Norwegian University
of Life Sciences

Master's Thesis 2017 60 ECTS
Faculty of Environmental Sciences and Natural Resource Management

The use of camera traps to identify seed removal agents in an East African savanna

Rikard Olai Haugen
Master of Science in Ecology

ACKNOWLEGDEMENTS

Finished, at last! This thesis is the fruition of one of the greatest experiences of my life so far. I had the privilege to see warthogs, zebras and impalas every day in a unique savanna landscape right south of equator in western Uganda. When the original project couldn't be implemented as planned I was glad my supervisors had helped me prepare alternative projects, and I learned that in the field, few things goes according to plan. The analysis and writing process has rewarded me with improved writing, statistical and programming (R) skills as well as increasing my tolerance for taking constructive criticism.

I would like to first thank my supervisors Stein R. Moe (NMBU) and Douglas Sheil (NMBU) for making this project happen and for invaluable and continuous advice and feedback throughout my writing. I would like to thank Paul Okullo (NARO, Uganda) for coordinating and arranging access to do the research in Lake Mburo National Park and Erik Francis Acanakwo (PhD, NBMU) for valuable advice, especially in the field. I also want to thank Ronny Steen (NMBU) for technical help with the camera set-up, and Doreen Mugendi and Fred Matovu for everyday assistance during fieldwork and keeping motivation up. Finally, I want to thank all my other friends for good company and intellectual conversations during breaks when writing, and a special thanks to the lion that made my research a little bit more exciting. I am extremely grateful for all the help I have received during my work.

Ås, May 12th 2017

____

Rikard Olai Haugen

ABSTRACT

Camera traps are commonly used to capture vertebrate activity, but remote video recording of invertebrates may now be possible due to new technology. Video motion detection (VMD) technology can be used to record large invertebrates, but has not been tested on small invertebrates. Here, I investigated the ability of camera traps using VMD to record and distinguish seed removal agents on and off active termite mounds in the savanna in Lake Mburo National Park, Uganda. I observed eight different seeds, one each from eight species (5 native species and 3 crops) with removals replaced daily for 30 days during the dry season in five savanna and five mound habitats. Ants and vervet monkeys (*Chlorocebus pygerythrus*) were recorded removing seeds. Larger seeds were less likely to be removed than smaller seeds. Removal rates were higher during day than during night, likely due to the diurnal activity of vervets, and many smaller seeds being removed by an unknown nocturnal seed remover. Absence of termites from the viewed recordings on mounds substantiates the claim that termites do not eat or remove seeds. The camera failed in recording invertebrates below a certain size, but ants were sometimes recorded because of moving shade triggering the recording, while vertebrates and larger invertebrates triggered the camera consistently. With improvements, this method is viable for recording small invertebrates with VMD technology.

SAMMENDRAG

Kamerafeller har lenge blitt brukt til å fange aktiviteten til virveldyr. Også avsidesliggende videoopptakere har begynt å bli brukt etter hvert som slik teknologi har blitt tilgjengelig. Forbedret video bevegelsesdeteksjon (VMD) teknologi har demonstrert evnen til å filme store virvelløse dyr, men har ikke blitt testet på små virvelløse dyr. For å teste dette med VMD, undersøkte jeg frøfjerning hos dyr for å identifisere forskjeller i hvilke dyr som fjerner frø på og utenfor aktive termitt-tuer in en Afrikansk savanne i Lake Mburo National Park, Uganda. Jeg så på åtte frø, fra åtte forskjellige arter (5 lokale frø og 3 jordbruksfrø), og la ut nye frø hver dag i 30 døgn under tørke sesongen i en øst Afrikansk savanna i Lake Mburo National Park, Uganda. Maur og vervetape (*Chlorocebus pygerythrus*) var de artene som ble fanget av kameraet mens de tok frø. Store frø hadde mindre sannsynlighet for å bli fjernet enn mindre frø. Frøfjerning var høyere om dagen enn om natten, sannsynligvis på grunn av dagaktivitet fra vervetaper og at mange av de mindre frøene ble fjernet av en nattaktiv ukjent frøfjerner. Fraværet av termitter på termitt-tuer, underbygger påstanden om at termitter ikke spiser eller fjerner frø. Kameraet klarte ikke å fange små virvelløse dyr, men maur ble fanget av kameraet på grunn av bevegelse fra skygge som utløste kameraet, mens virveldyr og store virvelløse dyr utløste kameraet konsekvent. Med noen utbedringer på kamera-oppsettet, kan denne metoden brukes til og også fange små virvelløse dyr som maur ved hjelp av VMD teknologi.

CONTENTS

INTRODUCTION

Many animals, ranging from large herbivores (Janzen 1984) to small invertebrates (Wall et al. 2005) remove and predate on seeds, thereby influencing plant recruitment (Andersen 1989) and dispersal (Hulme 1998). Advantages to seed dispersal for plants include moving away from the parent plant where seed predation may be higher (Janzen 1970), and to suitable germination sites (Harper et al. 1965). Seeds are dependent on dispersal through either animals, wind, water or self-dispersal, and have developed attributes like fleshy nutrients, clinging structures, and chemical and visual attractants that often attracts a specific guild or species of animals (Willson & Traveset 2000). Seed predation by animals does not always lead to seeds being destroyed, but can be secondary-dispersed (Wall et al. 2005). To avoid the assumption that taken seeds are eaten, this paper used the term "seed removal" to describe any movement of seeds by vertebrates and invertebrates. Factors such as habitat and seed species, size and removal agent can affect seed removal rates (Holl & Lulow 1997; Hulme & Borelli 1999; Moles et al. 2003), and seed size can influence seed preference or avoidance (Harper et al. 1970).

Knowledge about what animals consume, remove and disperse seeds, could be important to predict future consequences of change in ecosystems based on different kinds of animals' role in seed removal. It would therefore be important to know what specific animals did the seed removal and what their preferences would be. Studies that only look at guilds and not specific taxa or species may fail to gather important details when it comes to seed dispersal outcomes. Hulme (1998)'s comparison between studies that include all seed removers and studies with selective treatments (insects, rodents, birds), found that in ecosystems with more than one guild of post-dispersal seed predators, the studies including all seed removers fail to describe seed predation appropriately because they don't estimate the guilds separate impact of seed removal.

In tropical savannas, the main seed removers are birds, ants and rodents (Linzey & Washok 2000). Tropical savanna ecosystems are either grassland, or scrubland depending on the density of shrubs and trees. Tree densities in savanna varies because of both abiotic and biotic factors like fire, herbivory and soil condition (Sankaran et al. 2005; Sankaran et al. 2008). In the african savanna, some species of termites build large vegetated termitaria or termite mounds that can become protruding structures (Korb & Linsenmair 2001; Sileshi et al. 2010). These termitaria have higher nutrient content and moisture levels due to termites' ability to fix nitrogen from the air and maintain an aerated soil, compared to open savanna soils. Termite mounds also support a greater variety of animal species compared to the savanna floor (Stoen et al. 2013). Because of the higher nutrient content and vegetation density, megaherbivores (Loveridge & Moe 2004) and other large ungulate herbivores (Mobaek et al. 2005) preferentially feed on termite mound vegetation when compared to plants growing on the adjacent savanna. Termite mounds are known to host a higher diversity of tree species than savanna areas (Joseph et al. 2015; Moe et al. 2009), and mounds function as habitat for smaller mammals with a higher species richness than savanna (Okullo et al. 2013). In

Acanakwo et al. (2017) study on Macrotermes, showed that post-dispersal seed removal is high in the savanna ecosystem and significantly higher on mound than off mound.

Since termites to such a high degree function as ecosystem engineers (Dangerfield et al. 1998), it is important to understand how they affect vegetation and other animals around their mounds. Tropical ecosystems holds several guilds of invertebrate seed predators (Hulme 1998) where ants are likely the most significant seed predator in arid and semi-arid ecosystems (Hulme 1998). Ants find food in close proximity to termites and termite nests (Deligne et al. 1981), indicating a competition or complementation of resources around termite mounds depending on the food habits of termites and ants.

The main interest of this study, was to explore what animal species removes seeds in savanna landscapes, and explore if there is a difference in the number and composition of seed removal agents between mound and savanna habitats. To do this, I tested a method employing video camera recorders with high sensitivity that triggers on movement. Camera-traps has a wide range of uses (Rowcliffe & Carbone 2008) and have been used to assess vertebrate compositions (Mugerwa et al. 2012) and identify vertebrate seed removers (Beck & Terborgh 2002). Using camera-traps to identify seed removers allows us to identify them without having to physically capture them in traps (Myster & Pickett 1993; O'Dowd & Hay 1980) or interpret foot-prints (Jansen & Den Ouden 2005). Camera traps that used infrared sensors to capture warm bodied animals (Beck & Terborgh 2002; Miura et al. 1997; Page et al. 2001; Yasuda et al. 2000) and video recorders that continuously film (Jansen & Den Ouden 2005), have been successful at identifying terrestrial animal seed removal agents. New technology, using video motion detection (VMD), where change in fixed images trigger a video recorder and records both before and after the events, has successfully been used to record pollinating bumblebees (Steen & Aase 2011). By using this triggering mechanisms for video recording, it is easier to apply remote recording of animals without running out of data memory storage, and simultaneously save time when analysing data, because the VMD makes videos of only the removal event. When analysing data, Jansen and Den Ouden (2005) had to look through hours of continuous videos to locate the seed removal event. This study attempts to record both vertebrates and small invertebrates with VMD camera traps.

