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The effect of seed foraging and utilization by the granivorous ant *Messor capensis* (Mayr) (Hymenoptera: Formicidae) on the grassveld composition of the central Orange Free State

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Messor capensis (Mayr) is a granivorous ant that is widely distributed in the semi-arid grassveld of the Orange Free State, South Africa. The effect it has on the grassveld of the central Orange Free State was examined. The foraged items are taken into the nests and redundant material is discarded in refuse heaps. One percent of *Tragus koelerioides* Aschers., 7.5 % of *Eragrostis obtusa* Munro ex Fix. & Hiern. and 58 % of the *Eragrostis superba* Peyr. seeds foraged were discarded on the refuse heaps. The nitrogen content of refuse heap soil was greater (0.15 %) than that of 0–3 cm topsoil in the adjacent veld (0.08 %). This, together with the viable seeds in the refuse heaps, contributed to increased density of plant cover on the nest. Colonies migrate, and the cycle of foraging, increase in plant cover and migration is continually repeated. The foraging pattern of *M. capensis* contributes to seed dispersal, a dense plant cover and progression towards a climax plant community.

Key words: *Messor capensis*, grassveld, seeds, plant cover, plant density, succession.

INTRODUCTION

A general perception is that all seeds removed from the soil surface by *Messor capensis* (Mayr) (Hymenoptera: Formicidae), a granivorous ant, are carried into the nests and consumed. As *M. capensis* is widely distributed in the semi-arid grassveld regions of the Orange Free State (Vorster *et al.* 1991), it was thought to contribute to the deterioration of the grassveld. The location of the subterranean nests can easily be detected by the surface foraging-holes, refuse heaps and elevated soil. *Messor capensis* ants are group foragers, which use main trails. At the end of each trail they change from group to individual foraging (Vorster *et al.* 1991). When a new food source is located, it is immediately utilized, with a marked decrease in the number of foragers using the other trails. The new trail becomes a major trail for at least as long as the food source persists (Vorster *et al.* 1991). Group-column foraging is an adaptation to exploit high density clumped resources (Davidson 1977; Whitford 1978), making *M. capensis* an efficient forager in grassveld environments. Foraged material is taken into the nest and unused items are later discarded on surface refuse heaps near the nest entrances (Vorster 1989).

The grassveld of the Orange Free State consists of a mosaic of shrubs and grasses, with the latter predominating (Vorster *et al.* 1991). Most of the grasses are perennials which form a continuous ground cover (Tainton 1981). These grasslands have, however, suffered widespread degradation through overgrazing and drought (Tainton 1981). If an overgrazed grassland is allowed to recover, the bare areas are colonized by unpalatable karoo bushes and pioneer grasses. Secondary plant succession may proceed fairly rapidly to the sub-climax grasses which, in turn, are replaced by species of the climax community (Tainton 1981). Succession can, however, be influenced by factors such as climate, soil, fire, man and animals.

Plant communities are directly affected by the relationship between seed and seed consumers (Reichman 1979). Seeds are valuable food sources for ants since they can be stored in the nest for long periods, and have a high nutritional value (Carrol & Janzen 1973), containing lipids, proteins and

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especially carbohydrates in the case of grass (Baker 1972).

The question arose as to whether these granivorous ants would have a beneficial or detrimental effect on plant succession in a grassveld environment. The aim of this study therefore, was to determine the fate of seeds collected by *M. capensis,* and the impact of seed collection on plant cover on the nest relative to the adjacent veld.

MATERIALS AND METHODS

Items foraged

During the period November 1987 to May 1988, 20 individual foragers together with their foraged items were collected once a month from each of five randomly selected nests. The nests occurred in natural veld bordering the University of the Orange Free State (29.06S 26.10E).

Foragers were collected by placing a small glass vial over single individuals as they returned to their nests. When the ant had climbed up the vial it was trapped, together with the item it had collected. The foraged item was collected and the ant released.

Each foraged item was identified to determine the species and number of seeds removed from the soil surface by *M. capensis.*

Refuse heaps

Refuse heaps from 10 nests in the same area as above, were collected at two-week intervals from February 1987 to March 1988, using a vacuum cleaner. As a result of migration, the number of nests monitored declined to eight during the period of investigation.

