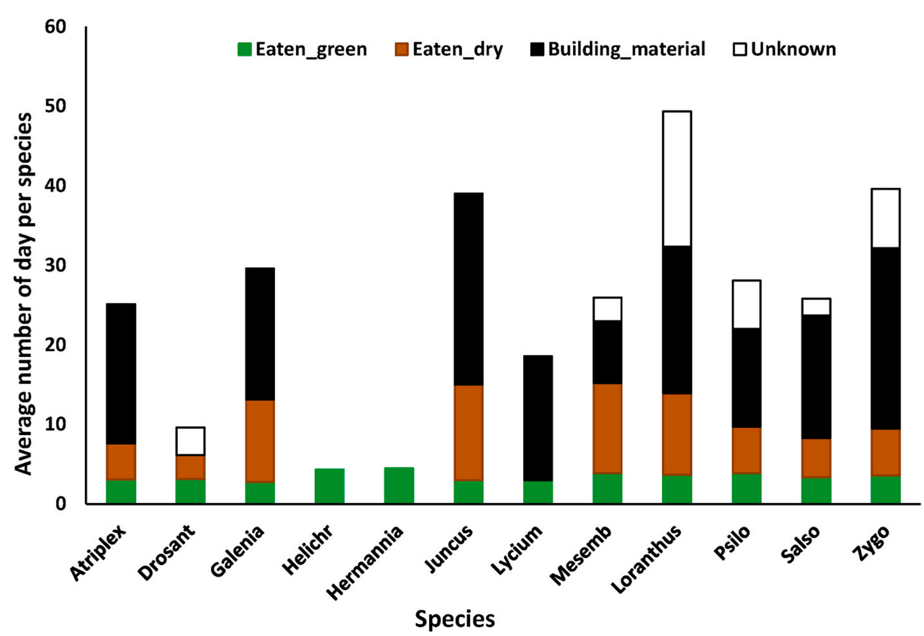

Fig. 2. Number of days until each plant piece of the different plant species collected by bush Karoo rats were categorised into their final fate. For example, Atriplex was eaten green within 2 days, within 6 days it was eaten as plantong, and within 26 days it was used as building material and never disappeared. Full species names: Atriplex (Atriplex lindleyi), Drosant (Drosanthemum hispidum), Galenia (Galenia sarcophylla), Helichr (Helichrysum sp.), Hermannia (Hermannia disermifolia), Juncus (Juncus acutus), Lycium (Lycium cinereum), Mesemb (Mesembryanthemum guerichianum), Loranthus (Loranthus sp.), Psilo (Mesembryanthemum (Psilocaulon)subnodosum), Salso (Salsola zeyheri), Zygo (Tetraena retrofracta, old name = Zygophyllum retrofractum).