Objectives

The overall aim of this study was to explore animal seed removal in an African savanna. I specifically asked the questions:

1) Which animal species are involved in seed removal?
2) Do seed removal species differ between savanna and mound?
3) Are specific animal species associated with removal of particular seed species?
4) Is seed removal related to seed size?
5) Is seed removal related to seed type (i.e. native or agricultural crop seeds)?
6) Is removal more frequent during the night or during the day?

Furthermore, I was also interested in evaluating the method of camera surveillance for the study of seed removal.

I asked:

1) How often are seeds taken while the animals responsible are not recorded?
2) Are there any improvements that can be done to the equipment or setup?

METHODS

Study area

The study was conducted in Lake Mburo National Park in the south-western part of Uganda between mid-June and mid-August 2016. The park is about 370 km^2 and has an elevation between 1220 – 1828 m above sea level. There are wet and dry seasons, with between 500 and 1000 mm annual rainfall and an average temperature of 27.5 °C, ranging between 21.5 – 34.0°C. The vegetation is composed of grass, open trees and woodland savanna with trees like *Acacia hockii*, *Acacia gerardii* (Mobaek et al. 2005), *Dichrostachys cinerea* and *Acacia sieberiana* (Okullo et al. 2013). In Lake Mburo NP, the savanna supports thickets that are associated with termitaria that are built by the termite genus *Macrotermes* (Moe et al. 2009). Lake Mburo National Park has a high density of termite mounds with 10.1 mounds per hectare (Davies et al. 2014; Moe et al. 2009). Compared with the savanna floor, mounds support higher densities of tree species that are often associated with lowland and riparian habitats (Davies et al. 2016). Woody species dominating the thickets include *Grewia similis*, *Rhus natalensis*, *Scutia myrtina* and *Maytenus heterophylla* (Mobaek et al. 2005). Common potential seed removers in the park are olive baboons (*Papio anubis*), vervet monkeys *(Chlorocebus pygerythrus)*, guineafowl *(Numida meleagris)* and ants *(pers. obs.)* in addition to several small mammals (Okullo et al. 2013) and a myriad of bird species.

Experimental setup

I conducted a seed removal experiment using camera traps at ten sites, five savanna plots and five active termite mounds with three days (approximately 72 hours) on each site. Savanna sites were used to compare against seed removal effect from termite mounds. When choosing a position in the open savanna, length from termite mound was 50 +/- 8 m (>20 m) to minimize any effects on seed removal from termites (Loveridge & Moe 2004; Stoen et al. 2013). Termite mounds were damaged with an iron rod to visually confirm termite presence, by either checking if the hole in the mound was repaired by termites after 24 hours, or by seeing termite presence while digging. When selecting camera position on the active termite mounds, I used south and southwest, aiming for the most vegetated side of the mound, and placed the camera on the lower third part of each mound.

I used a high sensitivity camera trap to video monitor the area of interest. The camera trap consisted of two standalone digital recorders (DVS) paired with a camera each, with different lens magnifications. The one with smallest magnification covered an area of 52 x 40 cm, aimed at capturing large seed removal agents, and the one with the largest magnification covered an area of 9 x 12.2 cm aimed to capture smaller animals. The camera pole was placed in the middle of a wooden platform measuring 26 x 80 cm (Figure 1). To make the platform level with the ground, soil was removed and placed along the edges. The platform was a wooden plank, while the camera itself was fixed to a stick and camouflaged with military camouflage-tape. A small square where the small area camera was directed, was marked to make it easier to know where to place the seeds. One set of eight different species of seeds were placed in the depressions on the platform that were carved inside this square (Figure 1). Seed species used were maize (*Zea mays* L.) (397.65 mg), g-nut (*Arachis hypogeae* L.) (337.32 mg)*, Acacia sieberiana* DC (290.4 mg)*, Grewia similis* K. Schum (101.9 mg)*, Dichrostachys cinerea* Wight et Arn. (25.4 mg)*, Scutia myrtina* (Burm. F.) Kurz (24.8 mg)*, Rhus natalensis Bernh. ex Krauss* (18.7 mg), and rice (*Oryza sativa* L.) (17.83 mg). Using different seed species allowed me to look for preferences of seed species between the different seed removers. The camera I used was Sony Effio-e 700TVL IR Led 1/3" Mini CCTV Camera, Shenzhen Harex Electronic Co., LTD, China, and the digital video recorder was Secumate H.264 Mini Portable DVR, Shenzhen Secumate Technology Co., LTD, China. The recorder has a video motion detection function (VMD) that detects changes in consecutive image captured by the camera, where events above a given threshold triggers the recordings (Steen 2016). The VMD works in the way that the picture frame is divided into cells, which reacts and triggers to changes in activity within each cell. Number of cells and size of area the frame covers determines the sensitivity of the VMD. Things far away or so small that they barely show any changes within a cell, will not trigger the VMD and the camera will therefore not record anything. I used a pre-recording buffer of 5 seconds (which is the duration of video that would be buffered already before a trigger is detected) and a post-recording buffer of 5 seconds (which was the duration of video recorded after a trigger event). The recorded video was stored in an SD-card locally in the recorder. A frame rate of 25 pictures per second was used (resolution 740 x 560 pixels, video file format AVI (H.264)). The cameras were equipped with automatic infrared lights (IR), allowing the cameras to record at night. They were protected inside a plastic waterproof housing, and camouflaged with camouflage tape (Figure 1).

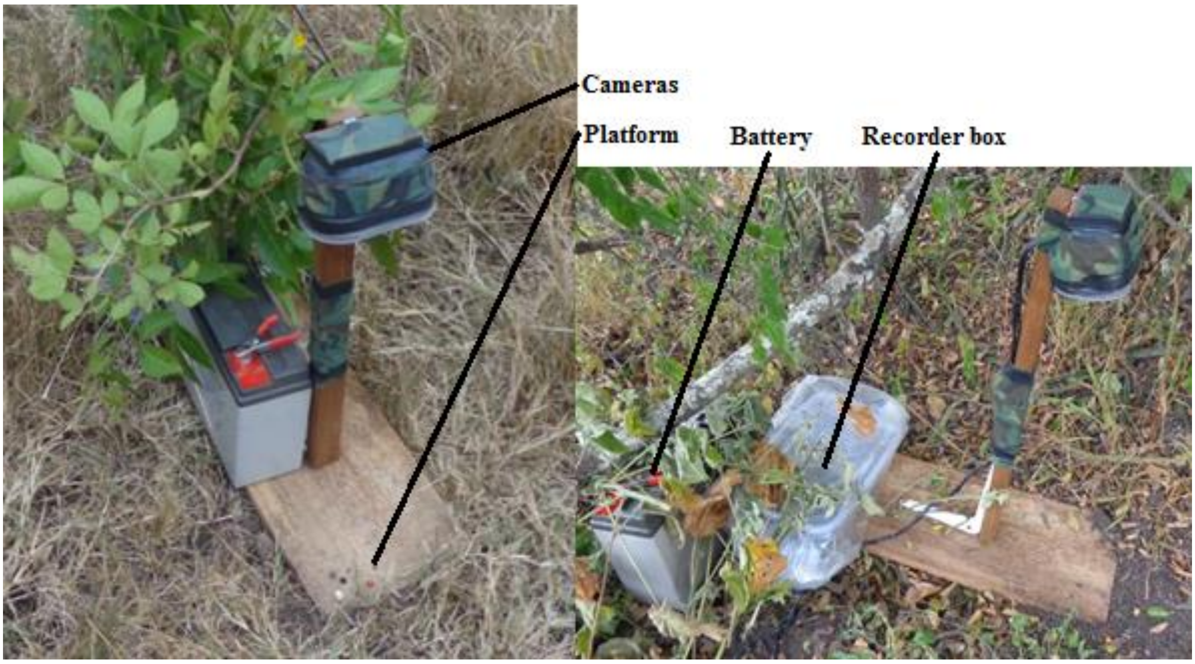

Figure 1. Camera set-up with camera directed towards the end of the platform. Seeds were located at the corner with battery and recorder box camouflaged behind the camera.