Plant and animal material were separated from inorganic matter by flotation in water. To facilitate further identification, the material was dried at 110 °C for 24 hours and separated into different size categories using sieves. The categories were: < 1.18 mm; 1.18–1.40 mm; 1.4–2.0 mm and > 2.0 mm. Since each size category frequently contained numerous seeds, subsamples were taken as follows: 0.5 g from the > 2.0 mm category; 0.3 g from the 1.4–2.0 mm category; 0.1 g from the 1.18–1.40 mm category and 0.1 g from the < 1.18 mm category. Seeds and related structures of each species were sorted and recorded: *e.g. Tragus koelerioides* Aschers. seeds and husks and *Themeda triandra* Forsk. seeds and awns. This was done to determine seed removal (*i.e.* ingestion and storage) from husks and spikelets, as well as seeds discarded on the refuse heaps after being taken into the nest. Seeds of *T. koelerioides* and *Eragrostis obtusa* Munro ex Fix. & Hiern. collected by *M. capensis* had no seed-related structures other than the husks. The reduction in mass of the seed and related structures of *T. koelerioides* and *E. obtusa* on the refuse heap provided a measure of seed removal by *M. capensis.* Similarly, the reduction in *Eragrostis superba* Peyr. spikelet mass is a reflection of seed removal. By contrast, fertile florets of *T. triandra* have awns which may be lost before collection or are removed by ants in the nest. Furthermore, the awns are fragile and readily break into small fragments which are deposited on the refuse heaps. This makes it impossible to establish a relationship between awns or awn fragments on the refuse heap and the number of seeds harvested. Estimation of the number of *T. triandra* seeds utilized was consequently not possible. It was similarly impossible to determine the number of *Aristida congesta* Roem. & Schult. subsp. *congesta* and *Nenax microphylla* Salter seeds used.

The mean number of husked and dehusked grains per refuse heap per month was estimated as follows:

Tragus koelerioides and *Eragrostis obtusa*

The number of husked and dehusked seeds (N)/subsample is given by:

$$a = (y \times c)\,N + [z \times (b + c]\,N \qquad (1)$$

where a = mass (mg) of *T. koelerioides* or *E. obtusa* seeds and husks in the subsample; b = mass of seed; c = mass of husk; $(b + c)$ = mass of husked seed; y = percentage empty husks in the refuse heap; z = percentage husks containing seeds in the refuse heap, subsample as a percentage of the debris in the refuse heap = 1.86 %.

If N/subsample = d, N/refuse heap is given by:

$$d \times \frac{100}{1.86} = e \qquad (2)$$

where husked seeds/refuse heap (f) $= e \times z$; and husks/refuse heap (g) $= e \times y$

Eragrostis superba

Number of spikelets (N)/subsample is given by: $a \div b = d$, where a = mass (mg) of E. *superba* spikelets in subsample; b = mean mass (mg) of discarded spikelets; c = number of seeds per discarded spikelet;

If N/subsample = d, N/refuse heap is given by:

$$d \times \frac{100}{1.86} = z \qquad (3)$$

Total number of seeds/refuse heap (y) = $z \times c$

Seed availability

The area occupied by five of the *M. capensis* nests from which the refuse heaps were removed, was demarcated. It was approximately 400 m^2 in extent. A metal frame measuring 0.5 × 0.5 m^2 was placed on the soil surface at 20 randomly selected points in the experimental site. All loose plant and animal material on the soil surface was collected with a vacuum cleaner and separated from inorganic particles by flotation in water. It was dried, and the debris, which seldom weighed more than one gram, was sieved as described above. The mass of material in each size category was recorded. Seed and related structures were removed and the seeds identified to species and weighed. Remaining plant and animal material was weighed separately. This sampling procedure was repeated every two weeks, from February 1987 to January 1988.

Plant density

Plant surveys were undertaken using the inclined point frame method (Allen *et al.* 1980), to compare plant density on *M. capensis* nests with that of the adjacent veld. The point frame used was 600 × 540 mm. Holes were set at 45° to the horizontal and accommodated 10 brass pins, each 750 mm long which were used for recording plant strikes. The inclined frame was placed on each of 20 randomly selected nests, in the same area as the nests from which the refuse heaps were removed, and the number of strikes recorded. Each plant struck was identified to species. The procedure was repeated at adjacent sites 2 m north, south, east and west of each nest.