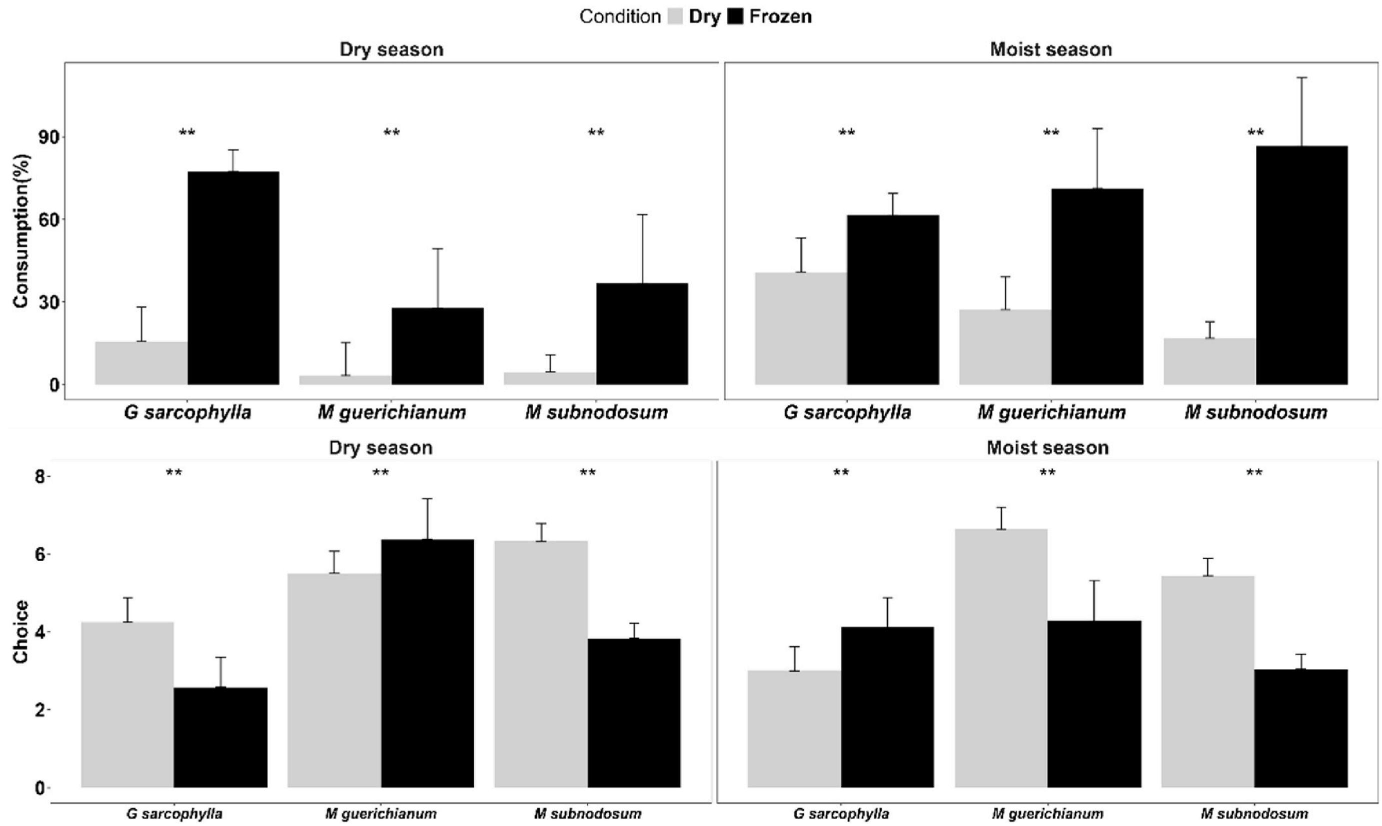

Fig. 3. Mean ± SD of the percentage consumption for plant pieces provided to bush Karoo rats and choice of which plant pieces were eaten first in the dry and moist season. Frozen vs Plantong treatment, N = 48 rats, with 24 individuals per season. For choice, a score of 1 represents the plant eaten first and 6 represents the last plant pieces eaten and 7 representing food plant that were not eaten. Species names: *Galenia sarcophylla* (*G sarcophylla*), *Mesembryanthemum (Psilocaulon) subnodosum* (*M subnodosum*), *Mesembryanthemum guerichianum* (*M guerichianum*. Asterisks: 0.05 (*), 0.01 (**), and 0.001 (***).

Table S11); season had a significant effect (LME; $t_{86} = 5.02$, P = 0.001) with bush Karoo rats eating more in the moist season. Bush Karoo rats first chose frozen plant pieces (LME; $t_{261} = -4.42$, P = 0.001) and there was no significant difference by season (LME; $t_{94} = -1.49$, P = 0.139; Fig. 3, Tables S11 and 13).