The camera setup was powered by a 12 VDC (40 Ah) maintenance-free sealed lead-acid solar battery. Power consumption will vary, but is under ideal conditions about 0.8 Ah for one unit, hence a fully charged 40 Ah battery should last for about 60 hours (Figure 1). To power the recorder, I had to use a step-down converter (12 to 5 VDC). By connecting a monitor, the cameras could be tested before starting the experiment. This check was done every time the battery was changed and every time the camera was moved to a different location. Recording-device and cables were protected inside a rectangular 20 x 30 cm plastic box. For camouflage, to prevent attention and possible theft, branches were cut and placed around the setup, making sure not to physically block out animals and that branches didn't trigger the cameras too easily with wind and shade. A 32 GB SD card (Sandisk Standard SDHC, class 2) was used in each camera recorder. Seeds were placed out, then counted and replaced every 24 hours and the SD cards were retrieved and replaced every 72 hours when the camera was moved to a new location. The card was formatted on the recording device every time it was changed to keep the same time and settings for the cameras.

Coordinates, date, elevation, rate of seed removal, and tree density was recorded from each site. After retrieving memory cards, the data was backed up and manually looked through to find when seeds were taken and what took them. All recordings of seed removal were logged. Removal without knowing the animal that took the seed(s) were registered as unknown and will be referred as such from now on.

Statistical analyses

The statistical software R, Version 0.99.491 – © 2009-2015 RStudio, Inc. (Team 2015) was used for statistical analysis. To determine whether seed removal was influenced by seed size, habitat, night or day and seed-type, I used generalized linear mixed-effects models (GLMM) with the function *glmer* from the R package *lme4* (Bates et al. 2015) and with binomial distribution. The ten different camera locations were set as the random variable. When selecting models, I used ANOVA chi-squared test and the lowest AIC (Akaike Information Critera) to compare and select the best models. Daily seed removal over the 30 days of the experiment was used as response variable to look for influence from habitat, seed species and seed type. A binomial (success or failure) was used for seed removal, because either zero or one seed was taken for every species per day. The same type of analysis was used for the data where the seed removal agents were recorded. In this analysis, I modelled seed removal as a function of seed removal agents and time of day. Seed removal as a function of seed weight was analysed using a general linear model (GLM) with the function *glm* from the package *mixlm* (Liland 2015) for both total seed removal and unknown seed removal separately. I used multiple comparison analysis Tukey tests from the R package *multcomp* to test for differences between all the seed species (Hothorn et al. 2008). I used the R package *ggplot2* to draw figures (barplots and boxplots) (Wickham 2009).

RESULTS

In total 84 of 240 seeds were removed. There were three observed removal agents, namely vervets, ants and crickets (Table 1). Since crickets were observed only twice, they were removed from further analysis. Of the 84 seeds removed, 48 removals were captured on camera (including the cricket). Vervets removed 26 seeds and ants 21 seeds (Table 1). Ants and vervets removed seeds from both savanna and mound, but ants did not remove agricultural crop seeds in the savanna (Table 1). There was no significant difference on seed removal between the two habitats (Figure 2, chi^2-test p-value = 0.07) and there was no difference in seed removal agents between the two different habitats.

Table 1. Presence and removal on different seed types and habitats. Total number of seeds removed is number of seeds taken in total in that seed-type and habitat (out of 120). Mean and SD is calculated from total removal over the 15 days and nights of recorded seed removal in each habitat.

Seed type	Treatment	Seed removal agents	Total no. of seeds removed	Mean (SD)
Native woody plant seeds	Savanna	Vervets	6	0.40 (1.02)
		Ants	11	0.73 (0.68)
		Unknown	4	0.26 (0.46)
		Crickets	1	0.07 (0.24)
	Active mound	Vervets	6	0.40 (0.80)
		Ants	8	0.53 (0.18)
		Unknown	14	0.93 (0.80)
Acricultural crop seeds	Savanna	Vervets	5	0.33 (0.79)
		Unknown	6	0.4 (0.51)
	Active mound	Vervets	9	0.60 (1.02)
		Ants	3	0.20 (0.40)
		Unknown	9	0.6 (0.51)
		Crickets	1	0.07 (0.24)

Vervets removed most seeds with a tendency of preferring the biggest seeds (maize, g-nut, *A. sieberiana,* and *G. similis*), while ants did not remove the three largest seeds maize, g-nut and *A. sieberiana* (Figure 3). Individually, rice was the seed that was removed the most (in total 21 out of 84), followed by *G. similis* (17 out of 84), *S. myrtina* (15 out of 84) and *R. natalensis* (11 out of 84), that all had a significant effect on the amount of seed removal (Table 2, Appendix 1). There was no difference between agricultural crops and native seeds (GLMM P-value = 0.59). Seed weight had a significant effect on seed removal, with smaller seeds being removed more often than larger (Table 3, Figure 4). Data indicates that ants and unknown removed predominantly smaller seeds, while vervets removed larger seeds (Figure 3).

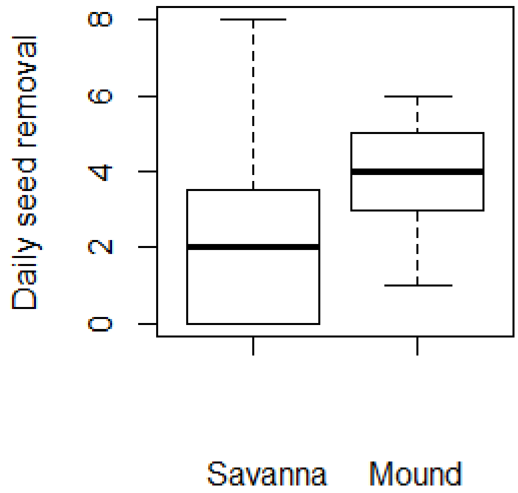

Figure 2. Variation in total daily seed removal over the 24-hour periods (n=15) in each of the two habitats, Savanna and Mound. Middle bar shows median seed removal, box edge shows 25 – 75 % of seed removals, and whiskers shows minimum and maximum amounts of seeds removed in one day.

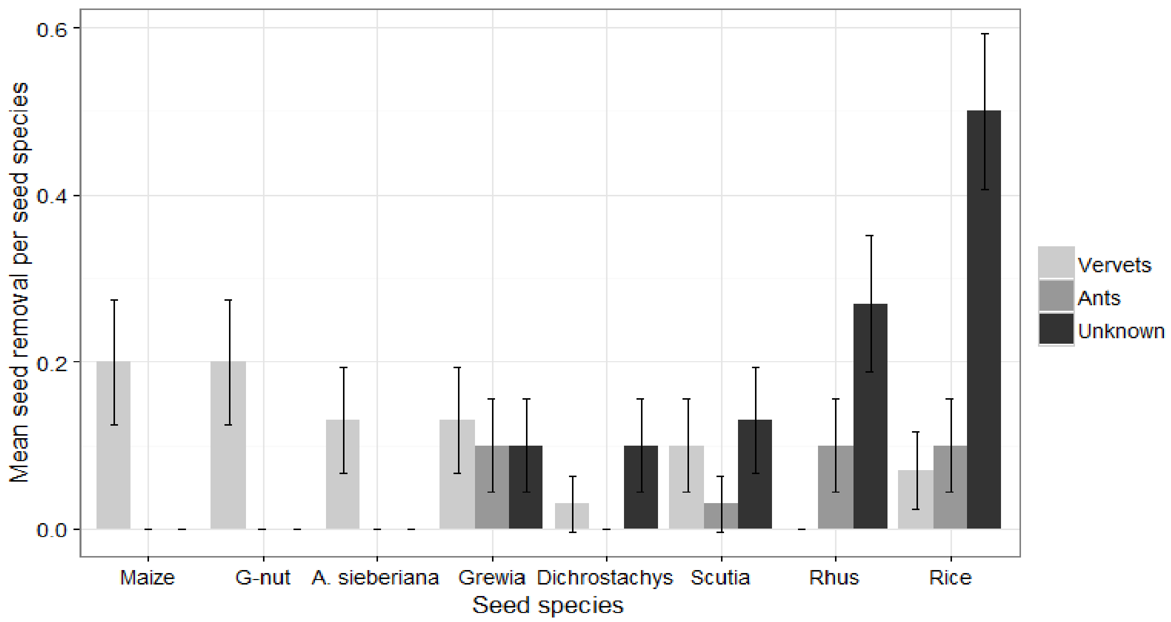

Figure 3. Mean seed removal with SE by ants, vervets and unknown for every seed species over 30 days sorted by seed weight (mg) from largest (maize) to smallest (rice) seed. Unknown shows the removal that was not captured on camera. Seed species are maize (*Zea mays*), g-nut (*Arachis hypogeae*), *A. sieberiana*, *G. similis*, *D. cinerea*, *S. myrtina*, *R. natalensis* and rice (*Oryza sativa*).