On the successional scale of grasses (Van Rensburg, pers. comm.), a value of three was assigned to climax, two to subclimax and one to pioneer grasses. A value of three was also assigned to nutritious, two to utilizable and one to non-utilizable shrubs for livestock (Van Rensburg, pers. comm.). The strikes at each site were multiplied by the value assigned to the species struck and the total for each site calculated, giving a plant-cover plant-succession rating. The rating on each nest was compared with the mean rating of the four adjacent observation sites.

Nitrogen content

The refuse heaps of six *M. capensis* nests were collected using a vacuum cleaner, while the topsoil (0–3 cm) surrounding each nest was scooped with a spade. Each refuse heap and topsoil sample was sieved separately. The soil which passed through the 1.18 mm mesh was analysed (n = 7 for each nest; n = 7 for each topsoil sample) for total nitrogen, using the conventional micro-Kjeldahl technique (Bremner & Mulvaney 1982).

RESULTS AND DISCUSSION

Messor capensis is an opportunist that collects a wide variety of items in its foraging areas. During the period November 1987 to May 1988, seeds constituted 85 % by number of the plant material foraged. Calculated over a year, the mass of seed and related structures of *T. koelerioides*, *A. congesta*, *E. obtusa*, *E. superba*, *T. triandra* and *N. microphylla* comprised 65 % of the available seed and related structures on the soil surface, but constituted 87 % of the total in the refuse heaps. No significant correlation (r = 0.125) existed between the mass of these species in the refuse heaps and in soil surface samples. As seeds were always present on the soil surface, it suggests that some choice had been exercised in the foraging process.

Calculation of the number and percentage of *T. koelerioides*, *E. obtusa* and *E. superba* seeds on the refuse heaps and in the soil surface samples yielded significant results. The mean mass of a *T. koelerioides* grain was 0.34 ± 0.008 mg (n = 30) and that of the husks 0.41 ± 0.009 mg (n = 30). Ninety percent of the *T. koelerioides* husks carried by foragers contained seeds, whereas only 1 % of the husks on the refuse heaps contained seeds. Ninety nine percent of *T. koelerioides* seeds taken into the nest were thus used, being either ingested or stored.

The mean mass of an *E. obtusa* seed was 0.14 ± 0.005 mg (n = 30) and that of the husk 0.10 ± 0.003 mg (n = 30). Once the *E. obtusa* spikelet has dropped from the plant it breaks into individual florets. Only florets containing seeds were foraged by *M. capensis*. On the refuse heaps 7.5 % of the florets contained seeds. Utilization of collected *E. obtusa* seeds was thus 92.5 %.

The mean mass of individual *E. superba* seeds was 0.56 ± 0.24 mg ($n = 30$) and that of the spikelet without seeds 13.80 ± 3.89 mg ($n = 30$). The mass of a spikelet foraged, was 17.72 mg and that of a discarded spikelet 16.04 mg. The *E. superba* spikelets retrieved from ants returning to their nests contained 7 ± 2 seeds ($n = 30$), whereas the spikelets on the refuse heaps contained 4 ± 1 seeds ($n = 30$). Forty three percent of the seeds foraged are thus removed from the spikelets in the nests.

There was no relationship between the number of *T. koelerioides, E. obtusa* and *E. superba* seeds available and those utilized, either during the same ($r = 0.60$) or the following month ($r = 0.38$). Since it is not known how long the seeds are stored in the nest, the composition of the refuse heap can only be used as an indication of the seeds utilized and not as an indication of preference. The mean number of seeds in the refuse heaps was much higher than that in 0.25 m^2 areas in the adjacent veld. Rissing (1981) also found that soil within 2 m of the refuse heaps of *Veromessor pergandei* (Mayr) and *Pogonomyrmex rugosus* Emery contained significantly fewer viable, native seeds than the refuse heaps. These ants consequently concentrate seeds in specific areas.