3.3.2. Experiment 2. consumption and choice of dry vs fresh plant pieces (moist season)

Of the 24 individuals tested, 9 individuals ate plantong and fresh plant material, while the remaining 15 individuals ate only fresh plant material. Bush Karoo rats ate significantly more fresh plant material than plantong (LME; $t_{114} = 11.42$, P = 0.001; Fig. S1, Tables S11 and S12), and they first chose fresh plant pieces (LME; $t_{134} = -11.52$, P = 0.001; Fig. S1, Tables S11 and S13).

3.3.3. Experiment 3. consumption and choice of dry vs fresh vs frozen plant pieces (between the moist and dry season)

Of the 24 individuals tested, 11 individuals ate the plantong as well as fresh and frozen pieces, while 12 ate only frozen and fresh plant pieces, and one individual did not eat anything. Bush Karoo rats consumed more frozen plant pieces followed by freshly harvested plant pieces and consumed plantong the least (Fig. S2, Table S11). Both frozen plant pieces (LME; $t_{188} = 10.51$, P = 0.001; Table S14) and fresh plant pieces were significantly eaten more often than plantong (LME; $t_{188} = 8.18$, P = 0.001; Table S11). The bush Karoo rats first choice was fresh plant pieces, followed by frozen plant pieces, with plantong being the least chosen (Fig. S2). Fresh plant pieces were significantly chosen sooner than plantong (LME; $t_{211} = -0.66$, P = 0.01; Table S14) while there was no difference between frozen plant material and plantong (LME; $t_{211} = -3.06$, P = 0.511; Table S15).

4. Discussion

In this study, we examined the function of dried plant pieces at bush Karoo rat lodges, as they could represent a preserved food source. Indeed, we found that more food plants were collected in the moist than in the dry season and that plantong was consumed most at the end of the dry season in autumn. Bush Karoo rats used most of the collected plant pieces for immediate consumption or construction, but consumed about 12 % of the food plants, after they became plantong, within less than a week. Overall, we found that while plantong is eaten by bush Karoo rats, it does not represent a form of food stored from one season to the next. Instead, plantong seems to represent leftovers from the green food brought to the lodge that is then eaten within days.

The area around occupied bush Karoo rat lodges mostly comprised of food plants, including plant species that become plantong. On the entire field site, a total of 30 different plant species were identified of which 20 were food plants. During observations, bush Karoo rats collected nearly 3000 plant pieces including all food plant species and those used for lodge building. Species that became plantong were mainly annual succulents (N=3) or succulent shrubs (N=4). All plant species that became plantong were also food plant species, which agrees with the hypothesis that they were collected as food and kept as plantong for potential later consumption.

If plantong were collected especially for food storage, we would have expected it to have a high nutritional value. However, plant species eaten or used as plantong were rather of lower than better quality when compared to other plant species, for example having a lower sugar concentration and very high ash content. One possibility could be that the species of highest nutritional value cannot be dried as plantong, but that doesn't seem to be the case (Table S3, Table S6). Rather, the lack of selecting plants of high nutritional value, such as protein or energy, could be a consequence of the high nutritional value of the plants around the lodges. This study could have benefited from additional analyses of the nutritional value of the plant, in addition to the analyses already performed for this study. All plants around the lodges had high nitrogen concentrations which was within the value ranges of savannah and dry lands from other parts of Africa (Feldt et al., 2017; Namukonde et al., 2023; Stolter et al., 2022). Yet, plants from the Succulent Karoo differed from plants in other regions by their exceptionally high ash content. This is matched by some of the plants consumed by gerbils in the Negev Desert (Kam et al., 1997). Ash represents all inorganic matter, such as salts or silica. The ash content was highly correlated with the water content of the plant samples and negatively correlated with sugar. Thus, if the animals had collected plants for high water content, as indicated by the higher water content of food plants versus non-food plants, they would have collected plants with high ash and low sugar concentration. This indicates that bush rats do not discriminate between plant species and simply eat whatever is there because most plant species provide sufficient nutritional value. This would match the lack of selecting high protein leaves by marsupials and primates once the protein content of leaves is above a certain threshold (Cork and Catling, 1996; Ganzhorn et al., 2017). Alternatively, bush Karoo rats could select sites for their lodges which are dominated by the occurrence of their preferred food plants.