Table 2. The effect of seed species and habitat on total seed removal. P-values below 0.05 shows a significant effect, and estimates represents how much it affects total seed removal (Seed species compared to D. cinerea and savanna habitat compared to mound). Models were selected by lowest AIC after an ANOVA chi^2-test. Estimates are presented on logit (log of odds) scale. Positive estimates are interpreted as an increase in removal. Seed species are maize (*Zea mays*), g-nut (*Arachis hypogeae*), *A. sieberiana*, *G. similis*, *D. cinerea*, *S. myrtina*, *R. natalensis* and rice (*Oryza sativa*).

Total seed removal	Estimate	SE	z	Pr(>|z|)
Fixed effects				
(Intercept)	-2.43	0.47	-5.13	<0.001
G-nut vs *D. cinerea*	0.45	0.48	0.95	0.34
G. similis vs *D. cinerea*	1.80	0.42	4.23	<0.001
Maize vs *D. cinerea*	0.45	0.48	0.95	0.34
R. natalensis vs *D. cinerea*	1.19	0.44	2.70	<0.01
Rice vs *D. cinerea*	2.13	0.42	5.08	<0.001
S. myrtina vs *D. cinerea*	1.61	0.43	3.76	<0.001
A. sieberiana vs *D. cinerea*	0.00	0.52	0.00	0.99
Savanna (vs mound)	-0.85	0.46	-1.85	0.06

Table 3. The effect of seed weight on total seed removal. P-values below 0.05 shows a significant effect, and estimate represents how much the seed weights affects the total seed removal. GLM model was selected by lowest AIC after an ANOVA chi^2-test. Estimates are presented on logit (log of odds) scale.

Total seed removal	Estimate	SE	z	Pr(>|z|)
Coefficients				
(Intercept)	-1.15	0.11	-10.38	<0.001
Seed weight	- 0.003	0.00	-4.79	<0.001

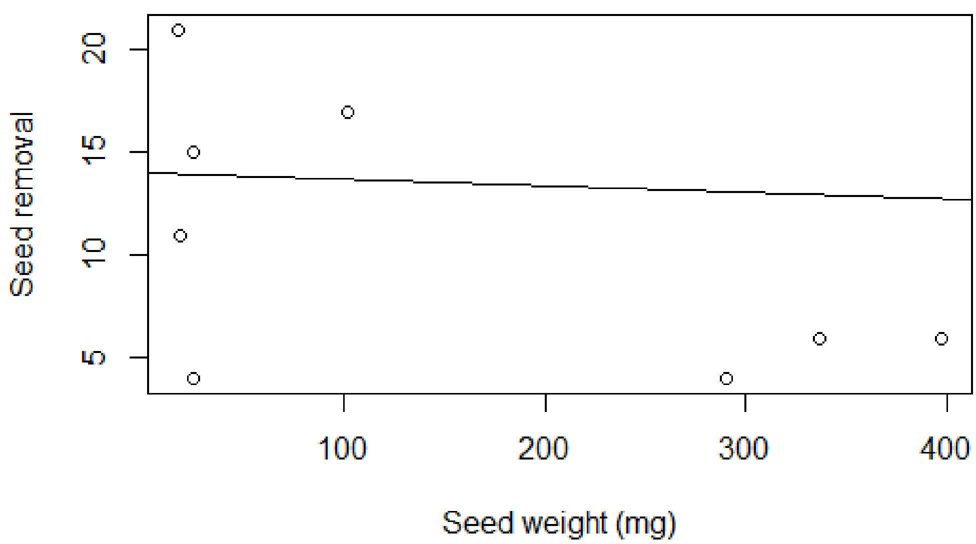

Figure 4. Scatterplot of total seed removal based on seed weight, with prediction line (Table 3).

Table 4. The response, seed removal, uses only the removal with the known seed removal agents, ants and vervets. Estimates show the effect on seed removal (night vs day, vervet vs ants, and the interaction between time of day and seed removal agents). The model was selected by lowest AIC after an ANOVA chi^2-test. Estimates are presented on logit (log of odds) scale. Positive estimates are interpreted as an increase in removal. Day is between 7 am and 7 pm, night is between 7 pm and 7 am.

Seed removal	Estimate	SE	z	Pr(>|z|)
Fixed effects				
(Intercept)	-2.78	0.31	-9.06	<0.001
Night	-0.96	0.49	-1.97	0.05
Vervet	0.61	0.34	1.80	0.07
Time x remover	-21.48	81.98	-0.26	0.79

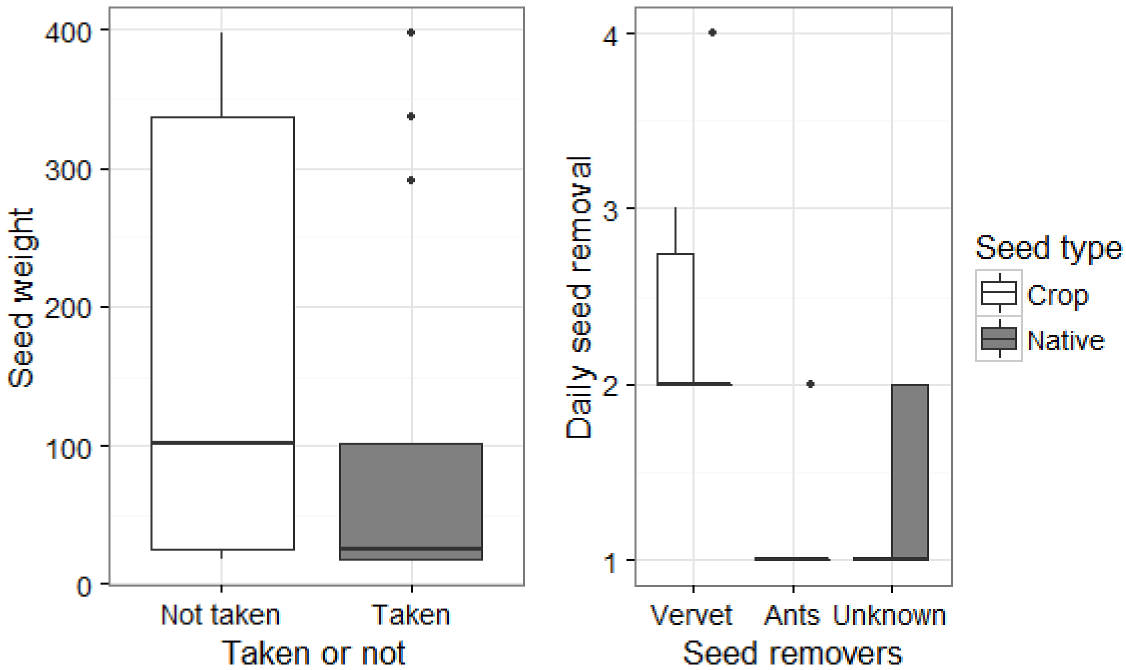

Figure 5. a) Variation between taken and not taken depending on seed size (seed weight). **b)** Variation in daily seed removal between native and agricultural seeds from the two main removers, ants and vervets over 30 days. Agricultural seeds include maize (*Zea mays*), g-nuts (*Arachis hypogeae*) and rice (*Oryza sativa*). Native seeds include *Acacia sieberiana*, *Grewia similis*, *Dichrostachys cinereal, Scutia myrtina*, and *Rhus natalensis*.

Removal was most frequent during the day (Table 4), with nearly twice the amount of removal during day compared to night (Figure 6, Table 5). Time had a significant effect on seed removal both with and without unknown seed removal agent, with the night reducing the seed removal rate (Table 4, GLMM, p-value = < 0.001 with unknown seed removal agent). There was no interaction between time of day and seed removal agent. Vervets showed a tendency of having positive influence on seed removal when compared to ants (Table 4).

The camera captured 55.4 % of the seed removal. G-nut, maize and *A. sieberiana* was removed only by vervets and caught on camera every time. There was a significant negative effect of seed weight on seed removal from the removal with unknown seed removal agent, with less removal of larger seeds (Table 6, Figure 7).

Table 5. Total seed removal based on time of day. Mean and SE is over the total 30 days of recorded seed removal.