Although the number of seeds in the refuse heaps was high relative to the adjacent veld, only a small proportion of the foraged viable seeds are discarded in the refuse heaps by harvester ants (Inouye 1980): a large number of viable seeds are consequently stored in their granaries. Seeds in the granaries of *M. capensis* do not germinate even though they are exposed to high humidity and favourable temperatures. Carrol & Janzen (1973) suggested that this is due to 'seed treatment' by ants. If a colony dies or migrates, seeds in granaries, especially those just below the soil surface can germinate, giving rise to a denser plant cover.

The mean number of plant strikes per frame on inhabited *M. capensis* nests (10.15 ± 1.04; $n = 20$) was significantly higher ($t = 11.24$; $P < 0.01$) than that in the adjacent veld (5.61 ± 1.48; $n = 80$). The highest and lowest percentage strikes on the nest were 100 % and 73 %, compared to 75 % and 23 % in the adjacent veld.

The number of plant species per frame on the inhabited nests varied between one and five, and those in adjacent veld between one and three. The mean number on the nests (2.95 ± 1.05), differed significantly ($t = 4.66$; $P < 0.01$) from those in the adjacent veld (1.78 ± 0.40). On a nest where only one plant species was recorded, the percentage strike was 100 %, compared to only 52 % in the adjacent veld where an average of one species occurred per frame. However, according to the Shannon-Wiener diversity index (Zar 1984), no difference was manifest between plant diversity on the nests ($J' = 0.98$) and in the adjacent veld ($J' = 0.99$), suggesting that the current results relate to species density rather than diversity.

The species in the various categories (Van Rensburg, pers. comm.) used for the plant-cover plant-succession rating were: climax grasses: *Aristida diffusa* Trin. var. *Burkei* (Stapf) Schweick, *Cymbopogon plurinodis* Stapf ex Burtt Davy, *Digitaria eriantha* Steud., *T. triandra*. Subclimax grasses: *Eragrostis curvula* (Schrad.) Nees, *E. lehmanniana* Nees, *E. obtusa, E. superba, Heteropogon contortus* (L.) Beauv ex Roem. & Schult. Pioneer grasses: *A. congesta, Chloris virgata* Swartz, *Digitaria argyrograpta* (Nees) Stapf, *E. nindensis* Fix. & Hiern, *Microchloa caffra* Nees, *T. koelerioides* Aschers. Nutritious shrub: *N. microphylla* Salter. Utilizable shrub: *Salsola kali* L. Non-utilizable shrub: *Ruschia hamata* (L. Bol.) Schwant.

The plant-cover plant-succession rating between *M. capensis* nests (22.15 ± 6.59) was statistically higher ($t = 6.86$; $P < 0.01$) than that in the adjacent veld (10.20 ± 4.20). Not only is the plant cover denser on the nests, but it also advances more rapidly to succession than in the adjacent veld.

The nitrogen content of refuse heap soil was 0.15 % and significantly higher ($P < 0.01$) than that of topsoil (0–3 cm) in the adjacent veld, which was 0.08 %. This was in accordance with the findings of Gentry & Stiritz (1972) who stated that harvester ant activity concentrates inorganic and organic nutrients at, or near the soil surface. The refuse heaps of *M. capensis* probably provide a continual source of inorganic nutrients and organic material for the seeds, making them ideal germination sites. Gentry & Stiritz (1972) speculate that gradual mineralization of nitrogen and other inorganic nutrients is responsible for the continual growth of plants at sites abandoned for many years. This, together with the viable seeds in the refuse heaps, may account for dense plant cover found on the nests in this study.

As the plant cover became denser, access to the nest entrances was restricted and movement on the nest surface became difficult; this could have initiated the migrations. The new sites, which were between one and six metres from the abandoned nests, were always on bare ground where the cycle of seed harvesting, increase in plant density and migration is repeated. An increase in the standing crop of plants at each new site could increase local seed production (Gentry & Stiritz 1972). Since the dense plant cover on the nests comprised mainly climax and subclimax grasses, local seed production of these species can be expected to increase. The foraging and migratory pattern of *M. capensis* thus contributes to seed dispersal, denser plant cover and progression to a climax community.

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