If plantong serves as stored food, most should be collected during the food rich moist season and consumed during the food-restricted dry season. Other small mammal species in semi-arid habitats adjust their foraging behaviour in response to fluctuations in nutritional content and water availability, such as the Mongolian gerbil (*Meriones unguiculatus*), spinifex hopping mouse (*Notomys* sp), fat-tailed gerbil (*Pachyuromys duprasi*), and desert pocket mouse (*Chaetodipus* sp), (Scheibler and Waiblinger, 2018; Pei et al., 2001), and some of these species hoard food (Nyby and Thiessen, 1980). Bush Karoo rats collected most of the plant pieces in moist winter. Thus, bush Karoo rats brought more food to the lodge and ate it there when overall more food was available. In sum, our results showed an influence of season on food collection in bush Karoo rats. A recommendation for future studies would be to include a measure of the quantity that plantong contributes to the food eaten by bush Karoo rats in relation to the fresh plant material that they consume.

The bush Karoo rat is a central place forager since it carries food plants back to its lodge and predominantly feeds and forages in the proximity of its lodge (Vermeulen and Nel, 1988; Makuya and Schradin, 2023). Central place foragers collect food within close proximities to their shelters and they can easily retreat into the shelter in case of any disturbance by a predator (Orians and Pearson, 1979). Feeding in a central place of the lodges is therefore advantageous to bush Karoo rats. This may explain why they carried more food back to the lodge in the moist season when food availability is much higher. During the dry season, food availability decreases with less cover, and collecting food plants during this time might pose danger from aerial predators.

Bush Karoo rats construct lodges using an assortment of available material, such as stones, herbivore faeces, wood, sticks, and food plants (Vermeulen and Nel, 1988; Brown and Willan, 1991). Several annual plants functioned both for lodge building and consumption, while perennial plants were mostly used for consumption, with shrubs used mostly for building (Table S7). Most plant pieces (68 %) carried to the lodges were consumed green. Some (12 %) plant pieces were consumed after they had dried and had become plantong, which typically occurred within 6 days of collection, indicating short-term storage. Another 11 % of the collected plant pieces became building material or part of the lodges after about 2 weeks, with the remaining 9 % disappearing, probably due to decomposition. In sum, we found evidence that the same plant species can function as food, plantong, or building material.

Scatter-hoarding rodents such as red squirrels (*Tamiasciurus hudsonicus*), Kangaroo rats (*Dipodomys* sp), and ground squirrels (*Callospermophilus lateralis*) consume food soon after collection, and they preferentially harvest and consume seeds with lower-tannin, cache higher-tannin alternatives, and retrieve cached high-tannin seeds in lower proportions (Lichti et al., 2017). Similarly, bush Karoo rats consumed mainly and most of the green plant material they carried back to the lodge, with only a few pieces being left over and finally drying out to become plantong. Thus, while the function of the collected plant pieces was often multifunctional, they served primarily as immediate food.

We observed bush Karoo rats eating plantong during nest observations. When presented with plantong during our experiments, most individuals ate plantong. Thus, plantong is a food source. But not a preferred one. The bush Karoo rats showed selective feeding behaviours when presented with food plant pieces in different states. When they had a choice between plantong and frozen or fresh plants, they mostly consumed frozen and fresh plant pieces. Food selection may be driven by a variety of factors, including nutritional content (e.g. energy, protein, fat, vitamins, minerals, all possibly influencing taste) (Kenagy et al., 1986; Green et al., 1997). Bush Karoo rats might have preferred fresh plant material over plantong due to higher moisture content and nutritional value of these pieces, which are essential for maintaining hydration and meeting their dietary requirements in arid conditions (Van Vuuren and Armitage, 1991; Randall, 1993; Kenagy et al., 1986).