	Removal	Mean (SE)
Day	55	1.83 (0.38)
Night	28	0.93 (0.21)

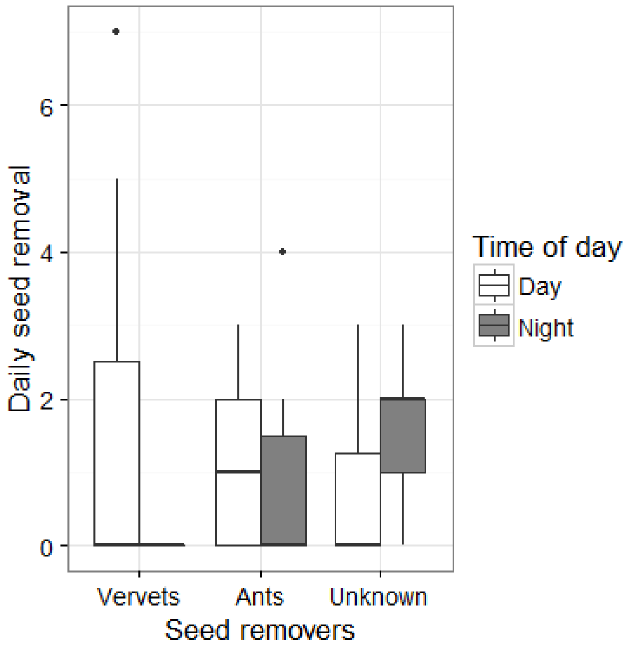

Figure 6. Variation in daily seed removal by each seed removal agent in relation to time of day. Day is between 7 am and 7 pm, night is between 7 pm and 7 am. “Unknown” is seeds removed where the seed removal agents were not captured on camera.

Table 6. GLM of seed removal with the unknown seed removers vs seed weight. Unknown is the seed removal that was not captured on camera. Estimates are presented on logit (log of odds) scale.

Total removal for unknown seed remover	Estimate	SE	z	Pr(>|z|)
Coefficients				
(Intercept)	-1.35	0.12	-10.97	<0.001
Seedweight	-0.005	0.00	-5.38	<0.001

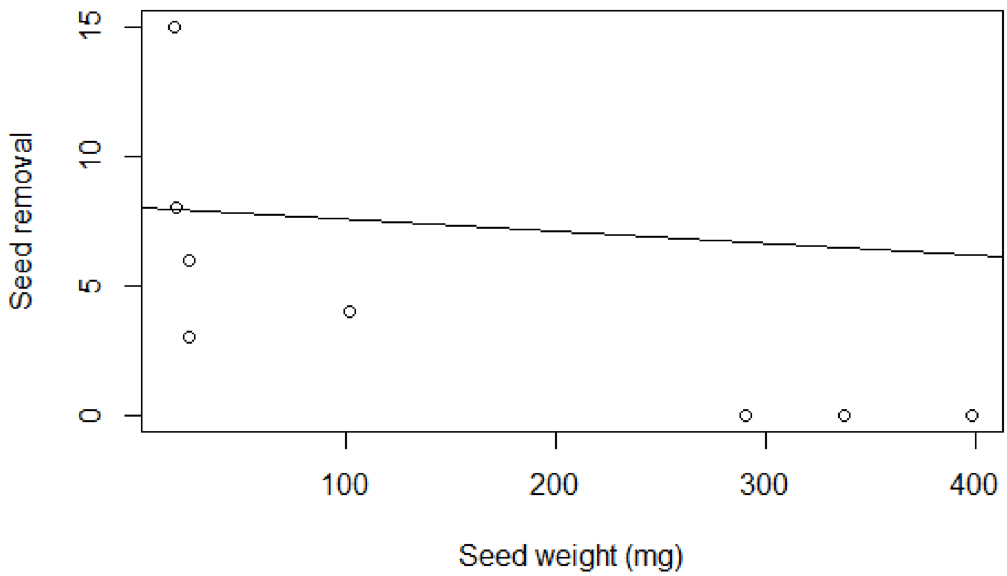

Figure 7. Scatterplot of seed removal with unknown seed removal agent and predicted line of removal based on seed weight (Table 6). Unknown is the seed removal that was not captured on camera.

DISCUSSION

Over the duration of the experiment, 35 % of the seeds were removed, and of the removed seeds, only 57 % of the seed removal agents were captured on camera. The vervets usually took several seeds at the same time and showed up six times on six different days removing a total of 26 seeds. The ants had 23 removals over 19 days. Rice was the most commonly removed seed, but for most of the removals, the seed removal agent wasn't captured on camera, most likely because the seed removal agent was too small for the VMD.

Animals involved and effect from habitat

Ants, vervets and crickets were captured on camera removing seeds. Ants and vervets were the two main seed removers, whereas the cricket only removed two seeds. Animals that was recorded on camera, but did not remove seeds, were a (male) lion (*Panthera leo*), a mouse, flies, spiders, moths, beetles, grasshoppers, and true bugs. Birds are considered important seed removers in African savannas (Kelt et al. 2004; Linzey & Washok 2000), but were completely absent. The lack of bird seed removers can be because it is the dry season with many species having migrated, although for some of the remaining birds, seeds should be an attractive food source (Alerstam & Christie 1993).

Vegetation works as cover against predators for small mammals such as rodents. Heavy grazing by herbivores and possible fires, and the fact that it was the dry season during the experiment could affect the density of these animals (Salvatori et al. 2001). Yet, the vegetation in the two different habitats in this experiment showed high difference in vegetation cover, with higher density of trees and thickets in mound habitat than in savanna habitat, but no difference in the species removing seeds in the two habitats, except for possibly different species of ants. There was, however, a trend of higher removal rates on mounds (Table 2), and with more vervets observed in the recordings from the mound habitat. The mound habitat had some removal every day, while the savanna had five days without any removal. The two habitats were separated by several km, which might have caused a regional effect. However, since the two habitats were selected to test for presence and absence of termites and the two sites were within the same national park and savanna landscape, the spatial distance is not likely to have any strong effect on the results. There was also a gap of three weeks in July between the two habitat treatments that could have affected the results, but the two habitats in the experiment were both completed during the dry season, with the savanna habitat enduring the longest dry period before implementation.

In most ecosystems (Hulme 1998), including in African savannas (Linzey & Washok 2000), rodents are common seed removers and are common in Lake Mburo NP (Okullo et al. 2013), raising the question why there was no rodent seed removal. This could be because of low populations of rodents. Rodent populations are generally low after longer dry periods, and rainfall patterns affect breeding (Delany & Monro 1986) and population outbreaks (Leirs et al. 1996), leading to larger populations when there is enough food. Furthermore, seed eating rodents may have difficulties surviving in dry climates when the duration between growing seasons becomes too long or annual plants fail to produce normal yields (Linzey &

Washok 2000). However, rainfall patterns in Lake Mburo National Park was within normal range during the study, thus longer dry periods cannot explain a low population and absence of rodent seed removal. Monadjem and Perrin (2003) reported that fire increased the abundance of *Mastomys natalensis*, while other species abundances declined. This was because matured vegetation was burnt and replaced by more suitable *M. natalensis* habitat. Perhaps the vegetation in the habitats used in this experiment were too matured and therefore unsuitable for some rodents.

Another limiting factor could be that the seeds were not visible enough, even though the set-up was at the same location for three days with at least some seeds present most of the time. This might be the case with birds if they can't see the seeds (Linzey & Washok 2000), but not with mammals, since both vervets and rodents were observed. The camera set-up most likely did not affect animal behaviour either, since cameras has been used in several studies recording vertebrates and birds (Steen & Aase 2011; Steen & Mundal 2013), and insects generally reacts to movement and wouldn't be affected by the set-up.

Both termites and ants are soil engineers (Dangerfield et al. 1998; Jones et al. 1994; Jouquet et al. 2011) and termites have been found to affect vegetation species composition (Moe et al. 2009) and invertebrate seed removal (Acanakwo et al. 2017) on the termite mounds. This could influence the number of seed removal agents on the mound habitat. However, despite the mounds being confirmed active with termites, there was no seed removal by termites captured on camera. *Macrotermitinae* spp.'s food habits consists of woody and grassy litter (Lepage et al. 1993; Schuurman 2006) and termites were not observed in any of the viewed recordings, even on mounds, although they might have appeared on unseen recordings. Seeds not being part of their diet might explain the lack of termite presence. Acanakwo et al. (2017) found that termite presence on active mounds reduced seed removal, indicating that *Macrotermes* are not seed removers, but rather decrease the presence and activity of other invertebrates.

Seed preferences

Overall, seed weight showed a statistically significant effect on seed removal, with a decrease of 3 removals for every 1000 mg increase in seed size (Table 3). This means that there is a slight decrease in removal the larger the seeds are (Figure 4). If vervets favours larger seeds, and ants usually remove small seeds (Inouye et al. 1980; Levey & Byrne 1993), we might not see if there is a different impact on total seed removal. The effect of seed weight on the removal including only the unknown seed removers, showed a significant decreasing effect of 5 removals per 1000 mg, a slightly stronger decrease than that of the total seed removal (Table 6, Figure 7). These results contradict other post-dispersal studies based on seed weight, where larger seeds generally increases seed removal (Moles et al. 2003). This indicates that removal of large seeds was more likely to be caught on camera than small seeds (Figure 3).

Statistically, no seed removal agents were associated with certain seed species, but my data strongly indicated that vervets preferred large seeds and ants (and unknown) preferred small seeds (Figure 3). Preference for different seed species can vary depending on seed size or other traits among different seed removal guilds (Kelt et al. 2004; Muñoz & Cavieres 2006), and since seed removers also work as seed dispersers, they can affect the diversity of specific plants on a site (Paine & Beck 2007). This could determine the composition of the plant community (Brown & Heske 1990), favouring seeds that are predated upon and are still viable after digestion. Vervets never removed the smallest seed in volume, *R. natalensis*, possibly because it was hard for the vervets to pick up small seeds. One recording showed a vervet struggling to pick up a rice seed, another losing a rice seed after it managed to pick it up and another dropping a g-nut seed. Seeds represents an important part of vervets' diet when they are available (Foord et al. 1994; Isbell 1995; Wrangham & Waterman 1981). Vervets can eat large quantities of *Acacia tortilis* seeds out of which many easily passes through the gut, improving seed germination potential (Lamprey et al. 1974). They are opportunists (Matlock 2013) and have been shown to feed on unripe *Acacia erioloba* seeds (Barnes 2001). It was documented from vervet faeces that they eat a broad range of fruits when they are available, and that many of these seeds are still viable after digestion. This signifies that vervets can be long range seed disperser within their range (Foord et al. 1994), thereby potentially affecting the plant community structure (Brown & Heske 1990).

Figur 8. *Left*: a vervet trying to pick up a rice (*Oryza sativa)* seed. *Right*: ants eating the juicy flesh from a *G. similis*.

Ants did not remove any of the three heaviest and largest seeds; maize, g-nut and *A. sieberiana*, but did eat all the smaller seeds except *D. cinerea*. *Grewia similis* and *S. myrtina* are diaspores with a seed and a soft elaiosome around that is attractive for the ants. Myrmecochory ants may spread diaspores up to a distance of 25 m (Christianini et al. 2007) and provide suitable germination conditions for diaspores after eating the elaiosome and discarding the seeds (Beattie 1985). Ants were observed either removing *G. similis* and *S. myrtina*, or consuming the fruit body and leaving the remaining seed on the platform. Rice and *R. natalensis* were always moved away. The surface of maize, g-nut, *A. sieberiana, D. cinerea*, rice and *R. natalensis* could be too hard for the ants to consume (Carroll & Janzen 1973). Since maize and *A. sieberiana* are also heavy, ants might have been unable to consume them, even though maize and g-nut are agricultural crops and easily digestible once they are cracked. *Acacia sieberiana* seeds on the other hand, have high phenolic content and insoluble proanthocyanidins, which may lower the digestibility of fibre and nitrogen (Reed et al. 1990;

Tanner et al. 1990). *Dichrostachys cinerea* is known for its efficient nitrogen-fixing abilities (Schulze et al. 1991) and has very high phenolic and tannin content (Mlambo et al. 2004). Wrangham and Waterman (1981) suggested that high tannin content in vervets' food worked as a deterrent, and determined which parts of an *Acacia* ssp. they chose to eat. Consequently, due to their high phenolic content, *A. sieberiana* and *D. cinerea* would be their least preferred seeds among the eight and is probably the reason they had the lowest seed removal.

Seed type and time of day

There was no significant influence of seed type (i.e. native or crop), and neither vervets nor ants seemed to prefer any seed type over the other. There was however a trend that vervets always removed the two largest seeds maize and g-nut which are both agricultural seeds. In a study by Hill (1997)'s on crop damage from wildlife in western Uganda, vervets were ranked third among farmers on crop damage, with maize being the most commonly grown crop. This supports the notion that vervets prioritize agricultural crop seeds, although it is more likely that seed size, with g-nut and maize having higher nutrient value than smaller seeds, had a higher influence than seed type, especially since size was statistically significant. However, no conclusions can be drawn from this experiment, and to learn more about both ant and vervet seed type preference, more specific experiments (Everett et al. 1978; Kerley & Erasmus 1991) of seed removal between selected native and agricultural crop seeds may be more elucidating.

Seed removal was almost twice as high during day than during night, and time had a significant impact on seed removal. Nighttime significantly decreased removal by nearly one seed per day. An interaction between time and seed removal agents showed no significant effect, but vervets by themselves showed a tendency of increasing seed removal. This is probable, since vervets are diurnal animals (Baldellou & Adan 1998), and vervet seed removal accounted for over half of the recorded removal and removed seeds 20% of the days of the experiment. Ants can be both diurnal and nocturnal (Sudd & Franks 2013) but had most recorded removals during day. This was probably due to a higher likelihood of being captured removing seeds during day because of a higher number of recordings during day compared to night, because of shadows triggering the camera during daytime.

Unknown seed removal and potential method improvements

Out of the 84 captured seeds, 36 seeds were taken without recording the seed removal agent. All the maize, g-nut and *A. sieberiana* seeds that were removed were recorded and taken by vervets. This indicates that all seeds taken by vervets were recorded. Over the six times vervets were recorded removing seeds, they took four or more seeds except one time where it took only two. Vervets were easy to capture on camera because of their size, while ants were not, leading to the conclusion that vervets were always recorded and could not be an unknown seed removal agent. This is supported by the fact that unknown seed remover(s) never removed any of the largest three seeds maize, g-nut, *A. sieberiana*. Additionally, camera-traps are good at capturing vertebrates (Trolliet et al. 2014), so the unknown seed removers were most likely invertebrates. Ants were present in most recordings, but not always eating or removing. When ants were removing seeds, there was always something other than the ants triggering the recorder, such as moving shadows from plants, raindrops, or other larger insects such as spiders, crickets and moths moving in front of the camera. Furthermore, since ants seemed to prefer smaller seeds similarly to the unknown seed removal agents, ants were most likely the main unknown seed remover.

Night-time seed removal was high for the unknown seed removal agent(s). Data examination showed that the camera did trigger multiple times during the night with sufficient movement such as rodents or larger invertebrates, indicating that the removers was most likely small invertebrates.

Over the 30 days of recording, 4070 videos were recorded with the small area camera, and 20223 videos on the large area camera taking up a total of 135.6 GB of data-space. Most of the recordings were triggered because of shade or other insects running across the platform or moving in front of the camera, and only recordings around the time of seed removal was viewed (around 1%).

Because most post-dispersal seed predation leaves little sign of the agents responsible (Hulme 1998), this type of experiment can give insight and the possibility to observe the removal and removal agents as well as sometimes the consumption of the seed itself. There are many studies confirming that camera-trapping is an effective way for recording vertebrates (Trolliet et al. 2014). However, using them for recording insects is new (Steen & Aase 2011; Steen & Mundal 2013). When Steen (2017) used an IPhone with a VMD application to record pollinating large vertebrates (bumblebees), he documented that there is a possibility for VMD technology to capture small invertebrates.

Catching small invertebrate seed removal on camera, especially ants, was unsuccessful. Nonetheless, a cricket was recorded removing seeds and triggered the VMD, indicating that this method can be used. But since ants is a major seed remover (Hulme 1998; Linzey & Washok 2000), and experiments excluding ants, but not other invertebrates is difficult, this set-up must be changed if it is to be successful at recording small invertebrates' seed removal. This camera set-up might be expensive in the short run, compared to exclusion methods, but can be used repeatedly.

Because the camera was mounted on a pole and wasn't facing the platform directly from above, it was hard to get an even focus on the seeds, ultimately giving an unclear picture and lower sensitivity the farther away from the camera objects were. The crickets triggering the recorder, indicates that it is possible to capture an insect the size of a cricket with this VMD set-up. The smallest insect triggering the camera on the platform surface without taking any seeds was a true bug from the order *Hemiptera*, including several smaller flying insects that triggered the camera when it flew close to the camera lens. With a closer set-up that would make ants fill a larger part of the picture so that the VMD grid detects changes, it should be possible for the ants to trigger the camera. To detect ants with the VMD, a set-up with a camera 20 cm directly above the seeds, may work. Yet, due to the high activity level of ants, a set-up with the ability to trigger from the movement of ants would also leave numerous recordings with ant movement that is not necessarily related to seed removal. The set-up should be designed to fit the objective of the experiment.

Since the VMD is set to be very sensitive because of the small area, it will inevitably be easily triggered by abiotic factors such as raindrops and shade effects. Over the 30 day experiment it rained twice, once in June and once in August, causing the camera to record repeatedly throughout the rainfall and moving seeds around. Rain and moving shade caused the camera to create a high number of recordings, hence using a roofing to protect the seeds from rain and shade-effects would be beneficial and limit the number of recordings, making it easier to analyse the data. Removing grass and branches a small distance away from the camera trap could help, and a set-up excluding vertebrates could easily be protected against shade and wind, removing this problem completely.

The batteries used were supposed to last for at least 48 hours in this set-up when fully charged, but was highly dependent on a solar panel that would charge the battery completely every day. Days with constant cloud cover where the solar power couldn't charge the batteries enough, forced me to change batteries more frequently and sometimes take breaks between locations to charge the batteries properly. High quality solar panels, preferably more than one, and a spare battery in case of cloudy days with inefficient solar charging should solve this problem.