Folivorous species face the challenge that leaves often have very low nutritional and energy content, especially when compared to seeds and fruits (Chapman et al., 2003). Foliage is high in fibre such that digestion is physiologically demanding, needing gut adaptations and a long retention time for fibre fermentation in contrast to plant species such as succulents and ephemerals which are easily digestible and contain more moisture (Seely and Louw, 1980; Rhoades and Cates, 1976; Chivers and Hladik, 1980; Cork and Kenagy, 1989). The nutritional content of food limits the body size, and it has been argued that folivorous species cannot be very small without special physiological adaptations (Demment and Van Soest, 1985; Foley and Cork, 1992). It is therefore surprising that a small African folivore rodent, the bush Karoo rat (approximately 100 g), can subsist on a folivorous diet. This seems to be explained by the differences in nutritional and energetic content of the leaves bush Karoo rats eat compared to small folivores species from other mammalian taxa. For example, its diet is by far more nutritious compared to the diet of the smallest folivorous primate species, the white-footed sportive lemur (*Lepilemur leucopus*; body mass about 500 g) that mainly feeds on succulent leaves of a euphorbia tree (*Alluaudia* sp.; Dröscher et al., 2016). Food plants included in the bush Karoo rat diet comprised much higher sugar concentrations, more lipids and less fibre (NDF), though food items of both species contain similar amounts of total non-structural carbohydrates (TNC), i.e.: the components that provide energy (compare Table S5 with Table 1 in Dröscher et al., 2016). Though the food items collected in our study did not only come from shrubs and trees as in case of *L. leucopus*, but also included annuals and ephemerals, the energetic value of the food was surprisingly similar.

In harsh arid environments, small mammals, especially rodents, store food for periods of food scarcity (Scheibler and Waiblinger, 2018; Pei et al., 2001; Price, 1978; Van Vuuren and Armitage, 1991). For example, kangaroo rats (*Dipodomys merriami*) are well known for their seed caching behaviour; seeds have a long storage potential (Huntley, 2023). The protective seed coat also allows for longer periods of storage compared to plants which usually dehydrate (Mortori and MacMillen, 1982). Compared to this, bush Karoo rats have a unique approach in which they temporally keep succulent leaves, termed plantong which are collected fresh, kept temporally and sometimes consumed. To our knowledge this is the first study demonstrating that food stored for a short period of days to one week can also consist of dried succulent leaves.

5. Conclusions

Bush Karoo rats feed on multiple food plants throughout the year, in relation to seasonal fluctuations in plant availability. Certain highly nutritious long-living shrub species like *Tetraena retrofracta, Lycium cinereum, Galenia sarcophylla, and Salsola zeyheri*, were eaten throughout the year. Additionally, there is multifunctional use of plants in lodge construction and gradual consumption as plantong, which highlights the means of bush Karoo rats responding to seasonal resource variations. However, plantong does not represent food stored during the food rich moist season for consumption during the harsh food restricted dry seasons several months later. Instead, plantong represents the leftovers of green plant pieces collected several days earlier, which dried up within a short period. Nonetheless, plantong offers an alternative food source which can be consumed without the need of risky foraging into open areas.

CRediT authorship contribution statement

S.P. Sangweni: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis. **N. Pillay:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **J. Ganzhorn:** Writing – review & editing, Methodology, Formal analysis, Data curation, Conceptualization. **R. Rimbach:** Writing – review & editing, Methodology, Formal analysis. **C. Schradin:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **L. Makuya:** Writing – review & editing, Writing – original draft, Supervision, Investigation, Formal analysis.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Lindelani Makuya reports financial support was provided by University of the Witwatersrand. Lindelani Makuya reports a relationship with University of the Witwatersrand that includes: funding grants. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jaridenv.2025.105385.

Data availability

Data will be made available on request.

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