CONCLUSION

Ants and vervets are important seed removers and dispersers in this savanna landscape, supporting the idea that *Macrotermes* most likely are not seed removers. There was a small, but significant decrease in removal rates from seed size with a smaller decline for total seed removal than the unknown seed removers, indicating that removal of large seeds were captured on camera more often than smaller seeds.

In most studies on post-dispersal seed removal, seeds are removed with no sign of the agent responsible. This study shows the possibilities to observe the removal agent and sometimes the consumption of seeds and demonstrates that it is possible to record even small invertebrates during seed removal. Future studies should make two different set-ups for vertebrates and invertebrates. When studying invertebrates, vertebrates should be excluded by creating a small protected platform with the camera close to and directly above the seeds to create optimal conditions for the VMD.

REFERENCES

Acanakwo, E. F., Moe, S. R. & Sheil, D. (2017). Termites and large herbivores determine seed removal rates in an African savanna [submitted ms]. *Journal of Ecology*.

Alerstam, T. & Christie, D. A. (1993). *Bird migration*: Cambridge University Press.

Andersen, A. N. (1989). How important is seed predation to recruitment in stable populations of long-lived perennials? *Oecologia*, 81: 310-315.

Baldellou, M. & Adan, A. (1998). Diurnal and seasonal variations in vervet monkeys' activity. *Psychological reports*, 83: 675-685.

Barnes, M. E. (2001). Seed predation, germination and seedling establishment of *Acacia erioloba* in northern Botswana. *Journal of Arid Environments*, 49: 541-554.

Bates, D., Machler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using {lme4}. *Journal of Statistical Software*, 67: 1-48.

Beattie, A. J. (1985). *The evolutionary ecology of ant-plant mutualisms*: Cambridge University Press.

Beck, H. & Terborgh, J. (2002). Groves versus isolates: how spatial aggregation of *Astrocaryum murumuru* palms affects seed removal. *Journal of tropical ecology*, 18: 275-288.

Brown, J. H. & Heske, E. J. (1990). Control of a Desert-Grassland Transition by a keystone rodent guild. *Science(Washington)*, 250: 1705-1707.

Carroll, C. R. & Janzen, D. H. (1973). Ecology of Foraging by Ants. *Annual review of Ecology and Systematics*, 4: 231-257.

Christianini, A. V., Mayhé-Nunes, A. J. & Oliveira, P. S. (2007). The role of ants in the removal of non-myrmecochorous diaspores and seed germination in a Neotropical savanna. *Journal of Tropical Ecology*, 23: 343-351.

Dangerfield, J., McCarthy, T. & Ellery, W. (1998). The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. *Journal of Tropical Ecology*, 14: 507-520.

Davies, A. B., Levick, S. R., Asner, G. P., Robertson, M. P., van Rensburg, B. J. & Parr, C. L. (2014). Spatial variability and abiotic determinants of termite mounds throughout a savanna catchment. *Ecography*, 37: 852-862.

Davies, A. B., Baldeck, C. A. & Asner, G. P. (2016). Termite mounds alter the spatial distribution of African savanna tree species. *Journal of Biogeography*, 43: 301-313.

Delany, M. & Monro, R. (1986). Population dynamics of Arvicanthis niloticus (Rodentia: Muridae) in Kenya. *Journal of Zoology*, 209: 85-103.

Deligne, J., Quennedey, A. & Blum, M. S. (1981). The enemies and defense mechanisms of termites. *Social insects*, 2: 1-76.

Everett, R. L., Meeuwig, R. O. & Stevens, R. (1978). Deer mouse preference for seed of commonly planted species, indigenous weed seed, and sacrifice foods. *Journal of Range Management*: 70-73.

Foord, S., Van Aarde, R. & Ferreira, S. (1994). Seed dispersal by vervet monkeys in rehabilitating coastal dune forests at Richards Bay. *South African Journal of Wildlife Research-24-month delayed open access*, 24: 56-59.

Harper, J. L., Williams, J. & Sagar, G. (1965). The behaviour of seeds in soil: I. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seed. *The Journal of Ecology*: 273-286.

Harper, J. L., Lovell, P. & Moore, K. (1970). The shapes and sizes of seeds. *Annual review of ecology and systematics*, 1: 327-356.

Hill, C. M. (1997). Crop-raiding by wild vertebrates: The farmer's perspective in an agricultural community in western Uganda. *International Journal of Pest Management*, 43: 77-84.

Holl, K. D. & Lulow, M. E. (1997). Effects of Species, Habitat, and Distance from Edge on Post-dispersal Seed Predation in a Tropical Rainforest. *Biotropica*, 29: 459-468.

Hothorn, T., Bretz, F. & Westfall, P. (2008). Simultaneous Inference in General Parametric Models. *Biometrical Journal*, 50: 346--363.

Hulme, P. E. (1998). Post-dispersal seed predation: consequences for plant demography and evolution. *Perspectives in Plant Ecology, Evolution and Systematics*, 1: 32-46.

Hulme, P. E. & Borelli, T. (1999). Variability in post-dispersal seed predation in deciduous woodland: relative importance of location, seed species, burial and density. *Plant Ecology*, 145: 149-156.

Inouye, R. S., Byers, G. S. & Brown, J. H. (1980). Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. *Ecology*, 61: 1344-1351.

Isbell, L. A. (1995). Seasonal and social correlates of changes in hair, skin, and scrotal condition in vervet monkeys (*Cercopithecus aethiops*) of Amboseli National Park, Kenya. *American Journal of Primatology*, 36: 61-70.

Jansen, P. A. & Den Ouden, J. (2005). Observing seed removal: remote video monitoring of seed selection, predation and dispersal. *Seed fate: predation, dispersal and seedling establishment*: 363-378.

Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *The American Naturalist*, 104: 501-528.

Janzen, D. H. (1984). Dispersal of small seeds by big herbivores: foliage is the fruit. *The American Naturalist*, 123: 338-353.

Jones, C. G., Lawton, J. H. & Shachak, M. (1994). Organisms as ecosystem engineers. In *Ecosystem management*, pp. 130-147: Springer.

Jouquet, P., Traoré, S., Choosai, C., Hartmann, C. & Bignell, D. (2011). Influence of termites on ecosystem functioning. Ecosystem services provided by termites. *European Journal of Soil Biology*, 47: 215-222.

Kelt, D. A., Meserve, P. L. & Gutiérrez, J. R. (2004). Seed removal by small mammals, birds and ants in semi-arid Chile, and comparison with other systems. *Journal of Biogeography*, 31: 931-942.

Kerley, G. & Erasmus, T. (1991). What do mice select for in seeds? *Oecologia*, 86: 261-267.

Korb, J. & Linsenmair, K. E. (2001). The causes of spatial patterning of mounds of a fungus-cultivating termite: results from nearest-neighbour analysis and ecological studies. *Oecologia*, 127: 324-333.

Lamprey, H., Halevy, G. & Makacha, S. (1974). Interactions between *Acacia*, bruchid seed beetles and large herbivores. *African Journal of Ecology*, 12: 81-85.

Leirs, H., Verhagen, R., Verheyen, W., Mwanjabe, P. & Mbise, T. (1996). Forecasting rodent outbreaks in Africa: an ecological basis for Mastomys control in Tanzania. *Journal of Applied Ecology*: 937-943.

Lepage, M., Abbadie, L. & Mariotti, A. (1993). Food habits of sympatric termite species (Isoptera, Macrotermitinae) as determined by stable carbon isotope analysis in a Guinean savanna (Lamto, Côte d'Ivoire). *Journal of Tropical Ecology*, 9: 303-311.

Levey, D. J. & Byrne, M. M. (1993). Complex Ant-Plant Interactions: Rain-Forest Ants as Secondary Dispersers and Post-Dispersal Seed Predators. *Ecology*, 74: 1802-1812.

Liland, K. H. (2015). mixlm: Mixed Model ANOVA and Statistics for Education. *R package version 1.1.0*.

Linzey, A. V. & Washok, K. A. (2000). Seed removal by ants, birds and rodents in a woodland savanna habitat in Zimbabwe. *African Zoology*, 35: 295-299.

Loveridge, J. P. & Moe, S. R. (2004). Termitaria as browsing hotspots for African megaherbivores in miombo woodland. *Journal of Tropical Ecology*, 20: 337-343.

Matlock, A. (2013). *Negotiating social space in vervet monkeys*: Lethbridge, Alta.: University of Lethbridge, Dept. of Psychology, c2013.

Miura, S., Yasuda, M. & Ratnam, L. C. (1997). Who steals the fruits? Monitoring frugivory of mammals in a tropical rain-forest.

Mlambo, V., Smith, T., Owen, E., Mould, F., Sikosana, J. & Mueller-Harvey, I. (2004). Tanniniferous *Dichrostachys cinerea* fruits do not require detoxification for goat nutrition: in sacco and in vivo evaluations. *Livestock Production Science*, 90: 135-144.

Mobaek, R., Narmo, A. K. & Moe, S. R. (2005). Termitaria are focal feeding sites for large ungulates in Lake Mburo National Park, Uganda. *Journal of Zoology*, 267: 97-102.

Moe, S. R., Mobaek, R. & Narmo, A. K. (2009). Mound building termites contribute to savanna vegetation heterogeneity. *Plant Ecology*, 202: 31-40.

Moles, A. T., Warton, D. I. & Westoby, M. (2003). Do small-seeded species have higher survival through seed predation than large-seeded species? *Ecology*, 84: 3148-3161.

Monadjem, A. & Perrin, M. (2003). Population fluctuations and community structure of small mammals in a Swaziland grassland over a three-year period. *African Zoology*, 38: 127-137.

Mugerwa, B., Sheil, D., Ssekiranda, P., Heist, M. v. & Ezuma, P. (2012). A camera trap assessment of terrestrial vertebrates in Bwindi Impenetrable National Park, Uganda. *African Journal of Ecology*, 51: 21-31.

Muñoz, A. A. & Cavieres, L. A. (2006). A multi-species assessment of post-dispersal seed predation in the central Chilean Andes. *Annals of Botany*, 98: 193-201.

Myster, R. W. & Pickett, S. (1993). Effects of litter, distance, density and vegetation patch type on postdispersal tree seed predation in old fields. *Oikos*: 381-388.

O'Dowd, D. J. & Hay, M. E. (1980). Mutualism between harvester ants and a desert ephemeral: seed escape from rodents. *Ecology*, 61: 531-540.

Okullo, P., Greve, P. M. K. & Moe, S. R. (2013). Termites, Large Herbivores, and Herbaceous Plant Dominance Structure Small Mammal Communities in Savannahs. *Ecosystems*, 16: 1002-1012.

Page, L. K., Swihart, R. K. & Kazacos, K. R. (2001). Seed preferences and foraging by granivores at raccoon latrines in the transmission dynamics of the raccoon roundworm (Baylisascaris procyonis). *Canadian Journal of Zoology*, 79: 616-622.

Paine, T. D. & Beck, H. (2007). Seed predation by neotropical rain forest mammals increases diversity in seedling recruitment. *Ecology*, 88: 3076-3087.

Reed, J., Soller, H. & Woodward, A. (1990). Fodder tree and straw diets for sheep: intake, growth, digestibility and the effects of phenolics on nitrogen utilisation. *Animal Feed Science and Technology*, 30: 39-50.

Rowcliffe, J. M. & Carbone, C. (2008). Surveys using camera traps: are we looking to a brighter future? *Animal Conservation*, 11: 185-186.

Salvatori, V., Egunyu, F., Skidmore, A., De Leeuw, J. & Van Gils, H. (2001). The effects of fire and grazing pressure on vegetation cover and small mammal populations in the Maasai Mara National Reserve. *African Journal of Ecology*, 39: 200-204.

Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S., Gignoux, J., Higgins, S. I., Le Roux, X. & Ludwig, F. (2005). Determinants of woody cover in African savannas. *Nature*, 438: 846-849.

Sankaran, M., Ratnam, J. & Hanan, N. (2008). Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography*, 17: 236-245.

Schulze, E.-D., Gebauer, G., Ziegler, H. & Lange, O. (1991). Estimates of nitrogen fixation by trees on an aridity gradient in Namibia. *Oecologia*, 88: 451-455.

Schuurman, G. (2006). Termite diets in dry habitats of the Okavango delta region of northern Botswana: a stable carbon isotope analysis. *Sociobiology*, 47: 373-389.

Sileshi, G. W., Arshad, M., Konaté, S. & Nkunika, P. O. (2010). Termite-induced heterogeneity in African savanna vegetation: mechanisms and patterns. *Journal of vegetation science*, 21: 923-937.

Steen, R. & Aase, A. L. T. O. (2011). Portable digital video surveillance system for monitoring flower-visiting bumblebees. *Journal of Pollination Ecology*, 5: 90-94.

Steen, R. & Mundal, D. (2013). New video registration of *Autographa pulchrina* (Haworth, 1809) (Lepidoptera, Noctuidae) and Sphinx pinastri L., 1758 (Lepidoptera, Sphingidae) pollinating *Platanthera bifolia latiflora* (Orchidaceae) in Norway. *Norwegian Journal of Entomology*, 60: 57-61.

Stoen, O. G., Okullo, P., Eid, T. & Moe, S. R. (2013). Termites facilitate and ungulates limit savanna tree regeneration. *Oecologia*, 172: 1085-93.

Sudd, J. H. & Franks, N. R. (2013). *The behavioural ecology of ants*: Springer Science & Business Media.

Tanner, J., Reeds, J. & Owen, E. (1990). The nutritive value of fruits (pods with seeds) from four *Acacia spp*. compared with extracted Noug (*Guizotia abyssinica*) meal as supplements to maize stover for Ethiopian highland sheep. *Animal production*, 51: 127-133.

Team, R. C. (2015). *R: A Language and Environment for Statistical Computing*. Computing, R. F. f. S. (ed.): R Core Team. pp. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Trolliet, F., Huynen, M.-C., Vermeulen, C. & Hambuckers, A. (2014). Use of camera traps for wildlife studies. A review. *Biotechnologie, Agronomie, Société et Environnement*, 18: 446.

Wall, S. B. V., Kuhn, K. M. & Beck, M. J. (2005). Seed Removal, Seed Predation, and Secondary Dispersal. *Ecology*, 86: 801-806.

Wickham, H. (2009). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.

Willson, M. F. & Traveset, A. (2000). The ecology of seed dispersal. *Seeds: The ecology of regeneration in plant communities*, 2: 85-110.

Wrangham, R. & Waterman, P. (1981). Feeding behaviour of vervet monkeys on *Acacia tortilis* and *Acacia xanthophloe*a: with special reference to reproductive strategies and tannin production. *The Journal of Animal Ecology*: 715-731.

Yasuda, M., Miura, S. & Hussein, N. A. (2000). Evidence for food hoarding behaviour in terrestrial rodents in Pasoh Forest Reserve, a Malaysian lowland rain forest. *Journal of Tropical Forest Science*: 164-173.

APPENDIX 1

Multiple comparative analysis with Tukey test of the seed species that compares the effect each species has on each other and if it is significant. Estimates describe how much effect the seeds has on each other in terms of seed removal, and can be related to seed weight. Seed species with the same amount of seeds removed shows 100 % correlation (p = 0.99).

Effects on amount of seed removal	Estimate	SE	z	P
G-nut vs Dichrostachys	0.45	0.48	0.95	0.34
Grewia vs Dichrostachys	1.80	0.42	4.23	< 0.001
Maize vs Dichrostachys	0.45	0.48	0.95	0.34
Rhus vs Dichrostachys	1.19	0.40	2.70	< 0.01
Rice vs Dichrostachys	2.13	0.42	5.08	< 0.001
Scutia vs Dichrostachys	1.61	0.43	3.77	< 0.001
A. sieberiana vs Dichrostachys	0.00	0.52	0.00	0.99
Grewia vs g-nut	1.34	0.37	3.60	<0.001
Maize vs g-nut	0.00	0.43	0.00	0.99
Rhus vs g-nut	0.73	0.39	1.88	0.06
Rice vs g-nut	1.68	0.37	4.56	<0.001
Scutia vs g-nut	1.15	0.38	3.07	<0.01
A. sieberiana vs g-nut	-0.45	0.48	-0.95	0.34
Maize vs Grewia	-1.34	0.37	-3.59	<0.001
Rhus vs Grewia	-0.61	0.32	-1.89	0.06
Rice vs Grewia	0.34	0.29	1.16	0.24
Scutia vs Grewia	-0.18	0.30	-0.61	0.54
A. sieberiana vs Grewia	-1.80	0.42	-4.23	<0.001
Rhus vs maize	0.73	0.39	1.88	0.06
Rice vs maize	1.68	0.37	4.56	<0.001
Scutia vs maize	1.16	0.38	3.07	<0.01
A. sieberiana vs maize	-0.45	0.48	-0.95	0.34
Rice vs Rhus	0.94	0.31	3.00	<0.01
Scutia vs Rhus	0.42	0.33	1.30	0.19
A. sieberiana vs Rhus	-1.19	0.44	-2.70	<0.01
Scutia vs rice	-0.52	0.29	-1.76	0.08
A. sieberiana vs rice	-2.13	0.42	-5.08	<0.01
A. sieberiana vs Scutia	-1.61	0.43	-3.77	<0.01

Norges miljø- og biovitenskapelig universitet
Noregs miljø- og biovitskapelege universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway