Hunger, Hiding, and Habitat: Observations and Game Theoretical Explorations of Foraging and Burrowing

BY

HILARY BETH OSBORNE
B.S., Northeastern University, 2000

THESIS

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Defense Committee:
      Joel S. Brown, Chair and Advisor
      Som B. Ale, Biological Sciences
      Tanya Berger-Wolf, Computer Science
      Thomas J. Park, Biological Sciences
      Christopher J. Whelan, Biological Sciences and Illinois Natural History Survey

working with me on what is now Chapter 6. And mostly Beth, without whom we'd all be forever lost in the red tape.

Contribution of Authors

I wrote the entirety of all manuscripts presented in this document, including generating all figures except where noted and the photograph in Chapter II, which was taken by Dr. Thom Park and used with his permission. The experiments in Chapter II were carried out by Dr. Joel Brown and Dr. Thom Park. The model in Chapter VI was a collaboration with Dr. Brian Powers and Dr. Matthew Borque. Dr. Joel Brown assisted in preparing all chapters by offering advice and critiques. None of the chapters have been previously published.

TABLE OF CONTENTS

TABLE OF CONTENTS (continued)

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES (continued)

LIST OF FIGURES (continued)

LIST OF ABBREVIATIONS

BRD   Behavioral resource depression

MNP   Mapungubwe National Park

NMR   Naked mole-rats

SRR   Slowly regenerating resources

TFCA   Transfrontier Conservation Area

VLNR   Venetia-Limpopo Nature Reserve

SUMMARY

The challenges of living include the need for food and the risk of predation. This dissertation explores several aspects of both finding food and hiding to avoid becoming food.

Naked mole-rats are subterranean eusocial rodents--or are they? We explored naked mole-rat foraging patterns via a laboratory study measuring how naked mole-rats allocated their foraging efforts when searching for hidden treats. We found that contrary to our expectations of cooperative foraging, they appear to forage only for themselves, and may even hide information about food patches from one another. This supports the idea that naked mole-rat society is despotic rather than cooperative.

On the other end of the sociality spectrum is the solitary aardvark. Aardvarks do not live fully underground like naked mole-rats, but they dig large burrows for themselves and feeding digs large enough to serve as burrows for other animals. We traveled to Mapungubwe National Park, South Africa, to look at the distribution of these burrows, how quickly they appear and disappear, and how frequently they are used. We confirmed what many suspected: they are distributed in a clumped pattern, and while these holes appear and collapse all the time, some last for years. All have a good chance of being visited by some animal at any time.

We also monitored dozens of burrows with camera traps to determine the identity of these burrow-users. It is not aardvarks. Instead, warthogs are king. This may reflect species abundance, as warthogs are quite numerous at Mapungubwe. The distribution of these burrows indicates that for their creators they are likely feeding digs, reflecting the clumped distribution of ant and termite nests.

We then considered what actually happens when an aardvark tears into a termite mound. The termites can run away, send soldiers to defend the mound, or both. This means that the food patch--in this case the mound--declines in food quantity at a rate higher than the rate at which the aardvark feeds. We created and explored a model of how this additional decline, a form of behavioral resource depression, affects the time the aardvark spends in the patch and how much food they actually consume. We made the model more general than aardvarks and ants/termites to account for other forms of behavioral resource depression, such as induced plant chemical defenses, that reduce the quality, and thus effectively the quantity, of plant biomass available to the herbivore. We also took the first step toward combining this with the fact that food sources can take a long time to regenerate after being foraged, and how a finite number of these patches can affect the forager's long-term harvest from the patch.

Finally, we modeled how hunger may affect a forager's willingness to risk predation and the predator's probability of hunting. Inspired by the well-studied gerbil–owl foraging game, including empirical studies on this subject, we developed a model which shows that the likelihood a predator will hunt increases with the forager's hunger level.

I. INTRODUCTION

A. Personal Background

Nature is complex. Individual lives are complex. And so, my adventures leading up to this document, and the document itself, are complex.

Once upon a time, I was a cynical kid. School was a horrible experience, not because of the academics, but because of the combination of having to be up at ridiculously early hours of the morning (who schedules physics for 7:30AM?) and having to be around teenagers. What got me through was the promise that high school was as bad as it got, and that college would be better. I hated English class most of all, but oddly enough some of my English teachers were my favorites, and I clearly learned a thing or two. Misplaced apostrophes make me twitchy. I also liked chemistry and never took biology.

Then college. At Northeastern University, chosen over Tufts for the simple reason of a full scholarship, I started out in Chemical Engineering, but quickly discovered that I hated engineering. I chose to switch to Biology for reasons unknown even to me. I did well, except for Organic Chemistry. I knew I wanted to someday get a doctorate, but as I was burned out on school and had no idea what I wanted my doctorate in, I went to work as a veterinary technician. For five years I worked full-time in the incredibly stressful, but also incredibly rewarding, specialty of Emergency and Critical Care.

After that, grad school seemed like a good idea. I ended up at UIC, with only a vague idea of what I wanted to do. Burrowing mammals—check. Game theory—check. Anything more specific—nope. I took some classes, had some ideas, then decided to head to South Africa, at a

private reserve owned by some people my adviser knew. They have aardvarks there. Aardvarks are nifty, so why not?

My first attempt at a field season was a disaster. Within three days of arriving in Johannesburg I was in an ICU in Polokwane recovering from life-threatening injuries. Turns out that gravity works the same way in South Africa as it does in the USA.

I decided to try again the next year, only based in the Limpopo Valley instead of the mountains. Mapungubwe National Park turned out to be perfect for me, having several habitat types in close proximity, plenty of aardvark activity, and a wonderfully supportive set of rangers. I spent a total of 9 months there over the next three years.

Like so much in my life, my research just kind of happened. I never had the detailed plan other people did, but I think that let me accept whatever my results were. With no particular attachment to a hypothesis, you don't mind seeing it disproven. It also helped while working in South Africa, as the culture there is simply not as regimented as here. One goes with the proverbial flow.

Throughout grad school, all 20 semesters, I was a Teaching Assistant. That of course had its highs and lows, but I generally liked it. Students tended to either love me or hate me. I was known as both "the mean one" and "the fun one," depending on whether or not the students followed my rules.

My desire to live comfortably instead of barely scraping by also led to taking more time but gaining invaluable experience. Throughout grad school I worked part-time as a tech at a veterinary ER. It's a mentally and physically exhausting job, but nothing beats the feeling of

saving a life. I also got to maintain my skills and keep on top of the rapidly changing standards of veterinary medicine.

I also picked up some freelance editing work. I had no formal training, or even informal training, but my mother had a book in progress that needed some resources checked for completeness, and content that begged for snarky commentary. Later, she got a job re-writing patient information for the American Academy of Ophthalmology, a project far too big for one person to handle. She hired me, and together we re-wrote more than 80 documents in one year. This means that I managed to have 80-something publications during grad school. Sure, they're just a couple pages long, really repetitive, and don't have my name on them, but I'll take it.

All that editing experience helped me qualify to take the exam for certification by the Board of Editors in the Life Sciences, which I passed easily. I realized that while I find writing up my own research painful, I love nit-picking others' work. Tearing it apart. And now I was qualified to do so professionally.

B. Research

In all that time, when not working at any of my three jobs, I actually managed to get some research done.

I began with an interest in burrowing mammals, especially the largest. That meant wombats and aardvarks. My advisor had contacts in South Africa--aardvark territory--who hosted undergraduate and graduate students studying the wildlife on their private conservation land, Lajuma. It sounded like a good idea, so I signed up. Two days after arriving in the country,

while exploring the mountains, I fell and was severely injured. After nearly a week in the hospital, I returned to do, well, nothing. I could not walk, and a deep depression prevented any sedentary research. I did manage to make some contacts at South African National Parks (SANParks), in particular a section ranger at Mapungubwe National Park named Stefan Cilliers. So a year later, having completely recovered, I came up with a better idea. With the appropriate permits in hand, I headed back to South Africa. This time, and the two years after, I only visited Lajuma but worked at the non-mountainous Mapungubwe. I went four years without experiencing summer.

At Mapungubwe, I spent countless hours walking around finding, describing, and photographing holes in the ground. For the first two years I had Nature Conservation students as assistants; the first year it was whoever was not assigned elsewhere, the second Samantha McCulloch. My final field season we had no students, and I didn't know until I arrived how it would work out. I ended up being accompanied every day by a ranger, Solly Zitha, who is also a fantastic wire artist. With my assistants, I documented hundreds of aardvark-dug holes, covering generally 8-10 km of ground a day. We set up camera traps all over the park, some of which still worked by the end of it all. I sifted through a disturbingly large number of pictures of grass to find the pictures of animals that form the basis for chapter 3. We revisited the same burrows year after year to monitor their existence, and Solly and I spent a few weeks figuring out how often these burrows were actually visited.

Back in Chicago, I built two game theory models. The first, an exploration of how behavioral resource depression combines with slowly regenerating resources to affect patch use in foraging. The second was developed along with some friends from the Math and Stats

department, and focuses on how hunger affects the decision of whether or not to forage for food. Game theory allows me to be the math geek I truly am.

C. The chapters

1. Field work

The order of the chapters presented here is not the order in which they were conceived.

While my initial attraction to burrowing mammals was simply that they're awesome, I had plenty of science to support actually studying them. I was intrigued by the concept of organisms as "ecosystem engineers," a term coined by Jones et al. in 1994. Ecosystem engineers work much like human civil and mechanical engineers, altering their environment to benefit themselves and, as a side effect, impacting their entire ecosystem. The example known even to the general public is the beaver, which creates massive and incredibly well-constructed dams and turns streams into ponds--or rivers into lakes (Jones et al. 1994, 1997; Jones and Gutiérrez 2007)

I was most intrigued by burrow-digging engineers. I don't know why. Perhaps I was unconsciously influenced by one of modern history's most impressive engineering projects, the Big Dig in my home town of Boston. The Big Dig involved putting a highway underneath an existing city and the neighboring harbor, which required moving more than 12 million cubic meters [24 million tonnes, assuming 2 tonnes/m^3] of dirt (Commonwealth of Massachusetts).

Aardvarks don't move anywhere near that much dirt (or cost nearly as much), but for individuals without machinery, their excavation work is impressive. To date, no one knows how much soil aardvarks move in a year, as no one has fully documented the number and size of

burrows dug, but our data allows for a very conservative estimate of approximately 300 tonnes per aardvark per year. Australia's hairy-nose wombat, another large solitary burrowing mammal, has been estimated to move 276 m^3/ha (552 tonnes/ha, assuming 2 tonnes/m^3), though no time frame was given (Bancroft et al. 2004).

One of my goals in South Africa, as seen in chapters 2 and 3, was to start to get a handle on the size and nature of aardvarks' impact. It turns out that another person, Gareth Whittington-Jones, had similar ideas, and his Master's thesis (Whittington-Jones 2007) and later paper (Whittington-Jones et al. 2011) cover areas that complement this dissertation. Whittington-Jones surveyed the small rodents and insects in and around aardvark burrows in several parks in South Africa with incidental sightings of larger animals; we focused on the larger animals though the use of camera traps. He also described the microhabitat within the burrows. We focused on the number, location, and external gross appearance of burrows.

My assistants and I, the royal "we," cataloged hundreds of aardvark excavations in three habitat types. Location, visual estimates of size, pictures. We revisited many of our sites year after year to see how things changed. Some burrows remained intact and in use for many years, others collapsed almost as soon as they were dug; this variation exists within a soil and habitat type, and undoubtedly varies among them.

At the same time, we used camera traps to figure out just who is actually using these burrows. Camera-trap technology (like all technology) is improving rapidly (Rovero et al. 2013), and even between field seasons we were able to switch to smaller yet higher-quality cameras. Out of the 20 or so cameras I brought to South Africa, only four were functional by the end of my final field season; I left them with the rangers to use for their own interests or to help catch

the poachers and smugglers that plague the park. Most of the rest were destroyed by hyenas,

elephants, or ants. One was stolen.

Camera-trapping started more than a century ago, when the method involved rigging up

a flashlight and a camera to be triggered by an animal tugging on a piece of food attached to a

wire (Carey 1926). Back then, they got one chance. Once film rolls were invented, camera traps

became more practical, and when the world went digital, camera traps became an easy and

useful way to survey the medium to large animals in an area (Rowcliffe and Carbone 2008),

though study designs are still being perfected (Tobler et al. 2008, Foster and Harmsen 2012,

Tobler and Powell 2013, Burton et al. 2015). Modern cameras can be left alone for months if in

a secure location, taking and storing thousands of pictures with a single set of batteries and a

memory card. Our cameras, made in 2008 or 2009, are not up to 2016's standards, but ours

were more than adequate for our purposes. One camera went missing, only to be found 11

months later, right where it had been left by a spotted hyena. It still worked.

I had the pleasure of sorting through tens of thousands of pictures to find just the ones

with animals and creating a spreadsheet database for them. There were already databases

created for this purpose (Tobler et al. 2008), but I chose to do it myself rather than navigate

new software.

Based on the data collected, aardvarks are clearly impressive creatures, rarely seen but

with significant, obvious impacts on their habitats. Their engineering efforts are not as widely

known as those of the builders or habitat destroyers, but have the same broad impacts.

2. Game theory

At UIC, in Chicago, I took two game theory courses and a math-based population ecology course. I decided to do some modeling.

When I was a kid, my dad (a health physicist) told me the terrible Spherical Cow joke and for some reason it stuck in my head. As rendered on Wikipedia (Spherical Cow 2015):

> Milk production at a dairy farm was low, so the farmer wrote to the local university, asking for help from academia. A multidisciplinary team of professors was assembled, headed by a theoretical physicist, and two weeks of intensive on-site investigation took place. The scholars then returned to the university, notebooks crammed with data, where the task of writing the report was left to the team leader. Shortly thereafter the physicist returned to the farm, saying to the farmer, "I have the solution, but it only works in the case of spherical cows in a vacuum."

It's a terrible joke but a very useful metaphor. Models of the real world, whether physics, economics, or biology, must be far simpler than the real world. Nature is complex. But we can use rough approximations to try to understand things a little better. It's like an artist drawing a cow. They don't start at the nose and try to get every little detail--they start with a few big ovals. It doesn't take much more than that to end up with a picture we would recognize as a cow. That is what we try to do with modeling. Not to get a realistic cow, but to end up with something sufficiently cow-like to be useful.

Thanks to decades of theoretical and practical work, we know quite a bit about how animals make foraging decisions. Each model and field study tends to focus on only one or two

factors, as the math and the number of variables and parameters can quickly become unwieldy (e.g., Wood et al. 2013, Sunyer et al. 2014, Fortin et al. 2015). Furthermore, the point of mathematical modeling is to discern how a particular factor may influence foraging. Including too many factors makes this task impossible or unproductive. One must make many simplifying assumptions so as to focus on the factor(s) of choice.

First up for my modeling was an exploration into behavioral resource depression (Charnov et al. 1976). Behavioral resource depression occurs when a resource such as a food supply, is depleted by means other than consumption. The simplest form of behavioral resource depression is prey animals running away from their predators, where they still exist but are not consumed. This concept applies to plants as well. Many plants have inducible chemical defenses--when an animal begins chewing on them, the plant begins to release noxious chemicals to render themselves less palatable or even toxic (Karban and Myers 1989). Some plants even let each other know that an herbivore is present so they can build up defenses before being eaten (Ueda et al. 2012).

Staying in defense mode may take a lot of resources (Neilson et al. 2013), and otherwise interfere with other fitness-enhancing activities (foraging, reproducing, etc.). The plant or animal which depresses its availability to predators needs time to return to its pre-predation state.

In reading papers on foraging, I found that most ignored two realities of many systems: sometimes the food runs away (i.e., behavioral resource depression) (e.g., Kotler 1992), and sometimes it takes a long time to come back (Brown and Rosenzweig 1986, Watts 1998). Many foraging studies use stationary food such as seeds, and the researcher replenishes the food

supply daily. My beloved aardvarks, however, eat ants and termites, which can both hide deeper within the nest and send soldiers armed with pincers and poisons to defend the nest (da Cunha et al. 2014). This encourages the aardvark to give up on the nest sooner, having done less damage. Then nest rebuilding begins, a process which takes far longer than the seconds or minutes the aardvark took to damage the nest. So I developed a model to explore how this behavioral resource depression, coupled with slowly regenerating resources, affects foraging behavior, giving-up densities (Brown 1988), and patch use. I used prey numbers, but the model can easily be adapted for other metrics.

Because the phenomena of behavioral resource depression and slowly regenerating resources exist in many systems, I kept the model, which I based on Charnov's Marginal Value Theorem (Charnov 1976), very general. Nevertheless, the model makes sense, and provides a basis for more sophisticated models.

While sorting through all of this, I also met regularly with a few friends from the Math and Stats department. We called it Game Theory Club. It was incredibly nerdy--we'd literally get together to do game theory. We read papers (on learning algorithms) and started our own model based on my idea. I was intrigued by the idea of state dependence, and that one's strategy in a foraging game could be affected by, for example, how hungry one is. If you're starving, you may be willing to head into a bad neighborhood if that's where the food is. If you're stuffed, even the kitchen may be too much effort (Clark 1994, Brown and Brooks 1991). State dependence can be applied to pretty much any game where a player's status may determine their available strategies and their outcomes. For example, both body size and

burrow-resident status can affect the outcome of contests between juvenile signal crayfish (Ranta and Lindström 1992).

Some work had been done in this area, and Game Theory Club's idea was sparked by one paper in particular (Berger-Tal et al. 2010). There was a simple model right in the paper, but we chose to start from scratch, or as they say in science, from first principles. The result is now chapter 5. Even with keeping our metaphorical cow pretty spherical (I'd say that it, like the Earth, is kind of an oblate spheroid), we can see how the normal predator–prey game can be affected by how hungry the prey is. While our models have some fatal flaws, they do indicate that owl hunting behavior may be driven by gerbil hunger state. This model will need to be altered before it is made more complex.

3. Naked Mole-rats

All throughout grad school I supported myself as a TA. At an end-of-semester lunch in 2014, one of the professors of the course I was TAing offered me a project. This professor, Thom Park, worked with naked mole-rats. He studies their bizarre physiology, but that's not what this project was. Way back in 1999 and 2000 he and my adviser, Joel Brown, had conducted a short foraging behavior study with two colonies of naked mole-rats (and one of gerbils, for comparison). They used Joel's favorite measurement, the giving-up density, or in this case the related proportion harvested, to try to figure out if naked mole-rats forage like they reproduce. Eusocially, that is.

Naked mole-rats are a weird species in many ways (Grimes et al. 2012). Physiologically, they are nearly ectothermic (unlike all other mammals, which are endothermic), resistant to

some forms of pain, can withstand extreme hypoxia, do not get cancer, can live ten times as long as other rodents their size, and show few signs of aging (though as the brilliant True Facts video (True Facts About the Naked Mole-Rat 2013) points out, that feat is somewhat less impressive when you're born looking like an old man). They are also one of the only mammals considered to be eusocial.

Eusociality in insects, most notably ants and honeybees, means that the colony effectively acts as a single organism. Individuals are literally born into their job, with little or no opportunity to switch castes (Sherman et al. 1995). Eusocial colonies have one or a few reproductive individuals, and non-reproductive members of the colony perform other tasks such as foraging or nest building. Naked mole-rats were first described as eusocial in 1981 (Jarvis 1981). Over time it became clear that naked mole-rats are not fully eusocial like the insects, and the popular definition for eusociality in mammals was restricted to "reproductive altruism (which involves reproductive division of labor and cooperative alloparental brood care), overlap of adult generations, and permanent (lifelong) philopatry," (Burda et al. 2000) and excluded things like fixed castes as criteria for eusociality.

But Thom and Joel had never really done anything with their data. Sure, they had collected and partially analyzed it, and knew that naked mole-rats do not forage eusocially, but had never gotten around to writing it up. They needed a grad student who knew them both. I fit that criterion (and needed another chapter), and since this involved burrowing mammals and eating, it was a perfect match. In this chapter, the royal "we" generally means "they," instead of the usual "I" or, occasionally, "we."

D. Conclusion

Nature is complex, but the following chapters try to make little spherical cows out of some bits

of it.

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II. NAKED MOLE-RATS ARE NOT AS COOPERATIVE AS THEY APPEAR

A. Introduction

1. Eusociality

Animal social systems vary from totally solitary to completely eusocial. Eusocial animals live in groups that have a reproductive division of labor, overlapping generations, and cooperative rearing of the young (Jarvis 1981, Sherman et al. 1995, Burda et al. 2000, Wilson and Hölldobler 2005, Jones 2014). Eusociality is most extreme in insects, in which individuals may be permanently constrained to their roles and thus require the colony to perform other tasks in order to survive as a unit; the colony is effectively a single organism and thus the unit of selection.

While the generally accepted definition of eusociality in mammals only addresses reproduction (Burda et al 2000), it is reasonable to expect that other aspects of their ecology would be similarly group-oriented. For example, one would expect that a eusocially reproducing group would also engage in eusocial foraging, in which individual foragers share information about the best foraging opportunities. They would be willing to take risks and subordinate their own returns for the good of the group.

Bees and ants, as the epitome of eusociality, engage in eusocial foraging. Honey bee scouts seek possible nesting and foraging sites, then, rather than simply settling in to eat, will fly back to the colony to tell the rest of the group (Seeley and Visscher 2003). Fire ants make trails, signal their fellow scouts, and even provide samples of food to other ants. This allows the

colony to harvest and eat *en masse* rather than each individual foraging on its own (Cassill 2003).

Choices animals make while foraging can reveal a great deal about their perceptions of their environment and their social cohesion. Social foraging may allow for protection from predators through greater overall vigilance and safety in numbers. It can also allow the group to find the best places to forage in a heterogeneous environment (Ale and Brown 2007). Eusocial foraging is extreme social foraging. As a social unit, group benefits may outweigh the individual's risks associated with focusing on one's own food intake and safety.

2. Naked mole-rats

Little is known about naked mole-rat behavior in the wild. Their entirely fossorial existence makes observation difficult at best. Even in the laboratory, naked mole-rat behavior has not been described in great detail, and much of what we know in this area is based on informal or incidental observations during the course of other studies.

Naked mole-rats (*Heterocephalus glaber*) are the most eusocial of mammals. They live in large, closely related, multigenerational colonies in which a single female, the queen, is responsible for all reproduction while other individuals work in tunnel maintenance and foraging. Unlike insects, the division of labor is not fixed into castes, though transition between roles is rare. The queen breeds with one to three designated males. The queen and breeding males are in those roles for life, and other colony members fight to replace them upon their deaths (van der Westhuizen et al. 2013).

Naked mole-rat scouts appear to recruit others to food patches by vocalizing when they find high-quality food patches and by leaving an odor trail between the food and the main nest (Judd and Sherman 1996). However, even in the same study, there was no obvious intentional scent-marking observed. Naked mole-rats have also been observed tugging at food items held by others (Schieffelin and Sherman 1995). This suggests that the "recruitment" may be unintentional. Conflicts may arise between the interests of the individual mole-rat and those of its colony.

3. Patch use

Food sources are rarely, if ever, distributed uniformly. Instead, food occurs in patches. Foraging animals choose patches based on their knowledge of the nearest and other accessible patches. Patch quality is determined by a number of factors, including nutritional value of food items, ease of foraging, and number of food items, as well as the relative risk or safety of the patch. A patch will be profitable so long as its benefits outweigh its costs (Brown 1988).

Studies in squirrels (Morgan et al. 1997) show that the pattern of patch choice, and the extent to which a given patch is depleted, is affected by the spatial scale of the patches. Simply put, the further away a patch is from the animal's current location, the less accessible and therefore less desirable it is. Animals are less likely to be aware of the quality of distant patches, even if they know the patches exist.

There are two ways in which an individual may glean information about distant patches: exploration or communication. Given a large enough spatial scale, exploration may not be possible due to time and energy spent on search and increased predation risk while travelling

between patches. Communication with other conspecifics allows for information transfer without increased individual risk. Communication may be via vocalizations, scent cues, or even dances (e.g., Jackson and Ratnieks 2006, Seeley et al 2000).

One factor which can influence the amount harvested from a given patch is the forager's information about, and ability to find and use, other patches. If there is only one food patch, the forager has no options and must exploit it to the best of their ability. Conversely, if there are many patches to choose among, a forager can explore them, using only the best patches and only until they are no longer profitable. Not knowing about nearby patches is effectively the same as these patches not existing. Animals vary widely in their communication about food, from none whatsoever to complete information-sharing (Galef and Giraldeau 2001).

One way to "ask" foraging animals their opinion of a patch or set of patches is to provide them with a variety of patches of known quality, allow them to forage for a time, and then look at the absolute and relative quantities of food harvested—or not harvested. Patch quality can be based on the type or quantity of food, the type and quantity of non-food items in the patch, and how these are mixed.

Valone and Brown (1989) established methods of measuring patch assessment ability using food patches and analyzing the patterns of food consumption. In this study, we used this food-patch approach to determine if naked mole-rats are eusocial foragers. We varied food patch quality and spatial distribution because closely spaced patches allow for exploration, but more-separated patches force individuals to choose to explore to find better patches, to "make do" with the first patch encountered, or to share information with one another.

A forager, or group of foragers, will stop using a given patch when the gains no longer outweigh the costs. These costs include the metabolic costs of finding and handling the food items, the risk of predation posed by the patch location, and missing opportunities from not harvesting higher quality patches or engaging in other worthwhile endeavors. The quantity of food remaining at the point a forager leaves a patch is known as the "giving-up density" (GUD), and this measure is used in studies in which patches have similar starting quantities of food. One can also compare the quantity or proportion of food eaten rather than what is left. Which measure is used depends on the questions asked or hypotheses posed (Brown 1988).

Foraging experiments often use three spatial scales (Morgan et al. 1997): patch, station, and site. Patches are individual foraging containers such as shallow trays in which a small amount of food is mixed into a non-edible substrate such as sand. These patches are clustered close together within a station. A site may contain several stations. Patch qualities can vary among patches, stations, sites, or any combination of the three. For experimental purposes, quality is held constant at two scales and varied at the remaining one.

When patches are close together, a forager can easily move between them, and thus can obtain all of the information needed to forage efficiently. If the variation is at a larger distance, such as at the station and site scales, movement may not be as easy or even possible.

When patches within a station have varying initial food quantities, the forager is able to move among them freely, gaining information with negligible effort. It should consume food until each patch has roughly the same quantity remaining--that is, to the same final patch quality. This translates into a proportion harvested that increases with patch quality. To leave

10 items in a patch, a forager must consume only 10 items from a patch that started with 20 (50%), but 90 items from a patch that started with 100 (90%).

The quality of the patches in this study vary solely on the amount of food present, so how much the animals eat is the only reliable measure of their foraging approach. To keep the scale consistent between patches with varying initial food quantities, we use the proportion of food eaten—the proportion harvested—as our metric.

We shall refer to our experimental set-up in which patch quality varies within a station as the "mixed" spatial scale. All stations contain the same mix of patches.

If the patch types are spread far enough apart, complete exploration is difficult or impossible due to time spent or danger incurred, and foraging decisions are more difficult. What decisions are made will depend in part on communication between individuals within a social foraging group—or lack thereof. In this scenario (which we call "clustered"), patches within a station are equal to one another in quality, but stations differ in their patch quality.

There are three general strategies foragers may use when food patches are distributed in this clustered manner (Figure 1; see Valone and Brown 1989, Troxell-Smith et al. 2016):

1. Fixed quitting harvest rate (hereafter fixed harvest rate). In this strategy, foragers will use a patch until it is no better than the average patch within the reachable foraging area. This is the same strategy as when patches are mixed, and is most likely the result of individuals sharing information, intentionally or otherwise. Accordingly, the proportion harvested will increase with patch quality.

2. Fixed time. When foragers have no information about the available patches other than their existence, the optimal strategy is to spend an equal amount of time

searching for food in each patch. Assuming the food items are not too difficult to find and consume, foragers will harvest approximately the same proportion of food from each patch type.

3. Fixed amount. If a forager has no information about other patches, faces significant danger or other costs in getting to other patches, or simply needs very little food, the patch encountered first will suffice. The forager will eat as needed without exploring the area or seeking further information. When a group of foragers use this strategy, they will harvest the same quantity of food from each patch type. Consequently, the proportions harvested will decrease with increased patch quality.

Figure 1 Relative proportions harvested by foragers using (A) fixed harvest rate, (B) fixed time, and (C) fixed amount foraging strategies. (A) shows an increase in proportion harvested with patch quality. (B) shows a constant proportion harvested regardless of patch quality. (C) shows a decrease in proportion harvested with an increase in patch quality. The relative values, rather than the actual numbers, are important. L: low, M: medium, H: high.

4. Study design

We based our study on the design of Morgan et al. (1997). In that study, three spatial scales were used to test the foraging strategy of fox squirrels when presented with various patch qualities: different quality patches within a station, with all stations having the same mix; similar patches within a station but each station different from one another; and similar station variations at different sites. Their test subjects, fox squirrels (*Sciurus niger*), could move within stations at no penalty, among stations with some risk and time cost, and among sites only at great risk and time cost. The squirrels showed no signs of intentionally communicating with one another about patch quality (though they may have observed and gleaned information from

others' activities); that is, while they may have been foraging at the same time, they were foraging as individuals.

Using this design as a basis, we tested the foraging strategy of two colonies of naked mole-rats and one group of gerbils. Gerbil foraging behavior has been studied extensively, so they served as a control of sorts. Several gerbils may forage at the same time, but they do so independently (Kotler et al. 1991).

We varied patch quality (i.e., number of initial food items) at the patch and station scales. Variation between patches within a station we call "mixed," as the patches within a station are a mix of different qualities. In other trials, all of the patches within a station had the same initial quality but this quality varied by station. We call this "clustered." We did not test multiple sites.

5. Predictions

All animals should show a fixed harvest rate strategy on the "mixed" spatial scale. This is because the patches are close enough to one another that every individual can sample and explore all three patches within a station. Each animal should allocate time among patches so as to equalize the end-of-foraging quality at all patches of a station. This translates into an increase in proportion harvested with an increase in patch quality.

For the "clustered" scale, we expected the gerbils and naked mole-rats to exhibit different strategies. Gerbils, as solitary foragers, were predicted to show a fixed time strategy, which would be reflected as similar proportions harvested in each patch regardless of initial quality. This is because the gerbils do not actively share information, and the cost of sampling

all patches at all stations may not be worth the effort to an individual gerbil. Why try to sample

patches that other gerbils are exploiting or have already exploited? Naked mole-rats were

expected to continue using a fixed harvest rate strategy, communicating with one another and

thus maximizing overall foraging efficiency. Alternately, the naked mole-rats could employ a

fixed time strategy, where each forager picked a patch and foraged it for a set period of time.

These strategies translate into proportions harvested which increase with patch quality or

remain the same regardless of patch quality, respectively.

B. Methods

We tested two colonies of naked mole-rats (n = 36, n = 27) and one family group

(parents and three litters of their offspring) of Mongolian gerbils (*Meriones unguiculatus*) (n =

20). The mole-rats were tested in their normal housing condition of dim red light, 30°C

temperature, and 45–65% relative humidity. The gerbils were housed and tested in a room kept

under a 12-hour light, 12-hour dark cycle, 22°C, and ambient relative humidity. Each colony was

housed in an artificial tunnel system constructed of two-inch diameter PVC piping and standard

laboratory mouse cages. The experimental protocol was approved by the University of Illinois at

Chicago Institutional Animal Care and Use Committee. All animals were given free access to

their normal laboratory diets in the home tunnel system. For naked mole-rats this was sweet

potato, and for gerbil's rat chow and water.

During foraging experiments, the home tunnel system was connected to an open

foraging arena via a PVC pipe. This arena consisted of a central compartment with three

foraging stations connected via short lengths of PVC pipe. Each station, measuring

approximately 91 cm × 51 cm × 24 cm (l × w × d) and was further divided into three patches.

Figure 2 provides a schematic of the foraging arena; Figure 3 is a photograph of one of the

authors (JSB) setting up the actual arena. We initially tested our foraging arena with a cover

over it. In these tests, all patches were foraged to zero; that is, the naked mole-rats simply ate

everything everywhere. When left uncovered, the naked mole-rats foraged but considerably

less, likely due to a heightened sense of predation risk. Experiments were performed with the

arena uncovered.

Figure 2   Schematic of the arena. (A) Mixed (B) Clustered. L: low-quality patch; M: medium-quality patch; H: high-quality patch. Drawing is not to scale.
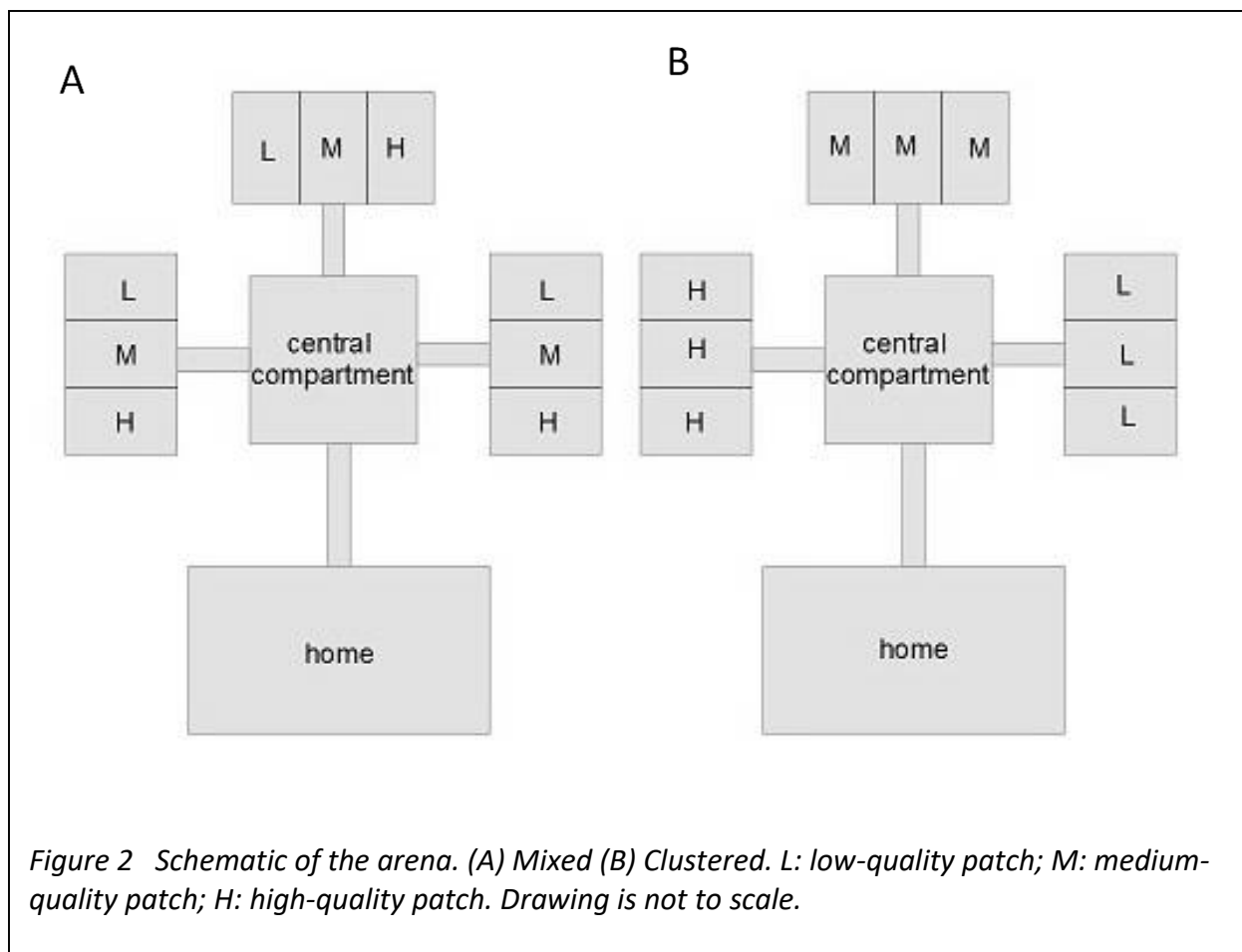
Figure 3 Author JSB setting up the test arena.

Abu Baker and Brown (2010) showed that stations just 1 m apart can be perceived by small rodents (four-striped grass mouse, *Rhabdomys pumilio*) as significantly different. Our animals are of a similar size to theirs and thus the spatial scale used here should be adequate to see spatial scale effects.

We used fresh apples cut into very small pieces (approximately 0.1–0.2 g each) to test naked mole-rat patch use behaviors. The naked mole rats prefer apples to their normal diet of sweet potato (pers. obs.). We used millet seeds (approximately 0.006 g each) for the gerbils. As gerbils are granivores, this food is sufficiently favored to ensure foraging within our food patches.

We conducted a week of trials to allow both species to habituate to the trays and allow us to establish the design of the patches and the quantity of substrate needed to achieve intermediate GUDs. Naked mole-rats consumed the entire allotment of apple pieces when they were offered in a single pile. All colonies (both gerbils and naked mole-rats) would eat all food items if the foraging arenas were covered, indicating that when experimental foraging ended it was not due to satiation. When the arena was uncovered, there was no difference between the number of food items eaten whether the animals were given 24 or 48 hours to forage, indicating that our choice of a 24-hour test period was adequate.

Prior to the experimental foraging rounds, we placed low, medium, or high quantities of food in each of the nine food patches, varying placement between rounds in a Latin square design while keeping average patch quality equal. We defined low as 20 food items, medium as 40 food items, and high as 80 food items (pieces of apple for the naked mole-rats, individual millet seeds for the gerbils). We covered the food items with 4 L of coarse bank sand.

In the "mixed," design, each of the three patches within each site contained a different initial quantity of food items (20, 40, or 80). In the "clustered" scenario, each of the three patches within a site contained the same initial food item quantity, with this number varying between sites.

The animals were then given access to the foraging arena and allowed to forage for 24 hours. At the end of this time, the foraging arena was closed off and all animals restricted to their home tunnel system. We counted the remaining food items in the experimental patches and calculated the proportion harvested. Each colony was tested under each treatment (mixed or clustered) for six trials.

We used SYSTAT 12 to test for effects of initial food quantity, spatial scale, and colony (for naked mole-rats) via ANOVA, using proportions harvested as the dependent variable. Effects were considered significant at $p < 0.05$. Naked mole-rat colonies were compared to each other with chi-square goodness-of-fit tests. Graphs of proportions harvested were compared (to one another and the theoretical graphs given above) visually and, in the case of naked mole-rats, compared to an equal-harvest strategy with chi-square tests.

C. Results

All colonies—both mole-rat and gerbil--performed as expected in the mixed-patch trials. The proportion of food harvested increased with patch quality, supporting a tendency toward a fixed quitting harvest rate strategy. The clustered patches, however, yielded some surprises. At the clustered scale, the gerbils continued to show a fixed quitting harvest rate rather than the expected fixed time strategy (Fig. 4). The two naked mole-rat colonies differed from one another in their proportions harvested at this scale, particularly among different initial food amounts. The colonies had different numbers of individuals (36 vs 27), and thus this is not surprising. However, these differences were not significant ($p = 0.638$), so we also considered the naked mole-rats as a single unit for analysis. Both colonies of naked mole-rats, whether

colonies were analyzed separately or pooled, showed a general decrease in proportion

harvested with an increase in number of initial food items—the opposite of our prediction (Figs.

5, 6, and 7).

Figure 4   Proportions of food harvested by gerbils in (Left) Mixed patches and (Right) Clustered patches. In both scenarios, gerbils tend to harvest a higher proportion of food from higher-quality patches, though harvest rates are always high. Bars indicate means ± S.D. n = 18 for each.
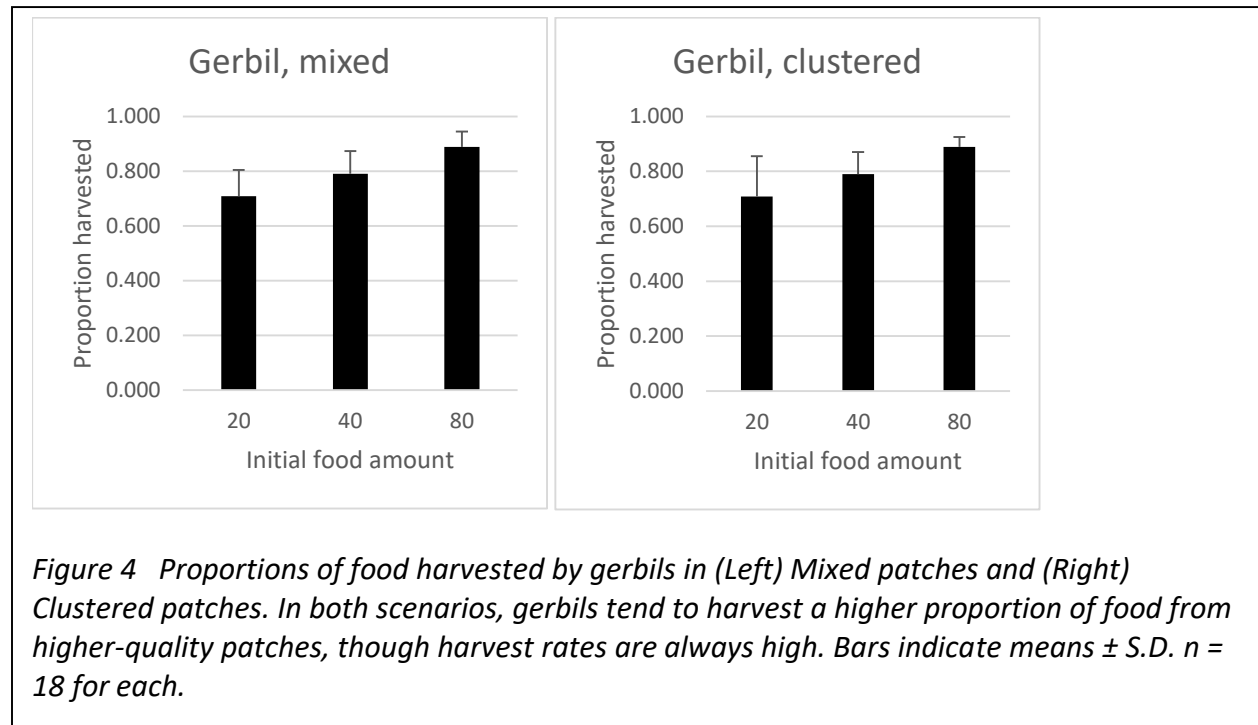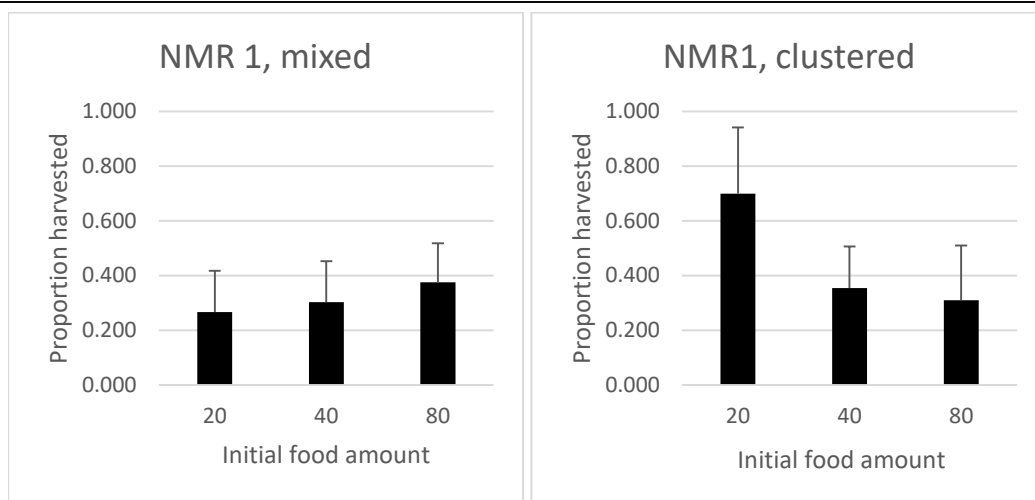
Figure 5   Proportions of food harvested by naked mole-rat colony 1 in (Left) Mixed patches and (Right) Clustered patches. Proportion harvested rose with patch quality at the Mixed scale, but declined with higher quality at the Clustered scale. Bars indicate means ± S.D. n = 18 for each.
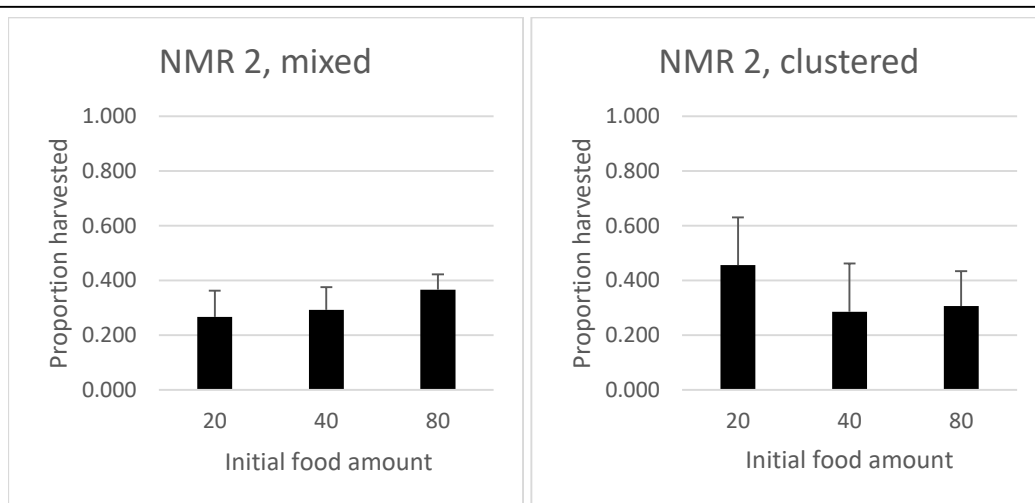
Figure 6   Proportions of food harvested by naked mole-rat colony 2 in (Left) Mixed patches and (Right) Clustered patches. Proportion harvested rose with patch quality at the Mixed scale, but declined with higher quality at the Clustered scale. Bars indicate means ± S.D. n = 18 for each.
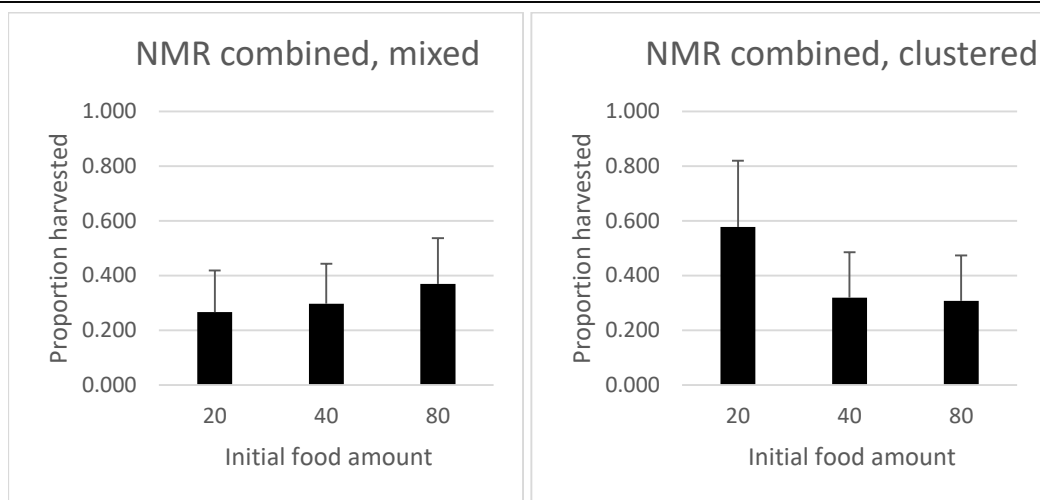
Figure 7 Proportions of food harvested by naked mole-rats in (Left) Mixed patches and (Right) Clustered patches. Proportion harvested rose with patch quality at the Mixed scale, but declined with higher quality at the Clustered scale. Proportions shown are the average of the two colonies ± S.D. n = 36 for each.

ANOVAs confirmed these conclusions (Table I): for gerbils, only the initial amount of food was significant, whereas the initial amount, scale, and the interaction of initial amount and scale were all significant factors for the naked mole-rats. Naked mole-rat colonies differed in their foraging. Colony 1 harvested a significantly higher proportion of food offered, but this difference was most striking in the interaction of initial amount and colony, where the colony harvested a much higher proportion of food from the low quality patch than did colony 2. The three-way interaction of initial amount, scale, and colony was not significant even though the interaction of initial amount and scale was highly significant.

Table I
ANOVA RESULTS FOR (A) GERBILS AND (B) NAKED MOLE-RATS[a]

a) Gerbils

Source	Type III SS	df	Mean Squares	F-ratio	p-value
Initial amount	0.520	2	0.260	32.042	**0.000**
Scale	0.011	1	0.011	1.349	0.248
Initial × Scale	0.002	2	0.001	0.129	0.879
Error	0.828	102	0.008		

(b) Naked Mole-rats

Source	Type III SS	df	Mean Squares	F-ratio	p-value
Initial amount	0.500	2	0.250	6.607	**0.000**
Scale	0.441	1	0.441	15.192	**0.000**
Colony	0.172	1	0.172	5.907	0.016
Initial × Scale	1.379	2	0.690	23.747	**0.000**
Initial × Colony	0.127	2	0.064	2.192	0.114
Scale × Colony	0.132	1	0.132	4.541	0.034
Initial × Scale × Colony	0.152	2	0.076	2.625	0.075
Error	5.925	204	0.029		

[a] Bolded values ($p < 0.01$) indicate factors that significantly affected proportion harvested

Both mole-rat colonies harvested similar amounts from the low- and medium- quality patches and significantly more in the high-quality patch, indicating that this was not a fixed-amount strategy despite the gross appearance of the graphs of proportions harvested (ANOVA: initial amount effect $p < 0.01$ for each colony). The large drop in proportion harvested from the low-quality patch to the medium-, then the leveling off in the high-quality patch, indicates a

strategy somewhere between fixed-amount and fixed-time. When increasing the spatial scale of the differences in patch quality, the tendency of the naked mole-rats to favor the rich patches broke down. Their inefficiency at the clustered scale is most pronounced in the low-quality patches.

Both naked mole-rat colonies foraged more from the low-quality patch and slightly less from the high-quality patches in the clustered scheme than in the mixed. Of the low-quality patches, colony 1 harvested 27% of the food items in the mixed configuration and 70% in the low-quality patches in the clustered configurations; colony 2 harvested 27% and 46% of the food, respectively, from these low quality patches. In the mixed scheme, Colony 1 harvested 38% of food from the high quality patches and only 31% in the clustered; colony 2 harvested 37% and 31% respectively.

D. Discussion

The gerbils showed a continued fixed harvest rate pattern when the foraging spatial scale was increased, implying that they must have information about patches other than the one first encountered. Gerbils are not known to be social foragers, but they were seen moving rapidly about the foraging arena. We conclude that the foraging arena was small enough, that they were able to easily explore the entire arena and concentrate their foraging efforts accordingly. A larger foraging arena, with more distance between sites, may be prohibitively difficult to explore and thus result in different patterns.

The naked mole-rats, which we expected to show a fixed quitting harvest rate response as eusocial foragers, in fact showed the opposite. Instead of increasing proportion harvested

with increasing patch quality, they showed a drop in proportion harvested as patch quality improved. Although the two colonies did not harvest the same proportions, the pattern was the same in both, and indicates a foraging strategy similar to a fixed amount approach when patch qualities were clustered. Individual naked mole-rats were clearly not gaining information about all patches, but were instead harvesting their food from the first patch encountered. They were neither exploring on their own nor sharing information.

The fact that naked mole-rats actually foraged from the high-quality patches less when the patch types were clustered together than when they were mixed with patches of other initial qualities implies that the naked mole-rats were actively avoiding the better patch. This implication is bolstered by the large drop in proportion harvested between the low-quality patches and the better patches. This could be due to competition among individual naked mole-rats and their not wanting to share information, to the point of refusing to gain any knowledge themselves lest they inadvertently signal their competitors. It is also possible that the fact that our naked mole-rats were not dependent on our experimental patches may have influenced their foraging strategy. If the only food source was our patches, the naked mole-rats may have shown a different foraging pattern than in our scenario, where the patches provided only supplemental treats.

As naked mole-rats are fossorial, the open arena top may have represented possible danger. The colony queen was never seen to investigate the foraging arena (except in the trials with the arena fully covered). Rather, the workers brought food to her. Other rodents are known to forage more in areas of cover than out in the open due to predation risk (e.g., Schmidt and Brown 1996, Kotler et al. 2002), and in a strictly fossorial species such as naked

mole-rats this risk may be exaggerated, as they are unfamiliar with aerial predators. When exploration of other patches presents danger, real or perceived, foragers are more likely to make do with what they find in the first patch they encounter.

Why might a reproductively eusocial species forage in such a manner? Eusocial foragers, such as ants and bees, may be willing to not only give up individual foraging opportunities for the overall benefit of the colony, but also to take on additional risk in seeking out the best foraging sites rather than settling for the first adequate site encountered. They behave as if the colony, not the individual, is the unit of selection.

However, there is some evidence that naked mole-rat workers, particularly those least related to the queen, will become lazy when able, increasing work output only when physically shoved by the queen. This effect is seen when a colony is fairly satiated (Reeve 1992; but see Jacobs and Jarvis 1996), as ours were.

Thus it seems that some of those workers tasked with gathering food will do as little as possible as long as they fill their quota. Because even our low-quality patches contained more than sufficient food items, and the colony as a whole had adequate food in their normal living quarters, there may have been little incentive to look for other patches. Combined with the potential risk of exploring open areas, this may explain why the naked mole-rats simply foraged in whatever patch they first encountered.

The results did not support a eusocial foraging strategy for the naked mole-rats, suggesting that they either cannot assess the comparative richness of food sites, or that they do not share information on the location of rich sites. It is possible that individuals fortunate enough to encounter high-quality patches keep this information to themselves, a possibility

consistent with observations of laziness. Foragers that do not share information do not need to compete with others to gather their quota of food. Those in lower-quality patches similarly do not want to invite competition and thus increase the effort required to meet the quota.

What does this mean for naked mole-rat society? It certainly shows that while they are generally considered reproductively eusocial, other aspects of eusociality do not apply. They in fact show what one may call an anti-social foraging strategy, failing to assist one another even if assistance would have little cost to the individual and great benefit to the group.

What of the apparent information-sharing vocalizations noted by Judd and Sherman (1996)? There are two possible explanations. One, the vocalizations are not intended as information-sharing but are for another, currently unknown, reason; and two, the cost of sometimes sharing information may be offset by the opportunity to potentially become reproductive in the future (Stiefel 2014). This is akin to game theoretical explanations of cooperation in general, where occasional acts of apparent self-sacrifice are found to be ultimately selfish (Brown and Vincent 2008, Doebeli and Hauert 2005, Gardner and Foster 2008, Nowak 2006).

When the breeding males and queen are removed, naturally or artificially, from a naked mole-rat colony, vicious fighting ensues in the competition to replace them (Clarke and Faulkes 1997, 2001; van der Westhuizen et al. 2013). This supports the idea that the non-breeding colony members are simply waiting until the breeding position opens up. They are essentially playing a waiting-then-warring game not unlike the potential rulers in the HBO series *Game of Thrones*. Naked mole-rats' long lives, upwards of 30 years (Grimes et al. 2012), and lack of senescence additionally support this hypothesis. Rather than fighting regularly, with all of the

associated risks, they wait until the dominant individuals die (or are removed by researchers), then fight with equals. This is consistent with Stiefel's theory of individuals cooperating—or at least pretending to—while waiting for the opportunity to take control of the "throne."

The idea that naked mole-rats' eusocial reproductive strategy may contribute to their longevity was explored by Williams and Shattuck (2015) in a review of lifespans of 440 ground-dwelling mammal species. Two factors seem to lead to longer lifespans in mammals: fossoriality and sociality. Naked mole-rats have both in spades, being both completely subterranean and reproductively eusocial. We do not know if these factors apply to animals other than ground-dwelling mammals. Workers and non-reproductives of completely eusocial species of bees and ants have very short lifespans, and they do not have time to wait for the queen to die so they can possibly take over. They also have considerably larger colonies. Individuals are expendable, and act as such. These colonies effectively act as a single organism, whereas naked mole-rats are more of a forced community.

While waiting for the opportunity to fight to become reproductive the colony works together, but perhaps only as much as they have to in order to avoid being shoved by the queen or a breeding male, or to gain trust ahead of the fight. Rather than the peaceful community that comes to mind when thinking of eusocial animals, naked mole-rats apparently merely tolerate one another, and then only as long as they have to. The dominance of the queen and breeding males, including physical violence against subordinates, indicates a despotic society. Each naked mole-rat individual forages and behaves as though it, and not the colony, was the unit of selection despite its non-reproductive status.

E. Conclusion

Whether naked mole-rats qualify as eusocial or not depends on your definition of eusocial. If we define eusociality in mammals as requiring only cooperation in reproductive matters (as in Burda et al 2000), then naked mole-rats are certainly eusocial. However, if we require a group effort in other aspects of their ecology, like foraging for food, then naked mole-rats are not. They fail the test of eusocial foraging.

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III. DEMOGRAPHY AND DYNAMICS OF AARDVARK-DUG BURROWS

A. Introduction

Animal burrows provide myriad benefits to those who occupy them even temporarily.

Burrows provide fairly stable temperature and humidity, protection from the elements, a place

to store food and raise young, and temporary refuge from pursuing predators (Kinlaw 1999,

Bulova 2002, Šumbera et al. 2004, Anderson and Richardson 2005, Read et al. 2008, Davidson

et al. 2012). Burrow benefits extend beyond the tunnel itself. The excavated soil can end up in a

pile, in some cases a rather large mound. A mound of excavated soil can be used as a lookout

(the "pitcher's mound" effect), a sunny basking site, or a source of previously buried seeds, now

available for foraging (Melton 1972). The soil itself is loosened and aerated, allowing seeds,

insects, and nutrients to be more available to animals and plants alike. This newly exposed soil

can allow for increases in plant diversity (Whitford and Kay 1999, Davidson et al. 2012, Fleming

et al. 2014).

Gopher tortoises, well-studied prolific burrowers, re-use about 78% of their burrows

from a previous year (Aresco and Guyer 1999). Female tortoises use an average of five burrows

per year, while males use twice as many (Eubanks et al. 2003). Among the mammals, the most

comprehensive studies of burrows have been of those of carnivores. Eberhardt et al. (1983)

found that Arctic kit foxes have favored and less-popular dens and that families will use

multiple dens, and multiple families use the same den, within a year. Arctic kit fox dens may last

upwards of 300 years, though age is difficult to discern from appearance. San Joaquin kit foxes

use even more dens, at an average of near 12 per year; individuals tend to use dens they had

previously used about half the time (Koopman et al. 1998). Northern red foxes have two types

of dens: natal (long-term) and temporary. Natal dens are well-maintained, some being used

throughout a 15-year study and probably longer (Nakazono and Ono 1987). Spotted hyena dens

may last for many years, whether large, multi-chambered dens or a closely clumped group of

smaller, simpler tunnels. These hyena dens are often burrows abandoned by other animals,

including the master digger the aardvark (Poiknes and Peterhans 2007).

Species other than the original digger may make use of the burrow, either at the same

time as the digger or after the digger has abandoned it (for example, Bright and Hogue 1972,

Campbell III and Clark 1981, Butts and Lewis 1982, Heidger 1988, Cocroft and Hambler 1989,

Hansell 1993, Kent et al. 1997, Alexy et al. 2003, Lomolino and Smith 2004, Anker et al. 2005,

Bangert and Slobodchikoff 2006, Gálvez Bravo et al. 2009, Martin 2011, Diedrich 2013). These

commensal species include insects, other invertebrates, and vertebrates large and small.

Burrow diggers too may be large or small, vertebrate or invertebrate. Among the mammals,

most burrow diggers are colonial or live in small groups (Davidson et al. 2012). Solitary

burrowers, and their burrows, are far less understood.

The aardvark (*Orycteropus afer*) is a large, solitary, burrowing mammal in Southern

Africa. In aardvark territory, one cannot help but notice the omnipresence of holes in the

ground. These holes often lead to tunnels 1 m or more in length, which for the purposes of this

study we call "burrows." The sheer size of the burrows and the appearance of the claw marks

show these to be dug by aardvarks. It has long been thought that the majority of burrows

occupied by warthogs (Bradley 1971) and many brown hyena lairs (Skinner 1976) were actually

dug by aardvarks, and our observations are consistent with these reports. Little is known

regarding the density of aardvark burrows, their primary utility to the aardvark, or how long aardvark-dug burrows remain intact.

A single aardvark may dig in up to 200 places in a single night, resulting in anything from shallow surface scratches to burrows 2 m deep (Taylor et al. 2002). Less frequent are larger excavations used as sleeping burrows. Aardvarks move between burrows frequently, and will re-use existing burrows within their home ranges (Taylor et al. 2002). Sleeping dens may exceed 12 m in tunnel length (Whittington-Jones et al. 2011). Reports of aardvark behavior are scarce and largely anecdotal, so it is unknown if aardvarks dig or maintain burrows for other reasons, such as as escape holes used to hide from predators. How long aardvarks maintain their burrows (including re-excavating collapses) is also unknown. Maintenance, renovation, and intentional destruction of burrows may also be performed by other species. While aardvarks can only use the largest of their burrows as home dens, their larger feeding digs may provide some benefit to other animals, especially those that are considerably smaller. Studies have shown that dozens of species of animals use aardvark-dug burrows for their own purposes (Smithers 1971, Whittington-Jones et al. 2011, Chapter 4 of this document).

We wanted to learn more about the burrows that aardvarks dig. Reports of burrowing vertebrates and their commensals are numerous, but the burrows themselves are often mentioned only as an afterthought. Studies on burrows proper, especially those dug by mammals, are relatively rare. They include burrows of common wombats (Borchard et al. 2009), woodchucks (Merriam 1971), and Great gerbils (Wilschut et al. 2013). The size and shape of burrows is studied relatively frequently, but methods tend to be destructive (e.g., Dentzien-Dias and Figueiredo 2015, Šumbera et al 2012). Non-destructive methods have been used

(Martin 2011) but are not yet common, likely due to financial limitations. Changes in burrows over time have gained some attention, particularly in recent years (Thomas et al. 2012, 2013).

What of the "demographics" and dynamics of the large and numerous burrows dug by aardvarks? We surveyed aardvark-dug burrows in three distinct habitats within and near Mapungubwe National Park, South Africa to learn more about these burrows. Specifically, we asked: How does the density of burrows vary across habitats?; How long do burrows remain usable?; How often do new burrows appear?; and is there evidence of active upkeep, whether by aardvarks or other animals?

B. Methods

1. Location

The bulk of this work was done at Mapungubwe National Park (MNP) in South Africa during the months of May-August of 2008, 2009, and 2010, which constitute the dry winter season. The 20,000 ha park, founded in 2004, lies along the Limpopo River at the northernmost point of South Africa, bordering Botswana (on the western side of the park), and Zimbabwe (on the eastern) (Fig. 8). The park is discontinuous, with several working farms within its boundaries, including farms that grow citrus and tomatoes. Sections of the northern border of the park are unfenced or have only a simple electrified fence (erected in 2009) to reduce elephant access without affecting other animals. The park is part of the Mapungubwe Transfrontier Conservation Area, which includes both public and private lands in South Africa, Botswana, and Zimbabwe. Animals are free to move among the countries, provided that the Limpopo and Shashe Rivers that form the borders are low, as they often are in winter.

Figure 8   Official Map of Mapungubwe National Park, 2005. Park borders were unchanged as of this study.
http://www.sanparks.org/images/parks/mapungubwe/maps/map2.png
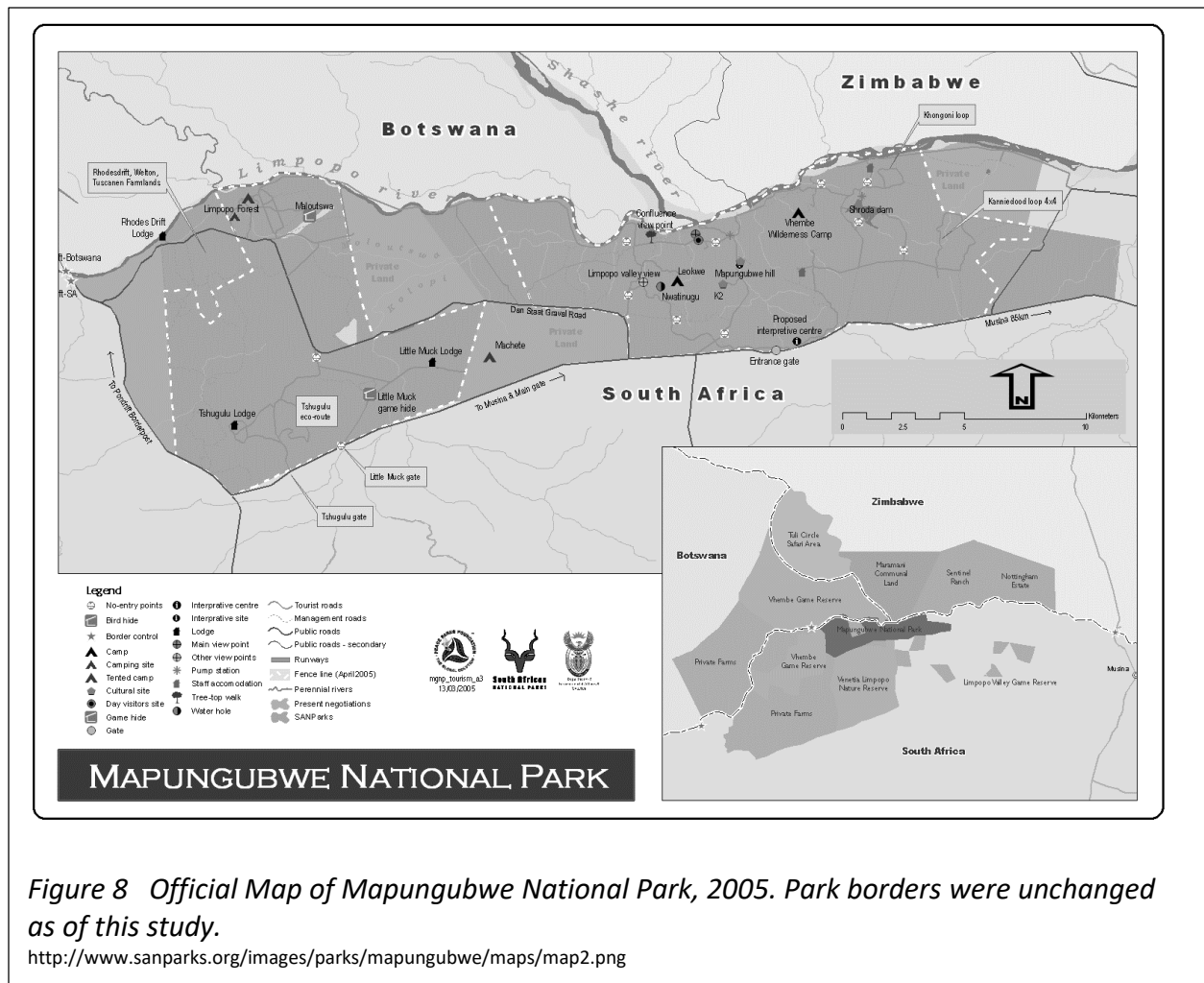
Humans have inhabited this area for millennia, and as a result none of the land is pristine. Remnants of human habitation are scattered throughout the park. The park's namesake, Mapungubwe, refers to an 11th century kingdom centered in the land that is now the park. The land has been used for agriculture, livestock, and building ever since. Parts of MNP were agricultural land until just before the park opened in 2004. Parts of MNP that were farms are still largely open fields, sometimes with remnants of furrows and irrigation circles

visible on satellite images. One section of these fields was subject to an attempt at restoring the natural riverine forest, but at the time of this study the restoration had yet to take effect.

Near the fields are patches of the endangered riverine forest habitat. Here too are signs of human habitation, such as pieces of irrigation pipes and remnants of buildings. The forest has largely recovered. The dominant trees are *Combretum imberbe* (leadwood), *Lonchocarpus capassa* (apple leaf tree or rain tree), and *Vachellia tortilis* (umbrella thorn acacia), reaching a crown height of > 7 m with 50% crown cover (Goetze et al. 2003). As of 2008, elephant presence was notable, and there was considerable damage to the woody vegetation. During our 2009 field season, SANParks erected a one-level electric fence in an effort to keep elephants (and only elephants) out of this habitat. The effort was fairly successful, greatly reducing elephant presence in the forest, stopping further destruction, and allowing plant regrowth.

In addition to the field and riverine forest habitats, there are also areas of dense mopane forests. Here, mopane trees (*Colophospermum mopane*) are a near monoculture. The mopane woodlands were largely ignored by humans except for travel between other areas. The soil in these mopane forests is often sandy and unsuitable for farming. Adjacent to and often within the grasslands and mopane forests are rock outcroppings (kopjes) some of which form extensive and contiguous tracks of rocky habitat (Fig. 9).

Figure 9 Habitat types at Mapungubwe National Park, South Africa. (A) Former agricultural field with a kopje in the background; (B) Riverine forest; (C) Mopane forest

MNP offers suitable habitats for a diverse and growing animal population including elephants, a wide variety of carnivores, and numerous antelopes. There is also a healthy aardvark population, as evidenced by the large number of burrows throughout the non-rocky areas of the park. A 2006 aerial census counted 114 elephants, 903 impala, 340 blue wildebeest, 271 eland, 228 Burchell's zebra, 88 greater kudu, 84 waterbuck, 48 giraffes, 20 red hartebeest, 125 gemsbok, 8 tsessebe, 4 white rhinos, 2 sables, and 3 donkeys. The census also

listed known but uncounted leopards, spotted hyenas, brown hyenas, black-backed jackals, African wild cats, lions, bushbucks, klipspringers, common duikers, steenbok, bushpigs, warthogs, baboons, vervet monkeys, mongooses, and unspecified rodents (Roerig 2006). Species not mentioned above include many more mammals, at least 15 species of snakes, and over 400 species of birds. In 2010, 165 elephants were counted within the park (Selier and Page 2010).

In 2009, we also surveyed the DeBeers-owned Venetia-Limpopo Nature Reserve (VLNR), which is just south of MNP, for aardvark-dug burrows. Plots at VLNR included open fields, mopane sandveld, and plots crossing both habitats. VLNR does not have riverine forest. These plots proved to contain few aardvark burrows or signs of aardvark activity. For this reason, they were not revisited.

2. Survey Plots

We chose plots haphazardly in each of the three habitats of open fields, riverine forest, and mopane forest. All aardvark-dug burrows within these plots were found and measured, and several randomly chosen burrows monitored with camera traps. The criteria for plot creation included that the entire plot would be within one habitat type, the plot would not cross a road, and the plot would not overlap others. We usually chose a corner point, then ran the plot east and south from that point. Plots varied in size (0.02–21.74 ha, average 2.39 ha) and shape (always quadrilaterals) depending on the continuity of the habitat type and ease of surveying.

In 2008 we surveyed 19 (total of 56 ha), 3 (9 ha) and 3 (9 ha) plots within the open field, riverine and mopane habitats, respectively, at MNP. In 2009 we resurveyed 13 of the plots in

the open field, and added 12 more (total 49 ha). We did not resurvey the 2008 riverine and mopane plots; instead we started 16 new riverine (23 ha) and 10 new mopane (10 ha) plots at MNP, as well as 2 field (29 ha) and 5 mopane (23 ha) plots at VLNR. In the last year, 2010, we resurveyed 15 of the field plots (38 ha), all 16 of the 2009 riverine (23 ha) and 2 of the mopane plots (2 ha) at MNP; we did not return to VLNR.

For the purposes of this study, we called all aardvark-dug tunnels greater than 1 m in length burrows. Such burrows, which can be attributed to aardvarks (Bradley 1971), are potential burrows and dens for aardvarks and other animals. They appear in great numbers, far disproportionate to the abundance of the aardvarks themselves. Clearly aardvarks are not maintaining all or even a majority of these burrows. To do so would require considerable time and effort. Aardvarks are constantly digging in new places to get at previously undiscovered ant and termite tests. This, combined with the ease with which the aardvarks could re-excavate a previous feeding burrow, means that they generally leave these burrows to the elements or other animals.

Burrows are often associated with conspicuous "fans" or mounds of excavated soil. The "fan" was defined as the area covered by soil removed from the burrow. In some cases, this was a mound, in others it was spread out nearly flat, thus inspiring the terminology. A few burrows that we believe to have been old had sunken areas just before the entrance, possible the result of a soil fan being compressed or washed away by heavy rains. The size of the fan should be related to the size of the tunnel, at least upon initial excavation. The amount of plant debris and, even more, the amount of plant growth, provides a clue to how recently the burrow has been maintained. When the soil is loose, even small rodents leave footprints, thus giving us

some indication of what type of animals have visited the area, and sometimes even if they went inside. The size of the entrance is another possible clue to the burrow's age. Aardvarks are large animals and therefore dig large burrows. Entrances and tunnels may partially collapse or be deliberately filled in. Smaller entrances should be older than larger ones. We noticed that many entrance holes had grasses growing over them, cobwebs across part of the entry, or both. These may provide clues as to recent activity. An entrance hole covered in grasses and cobwebs does not likely lead to a current burrow. Finally, the approximate length of the tunnel can tell us what kinds of animals may possibly make use of it. Large inhabitants, like aardvarks and warthogs, require large tunnels. Smaller burrows are not suitable for these species to use as sleeping dens, but could still provide temporary shelter.

For each burrow found, we recorded the GPS coordinates and several descriptors of the burrow entrance (Table II). Figure 10 shows examples of typical burrow entrances. We estimated the diameter of the soil fan in front of the entry hole, the diameter of the entry hole, and the minimum tunnel length. All measurements were estimated visually; tunnel length is the minimum based on visual inspection and measurements using fencing wire to probe the length. Descriptions were also categorical. Fan debris and growth referred to loose plant material on the surface and new plant growth on the fan, respectively.
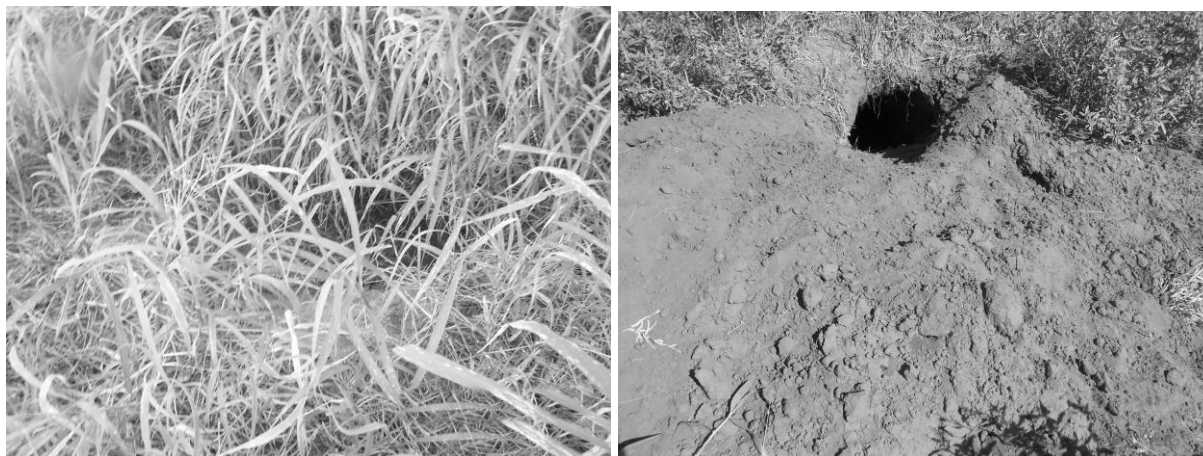
Figure 10   Examples of aardvark burrows at Mapungubwe National Park, South Africa. (Left) burrow entrance obscured by grass, no apparent soil fan; (Right) burrow entrance without any obstructions and a large soil fan.

Table II
BURROW DESCRIPTION CATEGORIES

Fan size	Fan debris	Fan growth	Fan prints	Hole size	Hole grass?	Hole webs?	Tunnel length*
None	none	none	no	Small < 20 cm	no	No	Small <2 m
Small < 1 m	light	light	yes	Med 20–30 cm	few	few	Med 2–5 m
Med 1–2 m	moderate	moderate	compacted	Large > 30 cm	many	many	Large >5 m
Large > 2 m	heavy	heavy			overgrown		
		overgrown					*minimum, may be longer

We used GPS Visualizer (gpsvisualizer.com) with Google Maps (maps.google.com) to create a map of plot and burrow locations, color-coded by the years found. To examine the spatial distribution pattern (random, clumped, or uniform), we used sub-plots of 1.0 +/- 0.05 ha following the method described in Odum (1961). Plots less than 1 ha were not counted, 1 ha plots were counted in their entirety, and larger plots were subdivided into 1-ha portions. We kept the sub-plots as square as possible while fitting as many as possible. Generally, the subplots were roughly the same shape as the larger plot. The method used to divide plots depended on the shape of the plot and number of subplots needed, but was standard across plots. We used Google Earth (Google, Mountain View, CA) with our maps to draw and measure these sub-plots.

Within each plot of each habitat, we counted the number of burrows in the first year that the plot was surveyed. As per Odum (1961), if the mean and the variance of the number of burrows per unit space are equal, then burrows are randomly distributed; if the mean is greater than the variance, then there is a uniform distribution; and if the mean is less than the variance, then there is a clumped distribution. We expected a clumped distribution, or possibly a seemingly random distribution on this fairly small scale, hypothesizing that the majority of these burrows were dug for feeding purposes (reflecting clumped or random prey distributions) rather than escape holes (which should have a uniform distribution).

3. Plugs

In 2010, to test for the frequency of use by any species, we loosely "plugged" the entryways of 107 burrows (52 riverine, 55 field) with grasses (Fig. 11). We revisited those

burrows one week later to see if the grasses had been moved. We then replaced the grass plug

and rechecked the burrow again a week later. Each of these entries was plugged up to 3 times,

and checked up to 4 times.

Figure 11   An aardvark burrow in the riverine forest at Mapungubwe National Park, South Africa, after our grass "plug" had been pushed down by an animal.

C. Results

We surveyed approximately 170 hectares across our sites, with 409 unique burrows

appearing across the years (Table III). Table IV shows the number of plots, total area per

habitat, and number of burrows within the plots by location, habitat, and year. Because many

plots and burrows were counted in multiple years, the sum of burrow counts in Table 3 is

greater than 409.

TABLE III TOTAL AREA SURVEYED AND NUMBER OF UNIQUE BURROWS, BY HABITAT		
	Total Area (ha)	Number of Unique Burrows
Field	96	214
Mopane	42	30
Riverine	32	165

TABLE IV APPROXIMATE AREA SURVEYED AND NUMBER OF HOLES FOUND, BY YEAR AND LOCATION[a]						
		MNP		VLNR		
		Total area (ha)	Number burrows	Total area (ha)	Number burrows	Average burrows/ha
Field	2008	56	137			2.4
	2009	49	101	29	7	1.4
	2010	38	58			1.5
Mopane	2008	9	19			2.1
	2009	10	2	23	9	0.3
	2010	2	2			1
Riverine	2008	9	41			4.6
	2009	23	106			4.6
	2010	23	77			3

[a] Counts include all holes with at least 1 m tunnel. Holes active for multiple years were counted in each year.

1. Burrow density

Individual plots varied by both area and burrow density; some large plots had zero burrows, and some very small plots had several. Had the density of burrows in the latter plots held across a larger area, we may have had 200 burrows per hectare. Of plots greater than 0.5 ha in area, the highest density was 17.4 burrows/ha (plot H, field). Our spatial distribution analysis of plots 1 ha or larger confirmed that burrows have a clumped distribution in the field. The field had an average burrow density of 2.66 burrows/ha with a variance of 19.79 (chi-square goodness-of-fit $p < 0.01$). In the riverine forest, burrows appeared to be clumped, though this was not statistically significant (density 3.47 burrows/ha, variance 7.71, chi-square goodness-of-fit $p = 0.21$); these densities were not significantly different from one another (chi-square goodness-of-fit, $p = 0.744$). When considering all plots at MNP (including those smaller than 1 ha and areas "left over" and thus not included in the subplot analysis), average field burrow density was 2.17 and riverine burrow density 4.63 burrows/ha; despite the larger difference, it was still not significant ($p = 0.345$). Figure 12 shows two adjoining field plots with very different burrow densities but no other obvious differences.
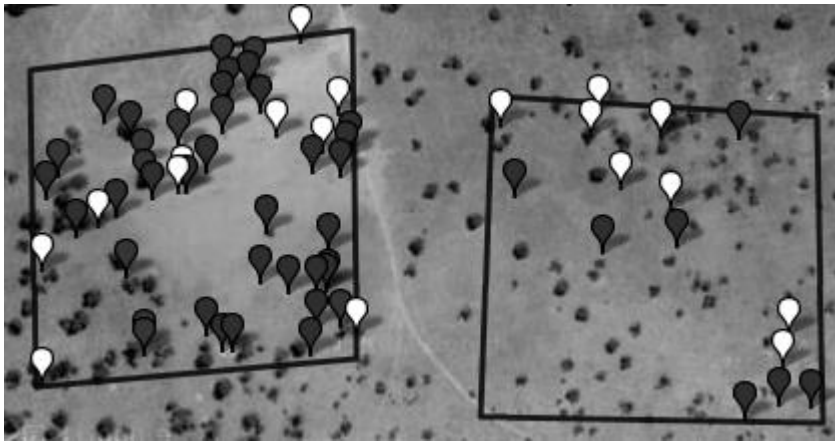
Figure 12   Burrow positions in two adjacent plots in the field at Mapungubwe National Park, South Africa, in 2008. Lines indicate plot boundaries. White markers indicate holes that collapsed by 2009. Burrow density of plot on left = 17.4 burrows/ha; burrow density of plot on right = 4.8 burrows/ha

This is consistent with the assumption that these burrows are mostly, if not entirely, dug in search of food, as the food—ant nests and termite mounds--also tend to be clumped. For example, Meyer et al. (1999) showed that termite mounds (all species combined) in the nearby Kruger National Park have a clumped distribution.

VLNR had very low burrow density in both fields and mopane forests (1.73 burrows/ha and 0.41 burrows/ha, respectively). VLNR has low animal density in general (pers. obs.). While VLNR is a larger reserve than MNP, MNP is open to other reserves and the Limpopo and Shashe Rivers, but VLNR is not, and VLNR has no significant bodies of water and few waterholes for drinking.

Twelve plots, covering approximately 34 hectares of the field at MNP, were surveyed in all three years. Thirty-one new burrows appeared in this area between the 2008 and 2009

surveys, and 30 new burrows appeared between 2009 and 2010, an average of 0.9 burrows per hectare per year. Of the 31 burrows that first appeared between our 2008 and 2009 surveys, 22 (71%) had totally collapsed by our 2010 survey. However, this is a single year, and all of these burrows were in a single habitat (open field), so we do not know if this is typical. There were 1.85 burrows/ha in the field and a similar 1.93 burrows/ha in the riverine that were present one year but not the next (chi-square goodness-of-fit, p = 0.965), indicating that burrow "death" may not be habitat-specific.

Burrows that existed across two or three of our surveys could not be distinguished visually from new burrows, and most had visible footprints indicating recent visitors. Burrow C1, in a former agricultural field, appeared "fresh" all three years, albeit with increasing amounts of vegetation (Fig. 13)

Figure 13   Burrow C1, in a former agricultural field, at Mapungubwe National park in (A) 2008, (B) 2009, and (C) 2010. This burrow saw considerable animal activity in all three years.

We had estimated both fan and tunnel measurements for 64 burrows in the field and 65 in the riverine (Figs 14 and 15). There was no apparent correlation between the two measurements in either habitat (Fig 16). Entry hole size estimates from 178 burrows in the field and 165 in the riverine are shown in Fig 17. The distribution of tunnel length was not different between habitats (chi-square goodness-of-fit; p = 0.0525). Fan sizes tended to be longer and entry holes larger in the field (chi-square goodness-of-fit; p < 0.001 for both).

Figure 14   Distribution of the diameter of the soil fan or mound in front of burrows. small: <1 m; med: 1–2 m; large: >2 m. n = 134 field, n = 129 riverine.
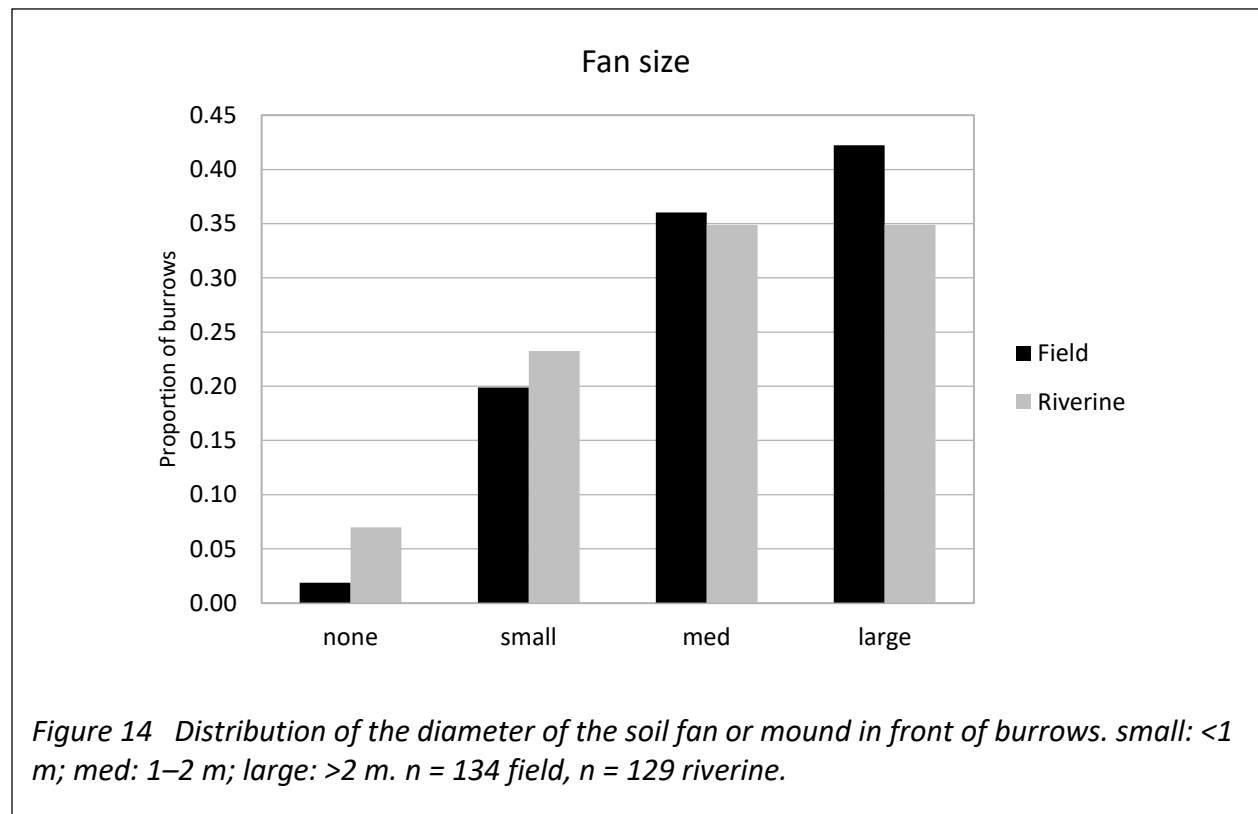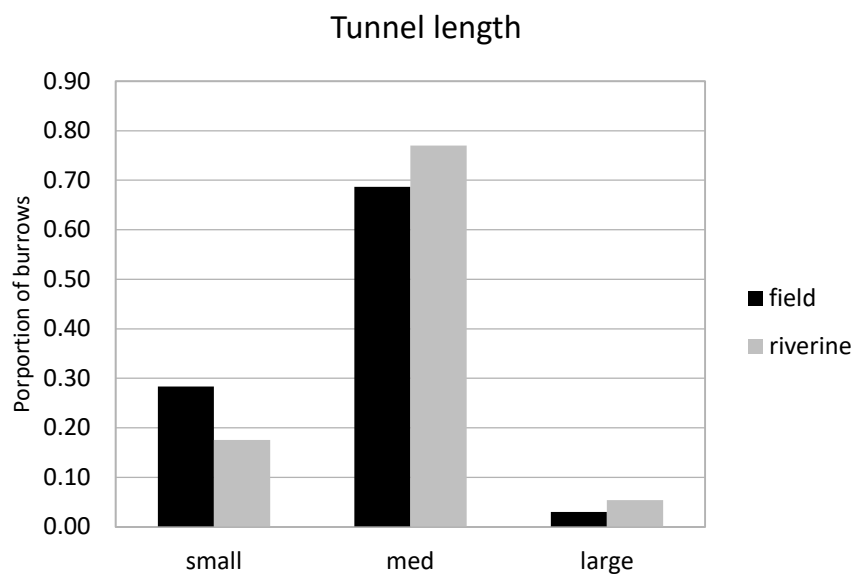
Figure 15 Tunnel lengths. small: < 2 m; med: 2–5 m; large: > 5 m . n = 67 field, n = 74 riverine. Most burrows were less than 5 m (minimum length).
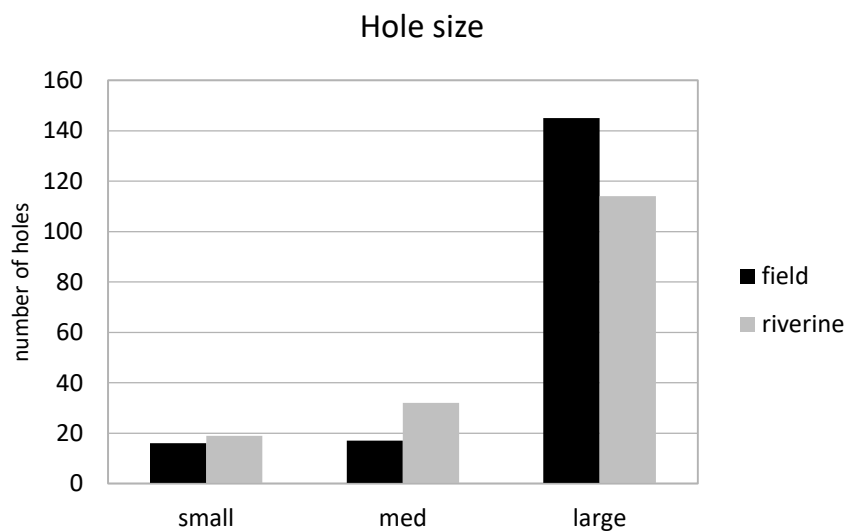
Figure 16   Entry hole size (diameter) based on visual estimate. small: <20 cm; med: 20–30 cm; large: > 30 cm. n = 178 field, n = 165 riverine.
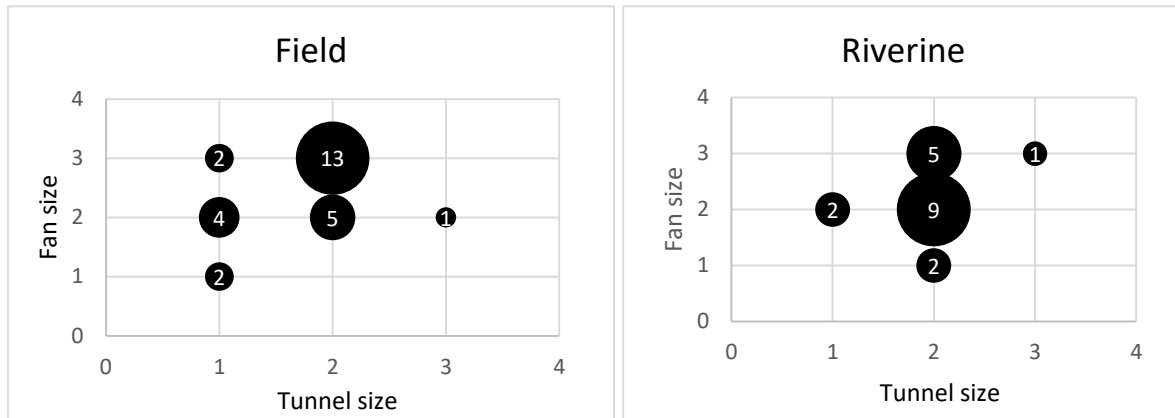
Figure 17   Bubble XY graphs for fan size vs. tunnel size. Values on axes represent estimated size category. 1: small, 2: medium, 3: large. Number within each bubble is the number of burrows fitting that description.

2. Plugs

We plugged a total of 107 different burrows (55 field, 52 riverine) for 2–4 weeks. On average, 39% of the burrows were visited in a given week. Twenty-five percent (27) of the burrows were never used in the weeks checked, while 16% (17) were used every week checked. There was no discernable pattern of use within a given burrow; that is, whether a burrow is used one week does not predict whether it will be used the next. Any given burrow was used 42.2% of the time on average. Burrows used at least once were used an average of 56.5% of the time (Table V).

TABLE V
FREQUENCY OF BURROW USE AS INDICATED BY GRASS PLUGS[a]

Number of burrows	Frequency of use
27	0
20	25%
9	33%
18	50%
10	67%
6	75%
17	100%
Total 107	Avg. 42.2%

[a] Each burrow was monitored for 3 or 4 weeks. Frequency of use is the percentage

D. Discussion

Burrow density varied by habitat and location. At MNP, the riverine forest had the highest density of burrows, followed by the field. The mopane forest had very few burrows, either in our surveyed plots or as seen in informal walks. There are many possible reasons for this. The first is animal activity. Aardvarks dig mostly for food, so their burrow density should reflect that of the aardvarks' food, ants and termites, which are both present in larger numbers in the riverine and field than in the mopane (pers. obs., consistent with Meyer et al. 1999). The second is physical features such as soil type. While we did not asses the soil types for this study, we did observe a range of types; the Limpopo Valley in which MNP is located has soils ranging from sandy loam to clay with high silt content (Götze et al. 2003). The influence of invertebrate burrows on soil properties is well-studied, but the influence of soil type on burrowing,

particularly in larger animals, is largely unknown. Soil type, along with the density of tree roots, can certainly affect the ease or difficulty of digging as well as structural stability. This has been shown in small mammals (Laundre and Reynolds 1993) and southern hairy-nose wombats (Walker et al. 2007). The variation in soil types undoubtedly affects the longevity of aardvark-dug burrows as well, though the short time frame of this study was not enough to discern a pattern in either habitat. Furthermore, soil type certainly affects the distribution of ants and termites, and aardvark feeding digs would thus follow this pattern. Finally, the riverine forest has significantly more water than the open fields, and this water affects both soil type and ant and termite distribution.

Taylor and Skinner (2003) excavated two aardvark burrows that had been used as sleeping dens. One of those burrows had two tunnels, the shorter 4.7 m long and ending in an enlarged chamber, presumably for sleeping. Our method of measuring tunnel length was crude, and only gave us a minimum length of a single tunnel. We had only 6 burrows with a minimum length of 5 m out of the 149 measured; however, they could have been larger, and some of our "medium" length tunnels were probably actually large enough to be sleeping dens.

Burrow attributes such as fan size and tunnel length did not appear to have any correlations, but our methods were too crude to provide conclusive results. For example, we did not test the depth or compaction of the soil fan, attributes that are vital in estimating the volume of soil. For this reason, we make no conclusion about burrow attributes in relationship to one another or their changes over time.

Burrow longevity, like burrow density at any one point in time, may be related to soil type, aardvark density, ant/termite density, and the density of other animals performing

burrow upkeep or destruction. Aardvark-dug burrow longevity appears to be highly variable, though our data do not permit calculation of averages. Of the burrows that appeared in the fields between our 2008 and 2009 surveys, 71% (22 of 31) had collapsed by our 2010 survey. On the other hand, there were 23 burrows in the same field that were dug sometime prior to our 2008 survey and were still viable at our 2010 survey. One of the few burrows found at VLNR was at least 16 years old: an assistant recalled finding an aardvark dead of a snakebite at this location 16 years prior to our visit, and camera-trap monitoring showed an aardvark using this burrow. One burrow at MNP was used by a minimum of two different aardvarks during this study: the first (which died in the burrow entry) in 2008, and at least one in 2009. An aardvark was also photographed at this burrow in 2010, but we do not know if it was the same aardvark as in 2009, as neither had distinctive markings. One burrow in the riverine forest (monitored by a camera trap) was closed by a warthog. We do not know the reason for this or if that burrow had other entrances.

We also do not know how much aardvarks contribute to this burrow upkeep as compared with other species. (Taylor and Skinner 2003) found that aardvarks change sleeping dens frequently; their observations found that a given burrow would be occupied for 1 to 38 days, with a mean of less than 10 days. They noted that there were many burrows available within each aardvark's home range and that aardvarks were not observed re-using any given burrow within their study.

In our plots, new burrows appeared at a rate of about 0.9 per hectare per year. Assuming an average of 1 m length and 30 cm diameter, that would mean about 0.7 m^3 of excavated soil per hectare per year, or about 1.4 tonnes per hectare per year (assuming an

average soil density of 2.0 g per cm^3). Measurements provided by Taylor and Skinner (2003), also allow for an estimate of the average volume of these burrows to be about 0.5 m^3. Aardvark home ranges may be around 200 ha (Taylor and Skinner 2003), so we can very roughly estimate the average turnover per aardvark to be 280 tonnes per year. This estimate is undoubtedly low, as an aardvark that digs even small amounts of soil every night will move many times more soil than can be estimated by visible burrows (smaller digs, burrows that collapse rapidly, renovation of existing burrows, and so on) and our estimate used a small burrow of just 1 m.

We can also compare soil turnover by other prolific diggers. The woylie (a kangaroo-like marsupial weighing approx. 1 kg) may dig in over 100 places in a single night to find its food, fungal fruiting bodies. A single woylie can displace 4.8 tonnes of soil annually (Garkaklis et al. 2004). If aardvarks move soil at the same rate relative to body size, we would expect aardvarks to move 336 tonnes of soil per year. That's 336 tonnes of soil turned over, aerated, and redistributed, which undoubtedly affects the plant community. Australia's hairy-nose wombat, another large (40 kg) solitary burrowing mammal, has been estimated to move 276 m^3/ha (552 tonnes/ha, assuming 2 tonnes/m^3), though no time frame was given (Bancroft et al. 2004). Aardvarks could easily match or best that number.

We found no correlation between the size of the "fan" of excavated soil by the burrow entrance and the minimum tunnel length. This may be explained by burrow longevity. It is possible that the soil fan erodes, compacts, and becomes completely covered over time, appearing much smaller than when it was new. Furthermore, we only estimated the fan diameter and tunnel length. Precise measurements would be required to confirm a breakdown in correlation, as it stands to reason that there must be a tight relationship between fan and

tunnel size at initial excavation. However, because new and older but well-maintained burrows are visually similar, this would also require monitoring the area for new burrows and then monitoring those over many years.

Burrows that aardvarks dig as burrows—that is, their sleeping dens—are more valuable to both aardvarks and other species, and are thus more likely to be maintained long-term, than the smaller feeding digs we called burrows but were not dug as such. Previous work (Taylor et al. 2002) found that aardvarks tend to move between existing burrows rather than always digging new ones, which supports this idea. The smaller burrows, which are likely nothing more than the result of foraging as far as the aardvark is concerned, are not worth the maintenance effort even by those smaller animals who may inhabit them, as such small burrows exist in large numbers in good habitat. However, our data do not provide direct evidence of this due to the relatively short time frame and crude measurements.

E. Conclusion

Aardvark-dug burrows serve two primary purposes for aardvarks: food and shelter. Some undoubtedly function as both. Aardvark-dug burrows appear and collapse at a high rate, but some may be maintained for many years. While they are intact, they can provide all sorts of benefits to other animals. Our data suggest that these animals make full use of these benefits.

Much about aardvark-dug burrows remains unknown. To truly understand the demography and dynamics of these burrows will require extensive, long-term monitoring along with regular precise measurements of burrow dimensions and other attributes. This should

include well-defined habitat variables such as distance to water and other habitats, vegetation

type and density, and a complete census of animals present.

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IV. CAMERA TRAPS REVEAL THAT AARDVARKS ARE THE INADVERTENT CIVIL ENGINEERS OF

SOUTHERN AFRICA

A. Introduction

1. Ecosystem engineering

Ecosystem engineering is the physical alteration of the environment by organisms, whether via their bodies (e.g., corals, trees) or by building structures or destroying or otherwise altering the landscape (Jones et al. 1994). The effects can be substantial: one study estimated an average 25% increase in species diversity thanks to local engineering species (Romero et al. 2014). Ecosystem engineers include diverse taxa of plants and animals small and large. It can be argued that all or almost all species alter their environments and therefore could be ecosystem engineers (Hastings et al. 2007), but generally speaking, most people seem to reserve the term for those with impacts disproportionate to their abundance in the community (Wright and Jones 2006).

The direct and indirect effects of ecosystem engineers are still being documented, as they are numerous and complex. In recent years, attempts have been made to better define the types of ecosystem engineers and classify and quantify their effects (Romero et al. 2014). Romero divided ecosystem engineering effects into three categories: bioturbation, habitat forming, and habitat modification. Other authors have devised their own ecosystem engineering classification schemes and others have challenged the usefulness of the term (e.g., Jones et al. 1997; Berke 2010), but the central idea remains.

The archetypal ecosystem engineer is the beaver (*Castor* spp.), which fells trees and builds dams that turn rivers into ponds (e.g., Wright et al. 2002). For pure destructive power,

one cannot beat elephants (*Loxodonta africana* and *Elephas maximus)* (Pringle 2008; Prugh and

Brashares 2012), though other species, like puffins (Jones et al. 1997), can have considerable

destructive effects. Other vertebrates that have been described as ecosystem engineers include

prairie dogs (*Cynomys* spp.) (Van Nimwegen et al 2008), seabirds (*Puffinus pacificus*) (Bancroft

et al. 2004), European bee-eaters (*Merops apiaster*) (Casas-Criville and Valera 2005), crested

porcupines (*Hystrix indica*) (Alkon 1999), giant armadillos (*Priodontes maximus*) (Desbiez and

Kluyber 2013), pileated woodpeckers (*Hylatomus pileatus*) (Duncan 2003), European rabbits

(*Oryctolagus cuniculus*) (Gálvez et al. 2008; Gálvez Bravo et al. 2009), gopher tortoises

(*Gopherus polyphemus*) (e.g., Alexy et al. 2003, Kinlaw and Grasmueck 2012), long nose

armadillos (*Dasypus hybridus*) (González et al. 2001), mole rats (Bathyergidae) (Hagenah and

Bennett 2013), badgers (*Meles meles*) and foxes (*Vulpes vulpes*) (Kurek et al. 2014), California

ground squirrels (*Spermophilus beecheyi*) (Lenihan 2008), and pocket gophers (*Thomomys

bottae*) (Reichman and Seabloom 2002; Romanach and Le Comber 2004).

Animals that excavate burrows have long been recognized as ecosystem engineers. They

fall into two of Romero's categories (bioturbation and habitat modification). The burrows

provide dens and temporary shelter for not only the species that create them, but for

potentially hundreds of other animal species, both invertebrate and vertebrate, who may share

the space with the engineer or move in after the engineer has moved on (Hansell 1993, Lill and

Marquis 2003, Dangerfield et al. 1998, Nummi and Hahtola 2008). Burrows provide, among

other things, refuge from extreme temperatures outside (Pike and Mitchell 2013). The soil

mound that piles up as the burrow is excavated also benefits other vertebrates. It may be used

for foraging for seeds which had been buried, as an open spot on which to bask, or as a

"pitcher's mound" lookout (Melton 1972). In addition to providing refuge and other uses for dozens of vertebrate species, burrows increase insect diversity and abundance, increase plant diversity via altered soil nutrient and water infiltration levels, and even help prevent establishment of invasive species (Davidson et al 2012). Fleming et al. (2014), in a review of the literature on Australian digging mammals, found that the recent loss of many of these animals has had significant negative impacts on Australian ecosystems. They noted that diggings lead to soil turnover and changes in soil properties, increase nutrient cycling, and promote plant recruitment.

Kinlaw (1999) summarized the myriad benefits of burrows: an anti-predator maze (for complex burrows with secondary exits); the mound of excavated soil for watching for predators; food hoarding; protection of vulnerable offspring; an amplifier for calls; a listening station; protection from the elements; and safety for living, reproducing, and recovering from injury. For those who occupy a burrow dug by another individual, group, or species, all these benefits accrue without the costs of digging it themselves. To these we add an ambush point, where predators can wait in shadow while unwary prey pass by or enter in search of food or shelter.

Studies of burrow commensals have revealed that dozens of vertebrate species can benefit from a single burrow, even if the original digger is still in residence (e.g., prairie dogs: Ceballos et al. 1999, Kotliar et al. 1999, Campbell III and Clark 1981, Butts and Lewis 1982, Bangert and Slobodchikoff 2006, Van Nimwegen et al. 2008, Lomolino and Smith 2004). Invertebrates, plants, and other forms of life have not been studied as much, but their role appears to be similar (e.g., burrowing land crabs: Bright and Hogue 1972; mussels: Commito et

al. 2005). Both predators and prey may inhabit the same burrows, though not at the same time (for long anyway). Kinlaw's 1999 review of the burrow literature included observational or sampling studies on burrow commensals; those papers' subjects included the aardvark (20 vertebrates; Smithers 1971).

For example, a single study found that burrows excavated by gopher tortoises are used by at least six reptiles, two amphibians, four mammals, two insects, and one spider even while the tortoises themselves are resident (Alexy et al. 2003). This list was compiled when focusing on the tortoises themselves, and thus is by no means comprehensive.

There has been a recent focus on social burrowers, particularly mammals (Davidson et al. 2012). Solitary burrowing mammals are less frequently study subjects. The most impressive solitary burrower is the aardvark.

2. Aardvarks

The aardvark (*Orycteropus afer*) is a semi-fossorial mammal found throughout sub-Saharan Africa (Fig. 18). Unlike many burrowing animals, aardvarks are solitary, though they do not appear to be territorial. Aardvarks can weigh upwards of 70 kg, and are impressively prolific diggers. Smithers (1971) reported that a team of men with shovels could not keep up with the digging speed of aardvarks even in soft soil. Aardvarks are myrmecophagids that consume tens of thousands of ants, termites, or some combination of the two, every night. To get at their prey, aardvarks dig into anthills and termite mounds aboveground and into underground nests. There they eat quickly, before the prey are able to escape deeper into the nest. Taylor et al (2002) found that a single aardvark, while foraging, might dig and eat in up to

200 places in one night, with bouts as short as 30 seconds. Most of these feeding digs are nothing more than shallow scrapes, but others may measure as much as 2 m deep. Aardvarks also dig significantly deeper holes to be used as sleeping dens. Some measure at least 12 m in length (Whittington-Jones et al 2011), and there are enough of these tunnels in aardvark territory for the aardvarks to move frequently without digging new ones (Taylor et al 2002).

Figure 18 Aardvarks at Mapungubwe National Park, South Africa. The aardvark on the left is outside a burrow dug into a termite mound at a former irrigation site.

Previous studies of aardvark burrow commensals (Smithers 1971; Whittington-Jones 2007, 2011) documented 49 distinct vertebrate species (see Table VI), and an unspecified number of unidentified rodents. These studies relied on small-mammal trapping, personal observations, and observations by local people. Whittington-Jones (2007) also identified insects

from six orders, 30 families, and 50 morpho-species in a pitfall trap survey. He found that aardvark burrows might increase overall plant diversity on a landscape scale, a finding consistent with our observations in the field.

TABLE VI
AARDVARK BURROW COMMENSALS IDENTIFIED BY SMITHERS (1971) AND
WHITTINGTON-JONES ET AL. (2011)

Scientific name	Common name	Scientific name	Common name
Agama aculeate	ground agama lizard	*Mabuya capensis* now *Trachylepis capensis*	Cape skink
Bitis arietans	puff adder	*Mastomys natalensis*	Natal mutimammate mouse
Bufo gariepensis	Karoo toad	*Mellivora capensis*	Honey badger
Canis adustus	side-striped jackal	*Merops pusillus*	Little bee-eater
Canis mesomelas	black-backed jackal	*Michaelamys namaquensis*	Namaqua rock rat
Crocodilus niloticus	Crocodile	*Mus indutus*	Desert pygmy mouse
Crocuta crocuta	spotted hyena	*Mus minutoides*	Pygmy mouse
Cynictis panicillata	yellow mongoose	*Myosorex varius*	Forest shrew
Desmodillus auricularis	Cape Short-eared Gerbil	*Myrmecocichla formicivora*	anteating chat
Felis lybica	African wild cat	*Mystromys albicaudatus*	white-tailed rat
Genetta genettta	Common genet	*Naja nivea*	Cape cobra
Genetta sp.	Genet	*Otocyon megalotis*	Bat-eared fox
Gerbilliscus brantsii = Tatera brantsii	Highveld gerbil	*Panthera pardus*	Leopard
Gerbilliscus leucogaster	Bushveld gerbil	*Phacochoerus africanus*	Warthog
Gerbillurus paeba	Hairy-footed gerbil	*Proteles cristatus*	Aardwolf
Halcyon leucocephala	grey-headed kingfisher	*Python sebae*	African rock python
Herpestes sanguineus	slender mongoose	*Raphicerus campestris*	Steenbok
Hirundo dimidiate	pearl-breasted swallow	*Rhabdomys pumilio*	four-striped grass mouse
Hirundo semirufa	red-breasted swallow	Rodent spp.	Rodent spp.
Hyaena brunnea	brown hyena	*Saccostomus campestris*	pouched mouse
Hystrix africaeaustralis	Cape porcupine	*Thamnolaea cinnamomeiventris*	mocking cliff-chat
Ispidina picta	African pygmy Kingfisher	*Varanus albigularis*	Rock monitor
Lepus capensis	Cape hare	*Vulpes chama*	Cape fox
Lepus saxatilis	Scrub hare	*Xerus inauris*	Cape ground squirrel
Lycaon pictus	African wild dog		

These studies give us part of the picture, but can miss the larger, and potentially more elusive, commensals. Furthermore, scattered stories do not provide information as to the frequency with which various commensals will take advantage of these burrows.

Here we used camera traps to document the use or avoidance of aardvark burrows by mid-sized and large animals, which is indirect evidence of aardvarks as ecosystem engineers—namely, the extent to which other animals make use of aardvark-dug burrows. This too gives only part of the overall picture, but when added to previous findings, we can get a general idea of the importance of aardvark burrows in the community.

3. Camera Traps

Camera-trapping has given us the opportunity to remotely "observe" animals in the wild for over a century (Carey 1926). In recent years, with advances in technology and decreases in price, the popularity of camera-trapping has dramatically increased. This method has been shown to be comparable to other census methods, only easier (Silveira et al. 2003, Yasuda 2004, Lyra-Jorge et al. 2008, Rowcliffe and Carbone 2008, Rowcliffe et al. 2008, Tobler et al. 2008, O'Connell et al. 2010). Camera-trap placement depends on the goal of the study, and placement can affect population density estimates (Foster et al., 2012). Our camera placement, as detailed below, was designed to capture animals both at aardvark burrows and in similar small cleared areas. It cannot be assumed to represent actual animal density, only confirmation of presence and relative activity.

4. Study goals

We sought to add to our knowledge of aardvarks as physical ecosystem engineers via their extensive burrowing and the benefits these burrows provide. For the purposes of this study, we defined a "burrow" as any aardvark-dug tunnel greater than 1 m in length. We used camera-trapping to determine which species may be more likely to be in the vicinity of a burrow for any reason, as well as those who may actively avoid them. We wanted to discern the extent to which aardvark-dug holes and burrows (hereafter "burrows") are an ecosystem service for other animals. How extensively are these burrows used? What proportion of burrows is in use at any given time? Can we determine from still photos how these burrows are being used? Is it aardvarks that are primarily using their own burrows, or are they more likely to be used by others? Which species derive benefit, directly or indirectly, from these burrows? Which species avoid them?

Our predictions were of a general nature. Burrows should be used frequently, by aardvarks and other species. Other species should include known burrow-dwellers such as warthogs and porcupines. Partially collapsed or filled-in burrows no longer suitable for such large animals may be home to smaller species such as springhares.

These burrows may provide dens or an escape from predators ("bolt holes"). If dens, we would see the same animals repeatedly over several days, weeks, or longer. If bolt holes, we would see only short visits. Our camera settings did not allow for detailed assessment of whether an animal entered the burrow and left shortly afterward, nor if they were being chased. Still pictures may give us some idea of how burrows are used, but this method is

limited. Not all use will be captured in a single photograph, as events may happen while the camera is latent and resetting.

If aardvarks use the burrows they dug more than other species do, then such burrows are less of an ecosystem service than it might otherwise seem, and function primarily as aardvark feeding holes or dens. If we see more use by other species, then these burrows are clearly performing a role in the community.

Known burrowing mammals such as warthogs and porcupines may favor aardvark burrows for their size and ease of use. If these species avoid burrows, it may be that the burrows are already occupied, or potentially occupied, by predators such as caracals, servals, pythons, or hyenas. Non-burrow-dwellers may also use the burrows in search of food (e.g., insects or seeds in the disturbed soil) or escape (bolt holes). Predators may use them for cover when ambushing prey. The soil mound that is a byproduct of burrow-digging may be favored by some species as a vantage point (the pitcher's mound effect). The plant species on aardvark burrows and the associated soil mound may differ from those in the surrounding landscape (Whittington-Jones 2007, pers. obs.), and thus may attract different herbivores. Antelope species, giraffes, and elephants may avoid burrows if they are potential sources of injury or loose footing (Kotler 2001, Abu Baker and Brown 2012). Avoidance of burrows would be shown indirectly by a significantly higher number of photographs at sites other than at burrows.

B. Methods

1. Location

This study took place within the western section of Mapungubwe National Park (MNP), a 20,000-hectare park managed by South African National Parks (SANParks) that lies at the northernmost point of South Africa, along the Limpopo River, which also serves as the national border with Botswana, and, to the east, Zimbabwe (Fig. 19).

Figure 19 Official map of Mapungubwe National Park, 2005. Park borders were unchanged as of this study.
http://www.sanparks.org/images/parks/mapungubwe/maps/map2.png
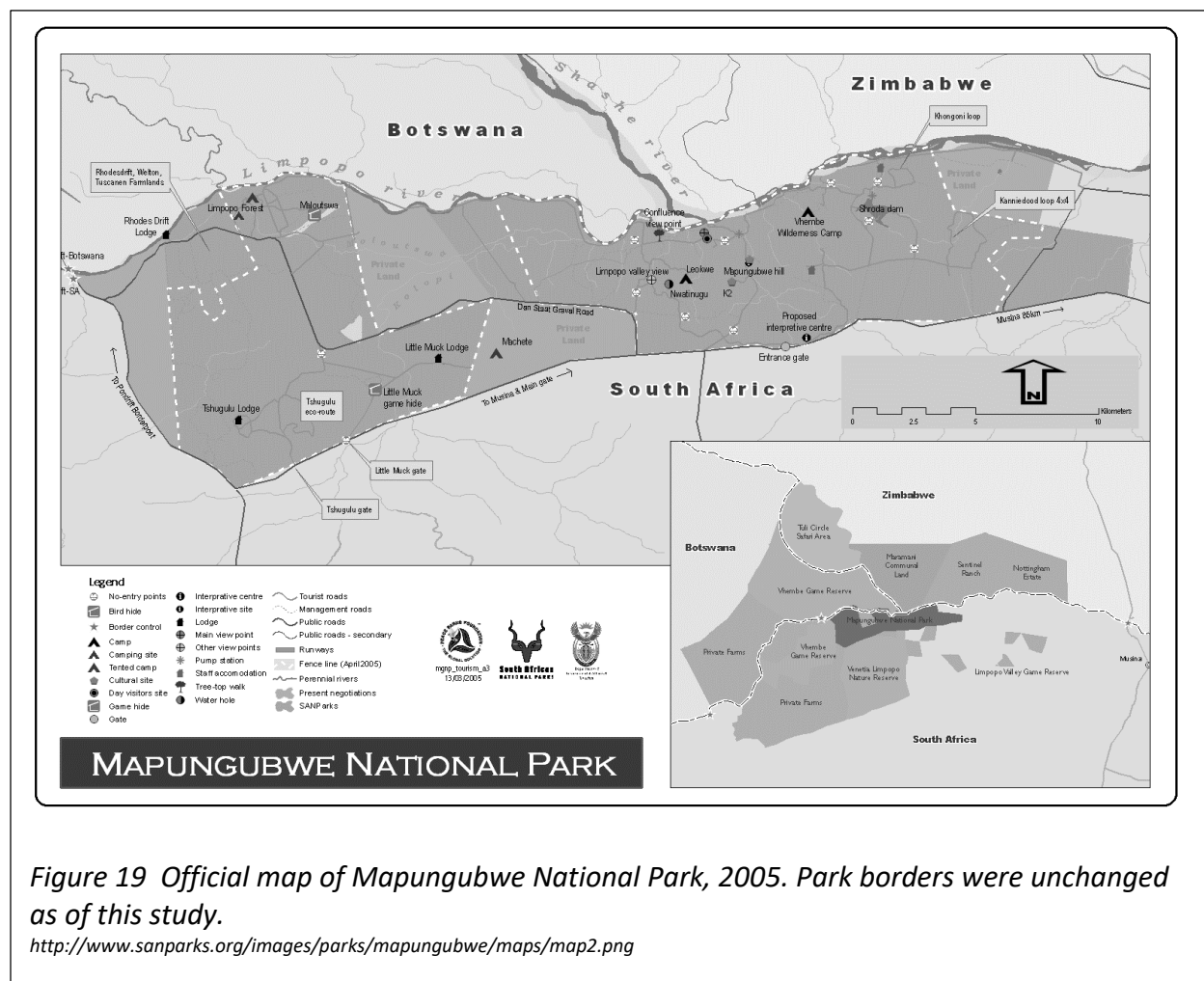
MNP was created beginning in 1999 and opened to the public in 2004, combining former farmlands either long abandoned or recently in use with wild areas. At the time of this study, working agricultural farms, growing primarily citrus or tomatoes, both abutted and divided the park. Neighboring private reserves in South Africa and Botswana and public land in Zimbabwe joined MNP as the Mapungubwe Transfrontier Conservation Area (TCFA). While part of the northern border is lined with high, multi-layered fences, other areas have only a single electrified wire elephant fence, a small barbed-wire fence, or no fence at all. Animals can move freely between MNP and adjoining land in the rest of the TCFA. This is a rapidly changing area and TFCA borders have been expanded since this study. This means that more animals now have access to burrows, and our findings may underestimate current burrow use.

MNP, despite its small size, has several different habitats. We used primarily former agricultural fields, a small portion of which were the site of experimental forest restoration, and riverine forest. The forest is not pristine, but has been allowed to return to its wild state for long enough that it is effectively so. In 2009, powerful electric fences were installed around much of the riverine forest in an attempt to exclude elephants and thus preserve the forest. These fences are just a few wires approximately one meter above the ground, so nearly all other animals can easily go under or over them. These fences are effective in limiting elephant movement, though elephants do break through on occasion. MNP also contains large areas of mopane forest, which proved to have nearly no aardvark activity. Hence, the mopane habitat represents only a small part of this study. The numerous rocky outcrops were not explored.

SANParks performs periodic aerial surveys by helicopter. The 2006 census counted 114 elephants, 903 impala, 340 blue wildebeest, 271 eland, 228 Burchell's zebra, 88 greater kudu,

84 waterbuck, 48 giraffes, 20 red hartebeest, 125 gemsbok, 8 tsessebe, 4 white rhinos, 2 sables, and 3 donkeys. Rangers reported known leopards, spotted hyenas, brown hyenas, black-backed jackals, African wild cats, lions, bushbuck, klipspringer, common duiker, steenbok, bushpig, warthog, baboon, vervet monkey, mongooses, and rodents (Roerig 2006). This formal census is the closest in time to our camera-trap work. Other species known to be present at the time but not included in that report include aardvark, honey badger, many small mammals, at least 15 species of snakes, and over 400 species of birds (MNP Rangers, pers. comm.).

All work for this study was performed during winter, during the months of May, June, July, and August, in 2008, 2009, and 2010. Daytime temperatures reached approximately 25°C, and nighttime temperatures dipped to around 1–2°C. Rain is rare this time of year; over the three winters of this study it rained one day.

2. Habitat types

While the vegetation of MNP is complex, for the purposes of this study we used three broad habitat categories (Fig. 20). "Field" refers to the former agricultural fields, whether under active restoration or not. These areas are very open and are dotted with trees, primarily umbrella thorn acacia (*Vachellia tortilis*) trees. "Riverine" is the riparian forest along the Limpopo River. This forest had been partially cleared and built upon in the past, but is well-recovered from the disturbance. "Mopane" refers to two different habitats dominated by mopane (*Colophospermum mopane)* but which differ in soil type. As both mopane-dominated habitats had low aardvark burrow density, we focused most of our efforts on the field and riverine habitats.

Figure 20   Habitat types at Mapungubwe National Park, South Africa. (A) Former agricultural field with rocky habitat in the background; (B) A clearing in the riverine forest; (C) Edge of the mopane forest.

3. Plot choice and camera placement

We placed cameras in each of the three different habitat types: field, riverine, and mopane. We chose plots to find and monitor aardvark-dug burrows haphazardly in each of the three habitats. The criteria for plot choice were that the entire plot would be within one habitat type, the plot would not cross a road, and the plot would not overlap others. We usually chose

a tree as a corner point, then ran the plot east and south from that point. Plots varied in size and shape (always quadrilaterals) depending on the continuity of the habitat type and ease of surveying.

Plots ranged from 0.02–21.74 ha, with an average 2.39 ha (most were 1–3 ha). Each plot was systematically explored for aardvark-dug burrows whether apparently in use by any animal or not. Each aardvark-dug burrow, no matter its age or condition, was photographed, and coordinates and other basic information about size and condition recorded. Minimum tunnel length was estimated by inserting metal fencing wire as far as possible. Each plot was assigned a letter code, and each burrow within a plot given a number. All large burrows (c. 30 cm diameter or larger) were assumed to be aardvark-dug, and in numerous cases claw marks were clearly visible. Other animals, such as warthogs and porcupines, are able to dig their own burrows, but not with the ease with which aardvarks do. It appears that at MNP these other animals may "renovate" or maintain burrows, but aardvarks do all of the initial excavating.

All burrows with a minimum tunnel length of 1 m were noted as candidates for camera-trap monitoring. Once plot exploration was completed, random burrows were selected for monitoring using polyhedral dice. The first number rolled which corresponded to an "eligible" burrow determined the burrow selection. The number of burrows monitored at a given time varied with camera availability.

A camera trap was then placed to monitor activity at the burrow (referred to as "Burrow" cameras). Cameras were mounted on trees or repurposed wood scrap (Fig. 21). Cameras were placed approximately 2 m from the burrow entrance, angled so as to capture activity both at the burrow entrance and in the soil mound or "fan" in front of it. It was

impossible to place all cameras ideally, leaving some of the area of interest outside the field of vision. As a result, some activity was undoubtedly missed. To avoid sun interference, cameras were placed facing south whenever possible. Nighttime photos were lit with infrared rather than a white flash, again to minimize potential interference as well as to avoid detection by poachers. Cameras were set to take one photograph when triggered, at no less than 5-minute intervals. This was to minimize photographs of moving vegetation but again likely led to an underestimate of actual burrow use.

Figure 21 Camera traps at Mapungubwe National Park. (A) Attached to a tree; (B) Mounted on a stick. We used trees when available, sticks and scrap wood otherwise, and the camera's strap and duct tape as needed.

In most cases in 2009 and 2010, a second, "Away," camera was placed in a similar fashion at a point within the plot that was 20–30 m away from not only the monitored burrow

but any other burrow. Natural clearings or areas with little vegetation were chosen when possible to emulate the lack of vegetation immediately around a burrow entrance and to minimize the number of photographs triggered by swaying plants. When camera availability did not allow for paired Burrow and Away cameras, we only monitored the burrow.

We cleared grasses and small branches from the area immediately in front of the camera only as needed to get clear photographs. Cameras were not baited to attract animals, but set to record the animals as they went about their usual activities.

Cameras remained in place for 3–76 days (average 12, mode 7). One burrow in the field, known as C1, was monitored for a total of 219 days over the three field seasons, with its Away point monitored 127 days (the discrepancy is due to not monitoring Away points in 2008 and ants disabling the camera in 2010). In 2009 we added a long-term monitored burrow in the riverine forest (97 days, 61 Away), but that burrow collapsed between seasons. A second burrow in the same plot was chosen for long-term monitoring in 2010, but equipment shortage meant it was only monitored 22 days and 22 nights, less than some other burrows.

We monitored a total of 85 burrows: 17 burrows in the mopane, 42 in the field, and 26 in the riverine. Away sites numbered 48: 6 mopane, 21 field, and 21 riverine. We gathered information over a total of 2050 camera-days and 2025 camera-nights. The number of days and nights are unequal due to camera malfunction or destruction. We ended up with a total of 3855 pictures with animals present.

Animals were identified to species, except for birds who were grouped to Family or Order (ex: doves) and small rodents, which were only identified as small rodents. Sometimes an animal could not be clearly identified. These subjects were classified simply as "antelope,"

"mammal," "bird," or "unknown." For analysis purposes, data were culled as to remove all photographs in these four categories. A mere 67 animal photos were taken in the mopane. We excluded this habitat from most analyses due to the small sample sizes for each species.

In addition, 53 photographs were removed from analysis because they showed an aardvark in the late stages of starvation laying out in the sun for several days, which is atypical and would thus skew our data unfairly (its first appearance was counted). This aardvark was found dead in the burrow entrance a few days after the photographs were taken. Rather than moving the camera as planned, we left it in place and were able to document brown hyenas scavenging the body (Fig. 22).
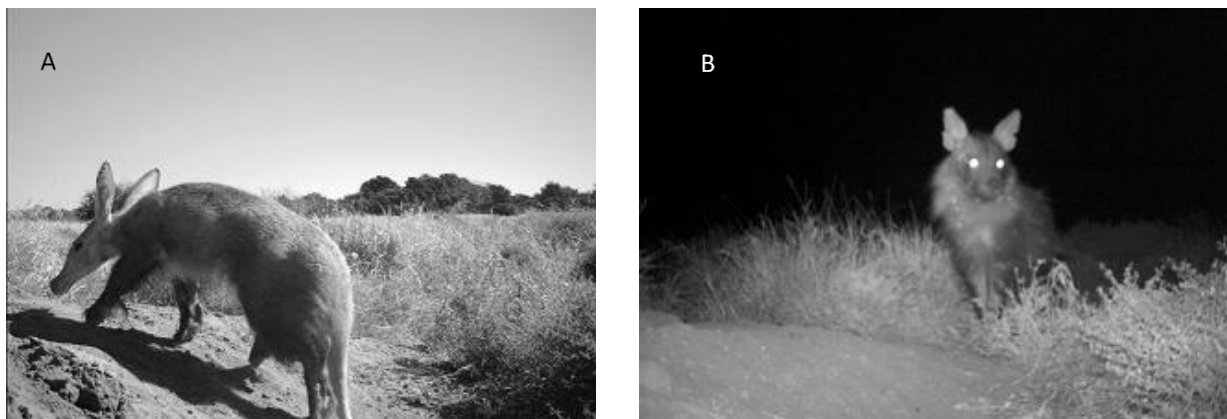
Figure 22 (A) A starving aardvark exiting its burrow during the day. The aardvark spent several days in the sun and nights in the burrow, and the dead body was later found in the burrow entrance. (B) The brown hyena that scavenged the aardvark. A second brown hyena was photographed a few days after this one. The aardvark body was dragged approx. 20 meters from the burrow and partially eaten.

Because of unequal sampling effort, we normalized all counts to the number of photographs per 100 camera-days. A camera-day is a unique combination of camera, date, and either day or night designation. Some species may appear several times in a single location on a single day, and therefore were counted multiple times. This reflects usage of the area. These numbers give a general picture of what is going on, but are too biased for certain statistical analyses.

To get at the question of how often a particular habitat, time of day, or burrow proximity was chosen, we counted the number of camera-days on which a species was photographed, regardless of the number of photographs of that species on that camera-day. We called this unique combination of camera, day, and species an "appearance." This eliminates the above bias of lingering.

For pairwise comparisons between habitats and Burrow–Away, all 3504 remaining photographs were used. Eighty-seven photographs were taken at either dawn (34) or dusk (53) and were therefore not included in day vs. night comparisons.

In our classification, there were 8 unique combinations of habitat, time of day, and burrow proximity. Our sample sizes were not large enough to permit full detailed analysis of these preferences and the interactions among them. We performed pairwise chi square goodness-of-fit tests to test for preference of location and time when the number of camera-day appearances would be expected to be at least 10 in each pair, (5 in each cell assuming equal camera-trapping effort but here calculated to reflect actual trapping effort). Each species could have a preference for habitat, time of day, and burrow proximity. Except for testing day against night, both day and night appearances were counted; factors were pooled as above. For

those species with 10–19 appearances, we tested burrow vs away; those with 20–39 appearances were tested for burrow vs away and day vs night; those with 40 or more appearances were tested for all three factors (burrow vs away, day vs night, and field vs riverine). Expected values for the chi-square tests were calculated based on the proportion of available camera-days and -nights and the total number of pictures.

We also noted whether these species were photographed definitely or apparently "using" the burrow in some fashion, such as entering or exiting, foraging in the soil fan, or using the mounded soil as a lookout.

C. Results

Only 71% of cameras located at burrows, in the mopane recorded any animal pictures, at an average rate of 12.5 pictures/100 camera-days+nights. Only 4 of the six (67%) Away cameras in the mopane had any animal pictures. By contrast, at least 90% of all other camera locations obtained at least one animal picture. Field burrows had an overall average of 50.8 pictures/100 camera-days+nights, and riverine burrows saw 187.5 pictures/100 camera-days+nights. In all habitats, fewer pictures were taken at the burrows than Away (Table VII).

TABLE VII
CAMERAS WITH PHOTOGRAPHS OF ANIMALS, BY LOCATION[a]

		Number of camera locations with pictures	Number of camera locations without pictures	Total number of camera locations	Proportion of camera locations with pictures	Average number of pictures per 100 camera-days+nights
Mopane	Burrow	12	5	17	0.71	12.5
	Away	4	2	6	0.67	17.7
Field	Burrow	39	3	42	0.93	50.8
	Away	19	2	21	0.9	66.9
Riverine	Burrow	26	0	26	1	132.7
	Away	19	2	21	0.9	187.5

[a] Number of pictures per camera-day+night is the total number of pictures taken either at or away from a burrow, including photos taken at dawn or dusk, divided by the [total number of camera-days plus the number of camera-nights].

1. Mopane

In the mopane, over the 152 camera-days and camera-nights at monitored burrows and the 87 camera-days and 77 camera-nights Away, we obtained a total of 67 pictures of animals. The most common animals in these pictures were baboons, appearing in 13 photographs (all Away, during the day), followed by mice (8, all at the burrow at night), aardvarks (6 at the burrow and 1 Away, all at night), and warthogs (5 at the burrow and 1 Away, all during the day). The 13 baboon photos were taken over 4 camera-days; mice, aardvarks, and warthogs each appeared once per camera-day. Remaining photographs showed African wild cat, black-backed

jackal, brown hyena, common duiker, elephant gemsbok, impala, kudu, scrub hare, steenbok, various birds, or unidentifiable antelopes or other mammals.

The low level of activity in the mopane meant that there were not enough photographs for statistical analysis. Therefore, all photographs taken in the mopane were removed from further analyses.

2. Field and riverine

Of the 3788 photographs taken in the two remaining habitats, 231 pictures contained unidentifiable animals (31 antelope, 56 bird, 71 mammal, and 73 completely unidentifiable) and were thus removed from further analyses. As described above, we also removed 53 pictures of an aardvark laying in front of burrow C1 in 2008, as it was clearly emaciated and dying, and thus represented atypical behavior that would have skewed the data.

After the above removals, we were left with 3504 photographs available for analysis. Given the unequal trapping effort and sample size, we present basic descriptive statistics only for the total photo count.

We observed 53 types of animals, largely mammals and birds. Most mammals were identified to species, excepting small rodents, which we grouped together. Only a few birds were identified to species.

Warthogs were by far the most photographed species, appearing in 842 pictures (24.0% of all pictures), many with more than one individual. They were followed by impala (565 pictures, 16.1%) and elephant (285 pictures, 8%) (Fig. 23). The ten most-photographed species

(warthog, impala, elephant, bushbuck, waterbuck, kudu, steenbok, porcupine, francolin, and

baboon) accounted for 75.0% of all photographs (Fig. 24).

Figure 23   The number of photographs of identifiable species taken in the field and riverine habitats at Mapungubwe National Park, South Africa, in the winters of 2000–2010. This total includes all cameras in all three years and does not correct for sampling bias.
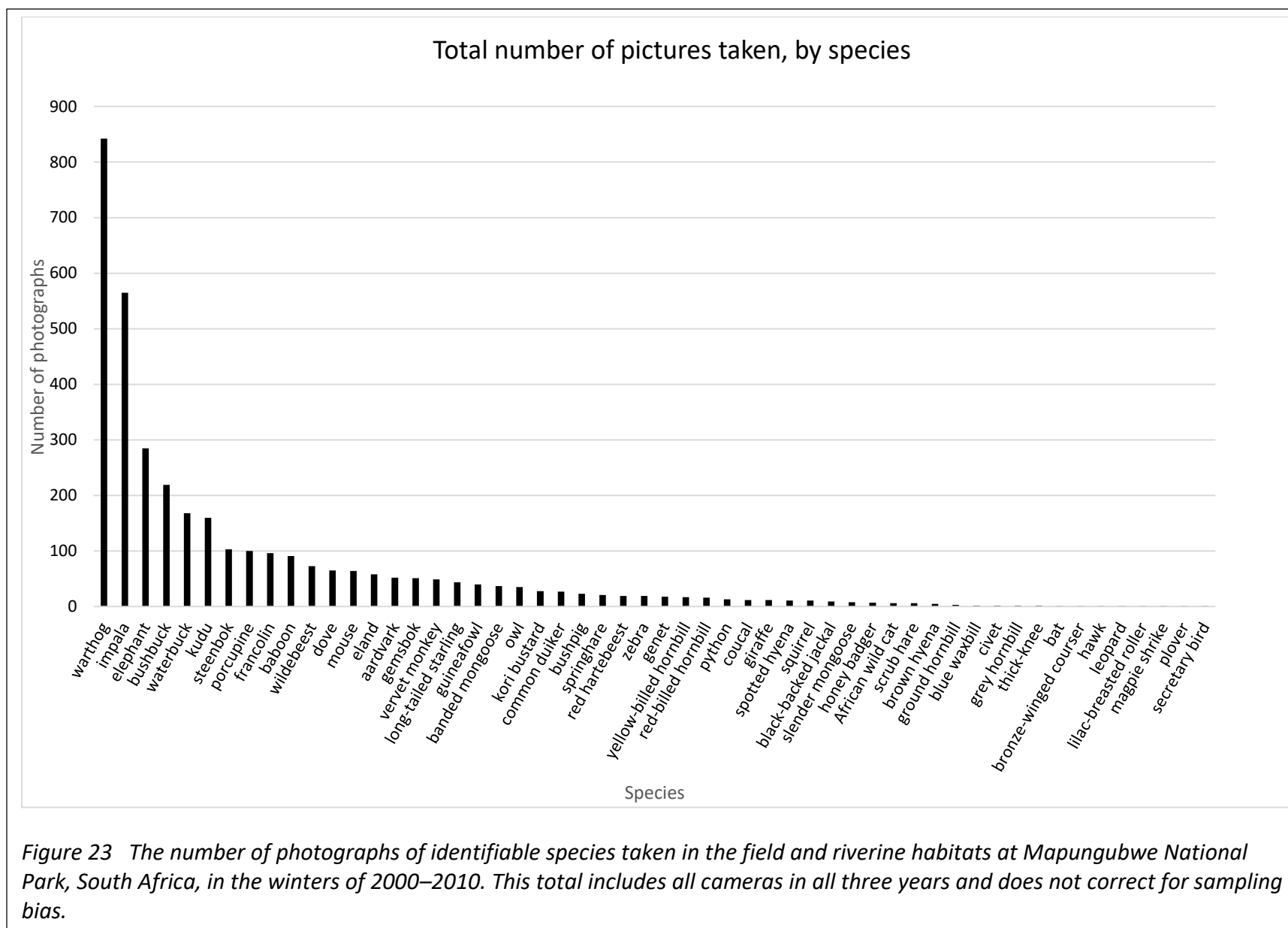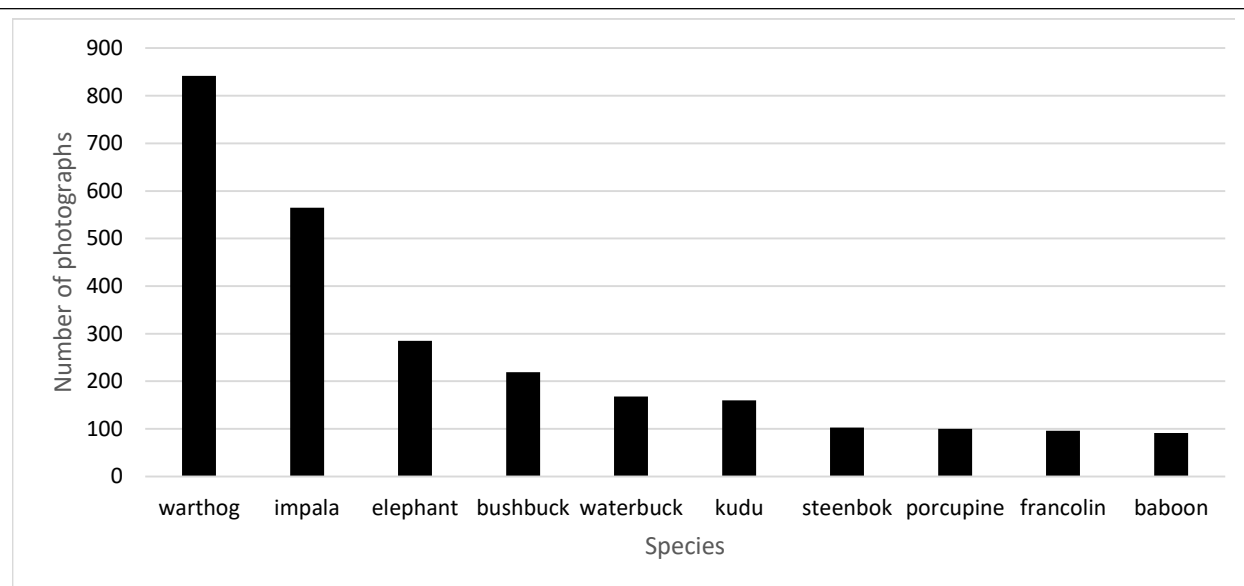
Figure 24   The number of photographs taken of the ten most-photographed species in the field and riverine habitats at Mapungubwe National Park, South Africa, in the winters of 2000–2010. These ten species were in 75.0% of all photographs taken.

To compare frequency of appearance of species across habitat, Day–Night, and Burrow–Away, we normalized all counts to number of pictures per 100 camera-days and -nights (Figs. 25, 26 27, and 28). For the Day–Night comparison, habitat and burrow proximity were pooled; for habitat, time and burrow proximity were pooled; and for burrow proximity, time and habitat were pooled. In all three cases, there were a total of 3607 camera-days or –nights available. The Day–Night comparison has lower totals due to exclusion of photos taken at dawn or dusk; these pictures are included in the other comparisons. Note that this method corrects

for unequal sampling but continues to reflect lingering—animals that spent considerable

amounts of time in front of the camera were photographed more often. For these graphs, each

factor was considered separately, so the total number of photographs shown may vary based

on the method of pooling other factors.

*Figure 25 Total number of pictures per 100 camera-days and camera-nights of identifiable species taken in the field and riverine habitats at Mapungubwe National Park, South Africa, in the winters of 2000–2010. Days and nights were counted separately but habitats and locations were pooled. Total available days = 1811; total available nights = 1796. Number shown is total number of pictures / 3607 * 100.*

Figure 26   Number of photographs per 100 camera-days+nights of the 15 most-photographed species in the field and riverine habitats at Mapungubwe National Park, South Africa, in the winters of 2000–2010, stratified by habitat.

Figure 27   Number of photographs per 100 camera-days or camera-nights of the 15 most-photographed species in the field and riverine habitats at Mapungubwe National Park, South Africa, in the winters of 2000–2010.

Figure 28   Number of photographs per 100 camera-days+nights of the 15 most-photographed species in the field and riverine habitats at Mapungubwe National Park, South Africa, in the winters of 2000–2010, stratified camera placement either at a burrow or away from any burrows.

Aardvarks appeared in 52 photographs. All were taken at night, with the exception of the dying aardvark and one that appeared at dusk. Aardvark photos were taken at 21 different burrows (7 riverine and 14 field) and 6 away points (4 riverine and 2 field).

Twenty-seven of the field burrow cameras and 23 of the riverine burrow cameras had pictures of animals definitely or highly likely to be actively "using" the burrow in some way. Animals were often photographed entering or exiting the burrow (not always distinguishable, e.g., warthogs enter backwards), or walking toward or away from it as though entry or exit were imminent. Birds and mice were seen foraging in the soil "fan" in front of the entrance, birds appeared to be using the soil mound as a lookout point, and several predators (African

wild cat, honey badger, genet, brown hyena) were seen apparently investigating the burrow,

likely for prey, and occasionally using a mound of soil for a lookout. Eight pictures showed a

steenbok looking into the burrow, and one picture showed a steenbok inside the burrow, all

while a second steenbok stood nearby.

Four of the field burrows (9.5%) and 2 of the riverine (7.7%) were used solely by

aardvarks during our monitoring period. Six field burrows (14.3%) and 3 riverine (11.5%) were

used both by aardvarks and at least one other species. Nineteen field (45.2%) and 18 riverine

(69.2%) were used by one or more species but not by aardvarks. In other words, both field and

riverine burrows were more commonly used by species other than aardvarks. Figure 29 shows

the burrow use in the two habitats.

Field

Riverine

Figure 29 Species using aardvark burrows. Numbers are the number of burrows used by that category (aardvark, non-aardvark, both, or neither) with percentages. The size of each circle reflects the unequal sample sizes but are not to scale. Total n for field = 42; n for riverine = 26.
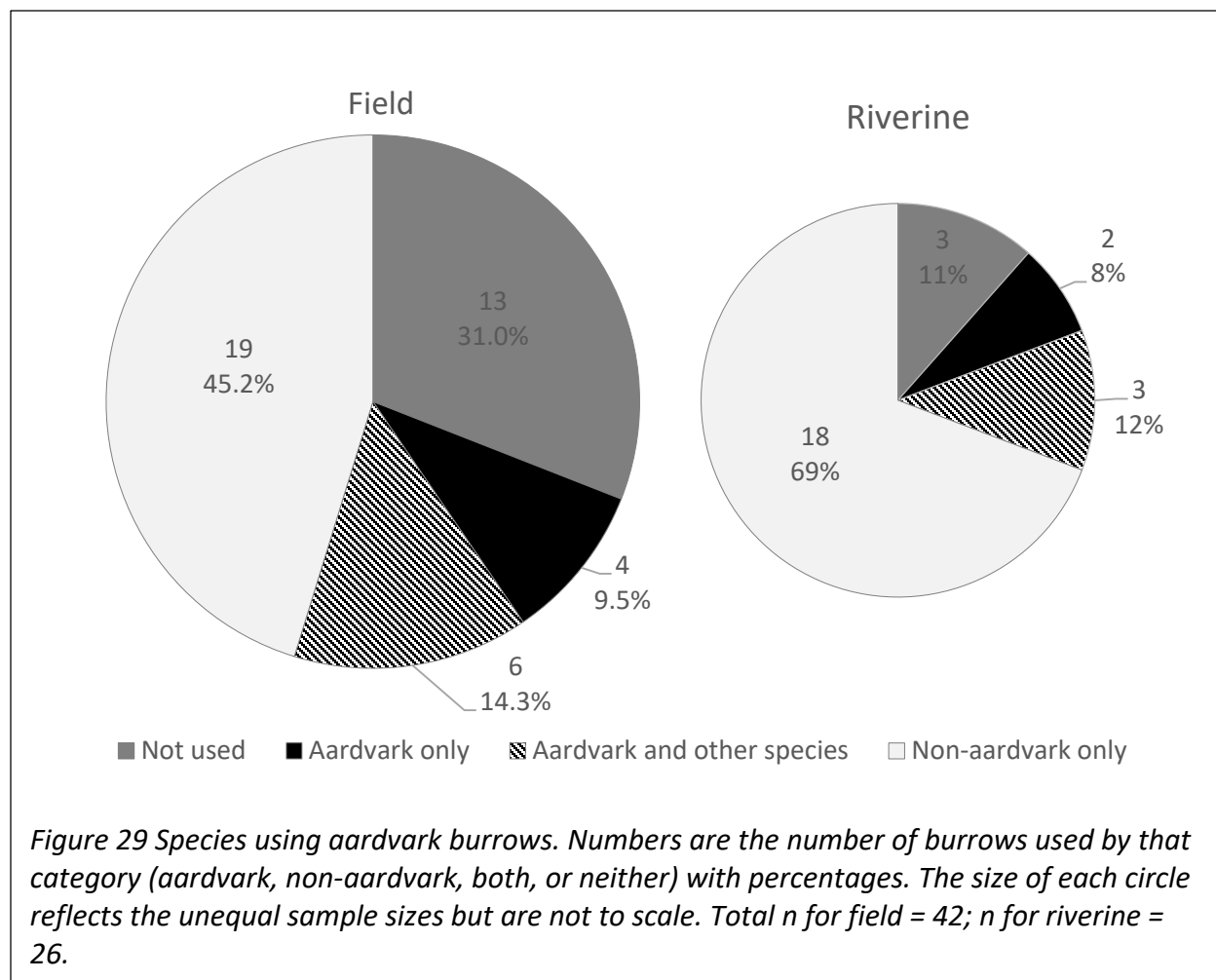
Figure 30 shows the total number of appearances (unique combination of species,

location, and day or night). As with total photographs, warthogs made the most appearances,

followed by bushbuck and impala.
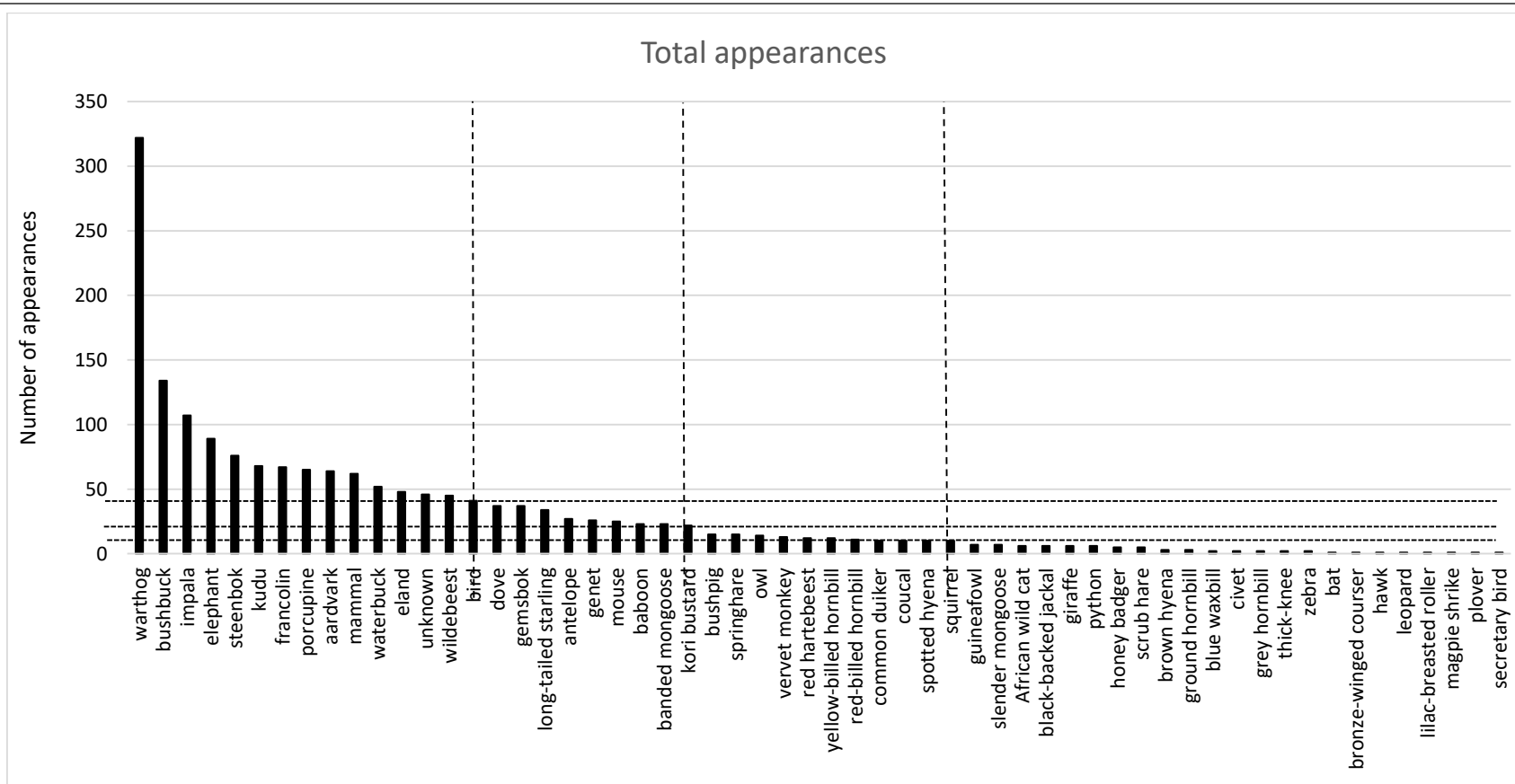
Figure 30 Number of appearances by species. One appearance is one or more photographs at a single location in a single day or night. Horizontal dotted lines represent 10, 20, and 40 appearances, the levels used for analysis. Vertical dashed lines indicate the species within each group by number of appearances.

Table VIII summarizes the results of our chi-square heterogeneity tests. None of the daytime preferences is particularly surprising save for the confirmation that impala seem to favor daytime over nighttime activity. Species that showed a significant nocturnal bias included aardvark, eland, gemsbok, kudu, small rodents, African grass owl, and porcupine Large antelopes such as eland, gemsbok and kudu favored the night. Bushbuck, elephant, steenbok, and wildebeest were active both day and night.

TABLE VIII

HABITAT, TIME, AND BURROW PROXIMINITY PREFERENCES FOR ALL SPECIES
PHOTOGRAPHED ON AT LEAST 10 DAYS OR NIGHTS[a]

Burrow or soil use	Species	preferred habitat	preferred time	preferred burrow proximity
Y	aardvark (*Orycteropus afer*)	n.s.	night	n.s.
	baboon (*Papio ursinus*)	Riverine	day	away
Y	banded mongoose (*Mungos mungo*)		day	burrow
	bushbuck (*Tragelaphus sylvaticus*)	Riverine	n.s	away
Y	bushpig (*Potamochoerus larvatus*)			burrow
	common duiker (*Sylvicapra grimmia*)		day	away
Y	dove spp.	n.s	day	burrow
	eland (*Taurotragus oryx*)	Field	night	n.s
	elephant (*Loxodonta africana*)	Riverine	n.s.	away
Y	francolin spp.	Riverine	day	burrow
	gemsbok (*Oryx gazella)*		night	away
Y	genet (*Genetta spp*)			burrow
Y	guineafowl (*Numida meleagris*)		day	away
	impala (*Aepyceros melampus*)	Riverine	day	away
	kori bustard (*Aepyceros melampus*)		day	away
	kudu (*Tragelaphus strepsiceros*)	n.s.	night	away
Y	long-tailed starling (*Lamprotornis mevesii*)		day	burrow
Y	small rodents		night	burrow
Y	African grass owl (*Tyto capensis*)		night	burrow
Y	porcupine (*Hystrix cristata*)	Field	night	burrow
	red hartebeest (*Alcelaphus buselaphus caama* or *A. caama*)			away
Y	red-billed hornbill (*Tockus sp.*)			n.s.
Y	springhare (*Pedetes capensis*)			burrow
Y	Steenbok (*Raphicerus campestris*)	field	n.s.	away
Y	tree squirrel (*Paraxerus cepapi*)			burrow
	vervet monkey (*Chlorocebus pygerythrus*)		day	away
Y	warthog (*Phacochoerus africanus*)	Riverine	day	n.s.
	waterbuck (*Kobus ellipsiprymnus*)	Riverine	day	away
	wildebeest (*Connochaetes taurinus*)	Field	n.s.	n.s.
Y	yellow-billed hornbill (*Tockus leucomelas*)			n.s.
	zebra (*Equus quagga*)			away

[a] Based on chi-square goodness-of-fit pairwise comparisons. A text entry indicates a significant preference at $p < 0.05$. n.s. = not significant. No entry = not tested due to small sample size.

Species that showed a significant preference for the field were eland, porcupine, steenbok, and wildebeest. Species that showed a significant preference for the relatively dense riverine were baboon, bushbuck, elephant (despite being largely excluded from the riverine in 2009), francolin, impala, warthog, and waterbuck. Aardvark, doves, and kudu showed no significant habitat preference.

Of the species included in these tests, aardvark, banded mongoose, bushpig, doves, francolin, genet, guineafowl, long-tailed starling, small rodents, African grass owl, porcupine, red-billed hornbill, springhare, steenbok, tree squirrel, warthog, and yellow-billed hornbill were photographed apparently or definitely "using" the burrow or its soil fan in some way (Fig. 31). These uses included entering or exiting the burrow, foraging in the soil fan, or using a mound of soil as a lookout. Other species photographed using burrows were African wild cat, brown hyena, honey badger, rock python (the only reptile photographed), slender mongoose, and spotted hyena. In all, 23 types of animals were photographed making use of the burrow or its soil.

Figure 31   Animals making use of aardvark burrows ay Mapungubwe National Park, South Africa. (A) genet, (B) warthog, (C) African grass owl (with its foot on a small rodent), and (D) springhare.

Burrow C1, located in the northernmost section of a former agricultural field, saw frequent activity in all three seasons, despite being relatively isolated from water. To the south of this patch of field lies a mopane forest, and beyond that a rocky area. The field and mopane

forest do not have significant sources of water, and the area is fenced. The closest water source is a small pool in the rocky habitat, several kilometers from this burrow.

In spite of the lack of nearby water, C1 was used by aardvark, brown hyena (scavenging the aardvark), porcupine, steenbok, warthog, python (witnessed entering burrow by author), and banded mongoose. C1's camera also captured pictures of kudu, eland, bat, gemsbok, ground hornbill, secretary bird, red hartebeest, elephant, black-backed jackal, African wild cat, bushbuck, honey badger, and coucal; these species were not photographed "using" the burrow in any way. Aardvarks were photographed at the burrow in all three years. Given that the aardvark seen in 2008 died, this means that at least two different aardvarks used this burrow over the three years.

In 2009, a warthog identifiable by a broken tusk was photographed leaving C1 around dawn on 51 non-consecutive days and returning in the evening on 53 non-consecutive nights between June 30 and September 20, often with several other warthogs. All but one of the evening pictures was followed by a morning picture, but there were occasional gaps in time between a morning picture and the next evening picture. Either the warthogs were sleeping somewhere else or something else triggered the camera and we missed the warthogs' arrival or departure. The camera was removed for the season on 1 October, and it is possible that the warthogs returned after that date. While the camera was active that year, the burrow was also visited by steenbok, porcupines, aardvark, banded mongooses, African wild cat, honey badger, coucal, and black-backed jackal (Fig. 32).

Figure 32   Some of the visitors to and residents of burrow C1, located in a former agricultural field. (A) Porcupines, (B) Aardvark, (C) Steenbok, (D) Warthogs, (E) African wild cat, (F) Black-backed jackal, (G) Banded mongooses, (H) Honey badgers, (I) African rock python. All pictures except (I) are from the camera-traps used in this study; (I) was taken by the author when maintaining the camera-trap.

How well did our cameras capture the diversity of the animals near and away from burrows or in the two different habitats? We investigated this by looking at the number of mammal species captured by each camera.

First, we combined data for all cameras based on the location (each of the four combinations of at and away from burrows in the riverine and the field) and calculated the mean number of species captured by cameras in each location (Fig 33). There were more

species photographed in the riverine than in the field. While they had similar total number of camera-days away from burrows, burrows in the field had about 830 camera-days while the riverine forest burrows had only about 385. The greater number of species captured in photographs despite the lower trapping effort indicates that mammal diversity was greater in the riverine.

Figure 33   Number of identified mammal species per camera location type. Values are mean ± S.E.M. and are not weighted by camera trapping effort (number of days).
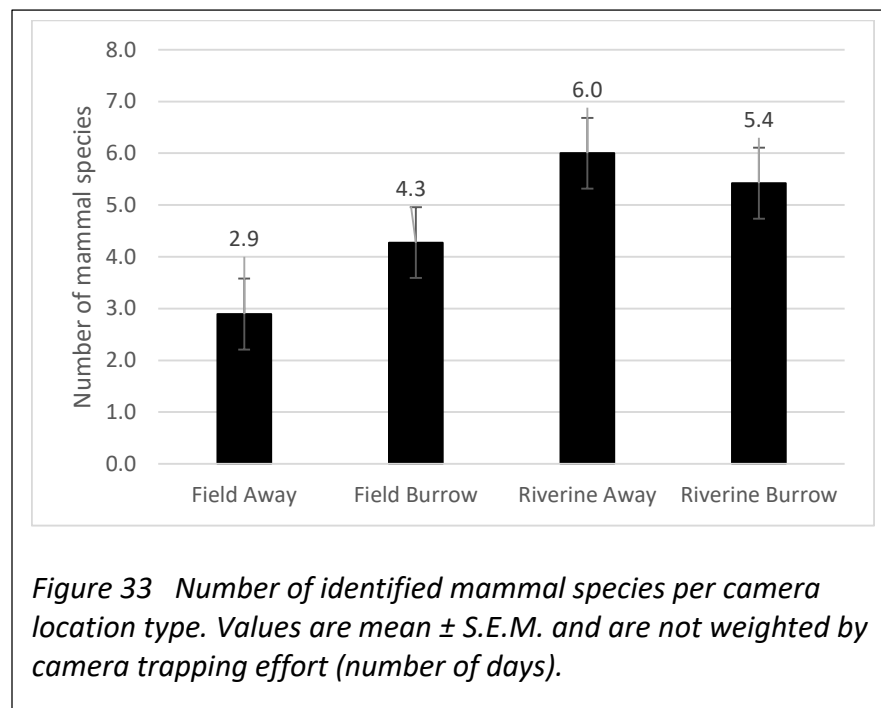
Because of the unequal camera-trapping effort across location types and individual cameras, we also looked into the number of mammal species captured by each camera and plotted that against the number of available camera-days. For this analysis, we added camera-

days and camera-nights then divided by two, to represent the approximate number of 24-hour

units. Figure 34 shows the results of this analysis. Most of the cameras had fewer than 30

camera-days and less than 10 mammal species. However, the few cameras that recorded

activity for longer periods captured more mammal species, with around 15 species captured in

60 or more days. This indicates that to be somewhat confident with the true diversity of

mammal species in this area at this time of year, one must monitor the area for at least two

months.

Figure 34   Number of mammal species versus the number of days (24-hour periods) monitored. Each point represents a single camera. Symbols represent location type.
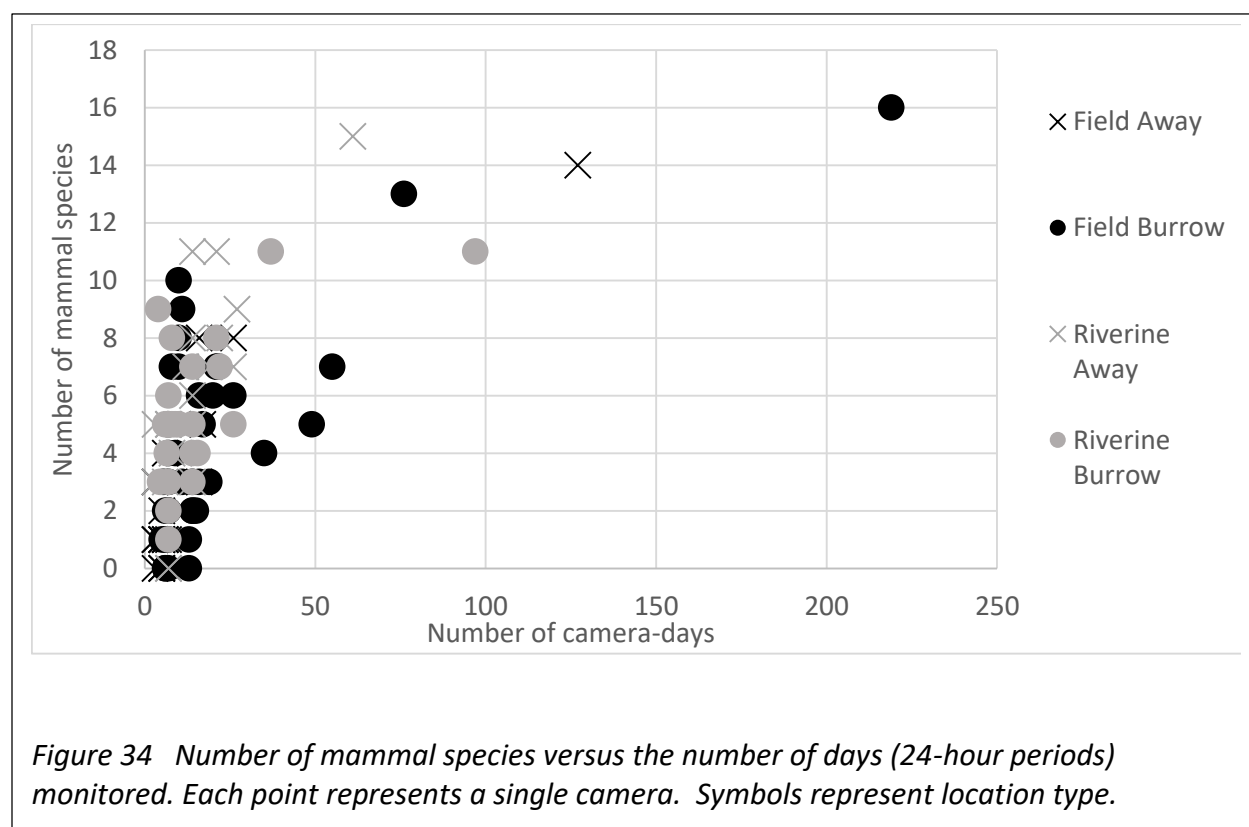
D. Discussion

Aardvark burrows are centers of bird and mammal activity. Nearly all of the cameras in the riverine forest and former agricultural fields captured photographs of animals, and half of those in the sparsely populated mopane forest did. It appears that most of the "burrows" are mere byproducts of the aardvarks' search for subterranean food (Chapter 3 of this document). Aardvarks were not the species making most use of the benefits these burrows provide. Burrow use at MNP can be summarized as "mostly warthogs."

The majority of burrows, as defined here, were used on a weekly and sometimes daily basis by a large number of species. Use of burrows was highly habitat-specific. In the riverine habitat, 23 of 26 (88.5%) randomly monitored burrows showed use during the time we monitored them. In the field, 29 of 42 (69.0%) had active use. In the mopane forest just 7 of 17 (41.1%) were used, and these were used infrequently compared to burrows in the other two habitats. While the aardvarks who dug these burrows likely intended few if any as dens, our hypothesis that they are widely used by other vertebrates is supported.

Many of our monitored burrows not only showed some animal use, but 13 in the riverine (50.0% of the 26 monitored) and 15 in the field (35.7% of the 42 monitored) showed use by more than one species, even in our generally short monitoring periods. The proportion of burrows in use was not significantly different between the two habitats (chi-square goodness-of-fit, p = 0.12). The most extensively monitored burrow, C1, saw definite use by seven different species (aardvark, porcupine, warthog, banded mongoose, python, steenbok,

and brown hyena) and apparent interest by another four (African wild cat, honey badger, black-backed jackal, and coucal), in its 219 days of monitoring across three winters.

Why are burrows in the riverine forest used so much more often than the other two habitats? Part of this may reflect animal activity in general. It stands to reason that if there are more animals present, more will be both attracted to and avoid aardvark burrows. The number of burrows is a similarly obvious factor: more burrows means that the animals present have more to potentially use (and less space in which to avoid them). Aardvark burrows are very clumped in distribution, but are more numerous in the riverine forest than the fields or mopane forest. We found that the mopane forest had about 1.1 burrows/ha, the field 1.8 burrows/ha, and the riverine 4.1 burrows/ha (Chapter III). Yet despite the increased number of available burrows, a higher proportion was used. This must be due to increased animal activity. While we do not have complete census data on the species and numbers present in these habitats, our cameras did appear to reflect the activity we observed. The riverine forest was relatively crowded, the fields less so, and the mopane nearly deserted except for baboons and elephants.

Our camera trap setup limited our ability to definitively determine the full nature and extent of burrow use. While we have many pictures of animals entering, exiting, and looking into the burrow, it is highly likely that we missed other incidents of use. If the camera was triggered, either by an animal or other motion, less than five minutes before the burrow use, we would not have a picture of the activity or even the species. This undoubtedly led to an underestimate of burrow use. For example, the warthog that spent much of our 2009 season using burrow C1 was photographed entering the burrow on 53 non-consecutive nights but only exiting on 51 mornings. On those days, other movement (such as that of vegetation) may have

triggered the camera just before he appeared, and thus we have no record of his exit. Alternately, he may have actually spent the night elsewhere.

While still photos, especially those taken five minutes apart as ours were, do not always provide direct evidence for why an animal chooses to be at or in the aardvark burrow, they can be used to get a decent picture of what may be going on. Our cameras showed ten mammal species, plus unidentified small rodents, definitely or likely using the burrows. Of these, five showed a statistically significant preference to be at burrows. Aardvarks and warthogs definitely use these burrows, but both are highly mobile and thus appeared in many Away pictures as well. Several birds (including unidentified species of doves) were photographed apparently foraging in the overturned soil (or hunting, as in the case of the grass owl in Fig. 4.14c), using mounded soil as a vantage point (e.g., coucal), or both (e.g., long-tailed starlings).

The burrows in this study did not appear to be used as bolt holes. Two pictures showed an animal, one a springhare the other unidentifiable, entering the burrow so quickly as to appear blurry; these may have been cases of the burrow being used as a bolt hole. Rather, the protection offered by burrows is more as temporary shelter rather than emergency escape. This makes sense. Predators could be hiding in the burrow as well as hunting out in the open. Aardvark-dug burrows are large enough to hide many smaller predators such as genets or snakes, and are easily modified into hyena or wild dog dens. Bolting into a burrow for protection from one predator may result in bolting into the mouth of another.

Another possibility for the lack of apparent bolting was the high abundance of prey animals relative to the predator populations. While many predators were photographed near burrows (mongooses, genet, honey badger, brown hyena, spotted hyena, wild cat, jackal, and

python) and others known to live within the park (leopard, visiting wild dogs and lions), they were greatly outnumbered by prey (warthogs, impala and other antelope, monkeys, and more).

To test this, the study should be repeated in a more predator-intensive/prey-poor region. In 2009, we used the same methods to survey the field, mopane, and mixed field-mopane habitats at the Venetia-Limpopo Nature Reserve (VLNR) that lies directly to the south of MNP. The two were separated only by two fences and a two-lane paved road with little traffic. VLNR was eliminated as a site for this study because of the low number of aardvark burrows. This site also had relatively large predator numbers, including lions and wild dogs, and few prey animals (pers. obs.). Because the climate and other factors are the same as at MNP, it could serve as a comparison site.

There is little information on the long-term use of burrows of any species. Evans (2008) found that common wombats (*Vombatus ursinus*) change sleeping burrows every 1–4 days; in that study, burrows were twice as dense as wombats, yet because of wombat movement burrows were used by an average of 2.2 wombats during the study. Finlayson et al (2005) found that southern hairy-nosed wombats (*Lasiorhinus latifrons*) similarly moved frequently between warrens (burrow complexes) and that they occupied 42% of the available warrens over a seven-month period. Grant et al (1992) showed that platypuses frequently share "resting burrows," and do not seem to have a single "home" burrow. Merriam (1971) found that woodchucks similarly move frequently. Holmes et al (2003) monitored burrowing owl (*Athene cunicularia*) nests and burrows over three breeding seasons and found that burrows were reused frequently, though they did not have data on the individual animals using them.

Taylor and Skinner (2003) radio-collared eight aardvarks and habituated two of them for direct observation. They monitored burrow use by three of these, one for three months and two for a year. The aardvarks spent 1–38 days in a given burrow (mean 6.9, 4.9, and 8.6 for the three animals), and the authors noted that when an aardvark moved to a new burrow it usually moved into an existing one within the home range rather than digging a new one. Aardvarks were rarely observed returning to previously used burrows, indicating that there must have been a surfeit of burrows to move among, though available burrows were not counted.

Aardvarks only used our monitored burrows occasionally. None of our monitored burrows appeared to be aardvark sleeping dens at the time of monitoring, with the exception of C1 and its dying occupant in 2008. Species other than aardvarks visited and inhabited the burrows frequently. At least three were used as dens by families of warthogs while being monitored. Given the low density of aardvarks relative to that of other species, and relative to the number of burrows, this is not entirely surprising. Our results support the hypothesis that most of these burrows were dug by aardvarks as onetime feeding digs and then left to be used or not. While aardvarks may re-use feeding digs, the sheer number of burrows dug by aardvarks suggests that few are actually re-used by the aardvarks for any reason. Taylor et al. (2002) observed aardvarks digging short tunnels, up to 2 m in length, solely for feeding purposes, which supports our conclusion that these "burrows," as we have been using the term, are nothing more than the remains of a meal as far as the aardvarks are concerned.

The proportions of burrows used by aardvarks, as compared to those used by any other species, are undoubtedly skewed by the relative populations of the various species. If one were to adjust for per-capita usage, the rates may be very different; however, we do not have the

census data to perform this calculation. An individual aardvark may well dig more burrows than an individual of any other species, but the sheer number of others and the low population of aardvarks makes it appear that aardvarks are not primary burrow users. However, this reinforces the hypothesis that these burrows are of great importance to species other than aardvarks.

Compared to expectations, aardvarks were underrepresented at burrows--they were seen just as often "away" from their burrows as at them. A likely reason is their highly mobile foraging. Another is the fact that a given burrow is probably neither the current den nor useful for foraging because the ant or termite population has not yet recovered from a previous aardvark attack. We do not know how often, if ever, aardvarks revisit previous feeding locations, or visit those dug by other aardvarks. That aardvarks were not preferentially photographed at burrows suggests that the majority of remnant burrows are unimportant to aardvarks while very important to others, such as warthogs and porcupines, that did prefer burrows.

Warthogs were by far the most numerous burrow-users at MNP, and the numbers are even greater when one considers that warthogs live in family groups. Photographs often showed multiple warthogs. Both porcupines and warthogs are capable of digging burrows, but the large number of holes left behind by aardvarks frees these other animals from having to make the effort. It would be interesting to know whether this public good simply makes life easier for warthogs and porcupines or whether this promotes larger population sizes of the two species.

Several antelope species significantly avoided aardvark burrows. The most likely reason is simply that burrows are holes in the ground. As burrows provide no benefit to these animals, the potential trip hazard is enough to make them avoid the immediate area. The trip hazard is paramount when running from predators, a time when one cannot be picky about where they place their feet.

Small rodents were only photographed in 2008. This was likely due to camera positioning. In 2008, we tended to place cameras closer to the ground and burrow entrances than in later years. Moving the cameras a little further away allowed for a more complete survey of the burrow entrance, but may have been too far for such small animals to trigger the cameras. Footprints of small rodents were a common sight at burrows with soft soil fans, and the animals were undoubtedly present.

What we do not know is how applicable these findings are to other aardvark-inhabited areas. MNP has a short history as a wildlife reserve and is bordered and interrupted by agricultural farms. Predators actively avoid humans, while prey species may use us as a "shield" and are quick to recolonize previously human-occupied areas (Berger 2007). One would therefore expect, as we observed, that in a new park such as MNP predators would exist in small numbers. The 2006 census did not count any predators, though rangers were aware of them.

Of the thousands of photos obtained in this study, we only obtained five of brown hyenas (which are mostly scavengers; Mills 1989), one of a leopard, 13 of a single python, 11 of spotted hyenas, two of civets, 18 of genets, six of African wild cats, and seven of honey badgers. Four of the five photos of brown hyenas were taken at the burrow entrance where an aardvark

died, in the week following the death. We found the aardvark remains some distance from the burrow several days later. The skull was crushed and one leg was missing entirely, probably the work of one or more of the brown hyenas.

Despite small numbers of predators overall, many of our photographs of them were near burrows (all 13 pythons, nine of 11 spotted hyenas, one of two civets, all 18 genets, all six African wild cats, two of seven honey badgers, and all five brown hyenas), and several of these were photographed apparently hunting in or around the burrow. This could indicate that burrows facilitate predator diversity as a potential prey source or a den; however, our sample size was too small to determine this. The python was present on the same dates as a family of porcupines, but it had recently eaten and so was not currently a threat. An aardvark had been present four nights before our first picture of the porcupines, and during the day in the same time period a pair of steenbok appeared to be investigating the burrow. There are anecdotes of multiple species sharing aardvark burrows, but this has not been formally documented. We do not know if these species were actually sharing the burrow or just taking turns.

Our cameras were not placed on trails or gathering places such as water holes, and were not baited to attract animals. We placed cameras in places similar to aardvark burrow locations—generally clearings or areas of low vegetation, but not trails. As we were looking at burrow use and avoidance, a full census was not the goal and our inventory should not be taken as such. Predators only appear incidentally in the Away pictures, or at burrows either incidentally or if hunting. The lack of evidence at hunting at burrows in the form of photos or other signs supports the idea that aardvark burrows are neither bolt holes nor ambush points, or that these are minor uses.

Previous studies (Smithers 1971, Whittington-Jones et al. 2011) collectively named 49 vertebrate species or groups associated with aardvark burrows in Botswana (Smithers) or South Africa (Whittington-Jones). We have expanded this list to 59, including the families of doves and francolins. Vertebrate commensals identified in this study are shown in Table IX, and the combined list in Table X. The species we added were mostly smaller mammals (mongooses, squirrels, and springhares) and birds. These species may be quick to leave the area when humans approach, too small to be noticed in the incidental observations employed by both Smithers and Whittington-Jones, too large for the traps set by Whittington-Jones, or some combination of the above. The only large animal we added was the bushpig, which may simply be present in relatively low numbers or be misidentified as the more common warthog when sighted.

TABLE IX
AARDVARK BURROW COMMENSALS IDENTIFIED IN THIS STUDY[a]

Scientific name	Common name
Crocuta crocuta	spotted hyena
dove spp.	dove
Felis lybica	African wild cat
francolin spp.	Francolin
Galerella sanguinea	**slender mongoose**
Genet spp.	Genet
Hyaena brunnea	brown hyena
Hystrix africaeaustralis	Cape porcupine
Lamprotornis mevesii	**long-tailed starling**
Mellivora capensis	honey badger
Mungos mungo	**banded mongoose**
Numida meleagris	**Helmeted guineafowl**
Orycteropus afer	Aardvark
Paraxerus cepapi	**tree squirrel**
Pedetes capensis	**Springhare**
Phacochoerus africanus	Warthog
Potamochoerus larvatus	**Bushpig**
Python sebae	African rock python
Raphicerus campestris	steenbok
rodent spp.	Rodent
Tockus leucomelas	**Yellow-billed hornbill**
Tockus rufirostris	**Red-billed hornbill**
Tyto capensis	**African grass owl**

[a] Bolded entries were not previously reported

TABLE X

AARDVARK BURROW COMMENSALS IDENTIFIED BY SMITHERS (1971), WHITTINGTON-JONES ET AL. (2011), AND THIS STUDY

Scientific name	Common name	Scientific name	Common name
Agama aculeate	ground agama lizard	*Merops pusillus*	Little bee-eater
Bitis arietans	puff adder	*Michaelamys namaquensis*	Namaqua rock rat
Bufo gariepensis	Karoo toad	*Mungos mungo*	banded mongoose
Canis adustus	side-striped jackal	*Mus indutus*	Desert pygmy mouse
Canis mesomelas	black-backed jackal	*Mus minutoides*	Pygmy mouse
Crocodilus niloticus	Crocodile	*Myosorex varius*	Forest shrew
Crocuta crocuta	spotted hyena	*Myrmecocichla formicivora*	anteating chat
Cynictis panicillata	yellow mongoose	*Mystromys albicaudatus*	white-tailed rat
Desmodillus auricularis	Cape Short-eared Gerbil	*Naja nivea*	Cape cobra
Felis lybica	African wild cat	*Numida meleagris*	Helmeted guineafowl
Galerella sanguinea	slender mongoose	*Otocyon megalotis*	Bat-eared fox
Genetta genettta	Common genet	*Panthera pardus*	Leopard
Genetta sp.	Genet	*Paraxerus cepapi*	Tree squirrel
Gerbilliscus brantsii = Tatera brantsii	Highveld gerbil	*Pedetes capensis*	Springhare
Gerbilliscus leucogaster	Bushveld gerbil	*Phacochoerus africanus*	Warthog
Gerbillurus paeba	Hairy-footed gerbil	*Potamochoerus larvatus*	Bushpig
Halcyon leucocephala	grey-headed kingfisher	*Proteles cristatus*	Aardwolf
Herpestes sanguineus	slender mongoose	*Python sebae*	African rock python
Hirundo dimidiate	pearl-breasted swallow	*Raphicerus campestris*	Steenbok
Hirundo semirufa	red-breasted swallow	*Rhabdomys pumilio*	four-striped grass mouse
Hyaena brunnea	brown hyena	Rodent spp.	Rodent spp.
Hystrix africaeaustralis	Cape porcupine	*Saccostomus campestris*	pouched mouse
Ispidina picta	African pygmy Kingfisher	*Thamnolaea cinnamomeiventris*	mocking cliff-chat
Lamprotornis mevesii	long-tailed starling	*Tockus leucomelas*	Yellow-billed hornbill
Lepus capensis	Cape hare	*Tockus rufirostris*	Red-billed hornbill
Lepus saxatilis	Scrub hare	*Tyto capensis*	African grass owl
Lycaon pictus	African wild dog	*Varanus albigularis*	Rock monitor
Mabuya capensis now *Trachylepis capensis*	Cape skink	*Vulpes chama*	Cape fox
Mastomys natalensis	Natal mutimammate mouse	*Xerus inauris*	Cape ground squirrel
Mellivora capensis	Honey badger		

We have no comparative data on the species that actively avoid burrows, either those dug by aardvarks or those dug by any other species. The few studies which do survey burrow commensals focus solely on these commensals. For a complete picture of the impact of burrows, one would need to not only take a complete census of the burrow itself, using a combination of techniques such as pitfall trapping and camera-trapping, but to repeat these methods at some distance from the burrows. One would also need to not just identify species, but to quantify individual numbers and document behaviors. Recording video rather than still pictures, which we did not do due to memory card limitations, is increasingly practical thanks to ever-increasing digital memory capacity at ever-decreasing costs. Most of the species we identified as burrow-avoiders are those which cannot benefit from burrows, such as large antelopes, elephants, and monkeys. Are there any animals that we would think may benefit from aardvark burrows but instead avoid them?

There is always a chicken-egg scenario in studies like ours. Are there a lot of warthogs because the predators have not yet moved in, because there are plenty of ready-made burrows to hide in, or some combination? How much are warthogs maintaining the burrows, and how would things change for other burrow commensals if the warthogs were to disappear? What would happen if the aardvarks were to disappear? Further study would be required to answer these questions.

E. Conclusion

Aardvarks dig a lot of holes large enough for vertebrates to use as a temporary shelter, a long-term den, a food source, or a lookout point. However, the aardvarks themselves appear to

have little use for most of these diggings once they have finished the meal that inspired their

excavation. Aardvarks move among burrows frequently, and often re-use burrows they or other

individuals dug, but it seems that the majority of aardvark diggings are, as far as the aardvarks

ae concerned, just the remains of a meal.

Vertebrates that are not aardvarks, however, make much use of these leftovers.

Warthogs were especially numerous at MNP, though this is likely to be site-specific. Aardvarks

truly are the inadvertent civil engineers of the southern African plains and forests, creating a

public good by creating big holes in the ground that others can use.

The full extent of aardvarks' effects on their community remain unknown, and while we

have expanded the list of commensal species, it too is likely incomplete. A full inventory of

vertebrate commensals would require more extensive camera trapping, physical trapping,

direct observations, and other census methods.

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V. A MODEL OF BEHAVIORAL RESOURCE DEPRESSION AND SLOWLY REGENERATING

RESOURCES

A. Introduction

Foraging and depredating, the acts of searching for, finding, and consuming food involve a number of steps and often complex, if unconscious, decision-making. Foragers and predators must decide what, when, and where to eat as well as how much time and effort to devote to this process, whether to forage with others or alone, and so on. Each facet is itself complex. Do you opt for a higher quality food which may require more risk to acquire, or play it safe but accept a lower-quality food? While it is true that these decisions are not conscious and even made by those with no capacity for conscious thought (e.g., plants, O'Brien and Brown 2008), they are nonetheless complex decisions that can be approximated with mathematical models. The early bird is not doing calculus when deciding to go for the early worm, it just knows that it's time to hunt. The long history of natural selection has left organisms of all types with adaptive foraging behaviors. Foragers behave as if they have done the math.

Food is never uniformly distributed; rather, it is clumped into patches. This is true whether one seeks nutrients in soil, forages for plants, hunts animals, or shops at supermarkets. The quantity and quality of food can vary among patches. Much of the existing work on patch use, both theoretical and empirical, makes the assumption that the food source is passive, politely remaining in place while it is eaten. The exceptions, of course, come when one is looking at predator-prey situations. In these, the prey attempts to evade the predator. But there are other cases in which the food source, be it plant or animal or otherwise, can make itself harder to eat, such as by arming itself with spikes or toxins. Defenses can be permanent,

but defenses, like everything else, require regular energy inputs or incur other costs. It takes a lot of food to avoid becoming food. Some species have instead turned to what we call behavioral resource depression, which is the decrease in the amount or value of a resource (here food) via its behavior. Examples of behavioral resource depression include animal prey hiding or running away, altering behavior as to appear dead and therefore unappealing to a given predator (Sargeant and Eberhardt 1975), and induced chemical responses in plants (e.g., Fraenkel 1959, Karban 1989, Harvell 1990, Walling 2000).

In 1976, Eric Charnov published a short but important paper defining the Marginal Value Theorem (MVT). His model assumed a single predator foraging in a patchy environment with an infinite number of two or more types of patches that the predator did not revisit. Foragers were assumed to have knowledge of the quality of their current patch, the existence of other patches, and the distribution of patch types in the environment (though not the quality of any other individual patch), and thus were able to act optimally. It showed that under these assumptions, a predator should leave a patch when the marginal rate of foraging drops to the average for the environment. That is, once a patch drops below some threshold of quality, a predator should forage elsewhere as the food availability is likely to be higher elsewhere.

The MVT has an important attribute in that the cost of foraging to an individual while in a patch is the missed opportunity of not leaving the current patch and finding another. Hence the benefit to a forager from a patch is the current harvest rate (marginal rate of return) and the cost is the average rate of return from searching for and exploiting a new patch. The key predictions are that a forager should spend more time in a rich patch than a poor patch, it should spend less time in patches of a rich environment than a poor one, and patch residence

time should increase with the time taken to travel to a new patch. Studies of the applicability and accuracy of the MVT followed. Nonacs (2001) noted that in most studies, foragers were found to leave patches sooner than predicted by the MVT.

Charnov et al. (1976) explored the implications of resource depression, which represents the decline in food availability in a patch because it is presently occupied by a forager. They identified three forms of resource depression: exploitation depression, in which prey is consumed by the predator; behavioral depression, in which the prey changes its behavior in a way as to reduce its availability to the predator; and microhabitat depression, in which prey move to another location to avoid predation. Microhabitat depression can be seen as an alternative form of behavioral depression, when the behavior is movement.

Along with resource depression, one must consider recovery of the resource—prey coming back to the location, reverting to pre-predation behavior, and increasing in population. Plants must grow and prey must creep back, seeking the resources they need while trying to avoid the predator. This recovery may be effectively instantaneous, very slow, or anywhere in between. This factor is even more poorly understood than behavioral resource depression. Foraging studies traditionally focus on the choice of a food patch and the food within, but do not consider that patches may be predictably dynamic. In foraging studies, artificial food patches are fully replenished daily, and while a given site may vary day to day, they do not do so in any predictable pattern. In nature, however, food takes time to become available, and in an environment with a limited number of food patches, this recovery time is as important as the initial patch quality. Some work has been done in this area. Brown and Rosenzweig (1986) modeled habitat selection in an environment with slowly regenerating resources, with the

assumption of a traditionally passive food source. Possingham (1992) provided a practical

application of the idea, using hummingbirds foraging on slowly produced nectar. However,

once the nectar was available it simply remained so. As a last example, Watts (1998) found that

gorillas will adjust the length of time between revisits to foraging areas to allow the vegetation

to recover from the previous visit.

Behavioral resource depression, including microhabitat depression, goes hand-in-hand

with slow regeneration of the patch. The decline in prey availability, above and beyond the

decline caused by food being eaten, should lead to a shorter foraging bout than if the prey just

stayed where and how it was. The rate of recovery to the pre-predation state determines when

the patch has recovered enough to be worth foraging again.

The models presented below begin to describe what may happen to prey numbers

during and after predation in a situation involving behavioral resource depression (BRD)

combined with a slowly regenerating resource (SRR). That is, what is actually happening when

food items make themselves unavailable and then take time to return. A major assumption in

our model is that prey will return at a predictable rate. We build a model in four stages,

beginning with the simplest situation, the Marginal Value Theorem, where a lone predator or

forager (we shall use the term "predator" for simplicity) travels among infinite food patches,

predating each until its quality is no longer greater than the average quality of all patches.

Because this is not a new model, we call this Stage 0. Stage 1 adds BRD, and reduces to Stage 0

when the BRD rate is set to 0. Stage 2 adds SRR with unlimited patches. It in turn reduces to

Stage 1 as infinite patches mean that the predator need not return to a patch that has not fully

recovered from previous depredation. Stage 3 introduces a limit to the number of patches such

that the predator may return at some point before the prey number has recovered to its initial level. This is a true model of BRD with SRR, and shows that in time prey will maintain an equilibrium population in hiding (or otherwise unavailable for predation) while available prey numbers vacillate between the predator's giving-up density (GUD, Brown 1988) and some number sufficient for being predated again.

B. The model Stage 0: the marginal value theorem

One can express the Marginal Value Theorem (MVT) in any number of ways, and add parameters as needed. Charnov's model used variables of energy gain and loss along with the proportion of patches of each type. Because our goals involve prey numbers rather than these variables, we will build a new model that will result in the MVT in terms relevant to our interests. We begin with an environment with an infinite number of distinct patches of prey, such as ant hills. Within each patch is a population of prey individuals. There is a single predator that encounters a patch, depredates it to some level, then moves on to another patch with greater prey numbers.

We define the variables as follows: let t be the predation time, starting at 0 when the predator enters the patch and maximizing at t^*, the time when the predator leaves the patch (quitting time); let T be the average time taken to travel between patches; and let N be the number of prey; let h be the predator's instantaneous harvest rate, the rate at which the predator is consuming prey at time t; let H be the average harvest rate for the set of patches under consideration; let a be the attack rate (Hassell 1978; also called encounter probability, Brown and Mitchell 1989), which is the probability that a predator will encounter and consume

prey within a given time step; and let N be the number of prey, where N_0 is the number of prey at time 0, and N_t is the number of prey available at time t. Table XI presents these variables for easy reference.

TABLE XI	
VARIABLES USED IN STAGE 0	
Variable	**Definition**
h	instantaneous harvest rate
H	average harvest rate
a	attack rate
t	time
T	time to travel between patches
t^*	patch quitting time
N_0	initial number of prey
N_t	number of prey at t

If the predator's attack rate a, is constant, then the predator exhibits a linear Type I functional response. Its instantaneous harvest rate is simply the encounter probability multiplied by the current number of prey within the patch. The number of prey items remaining at time t will follow an exponential decay curve. Therefore,

$$h = aN_t$$

and

$$N_t = N_0 e^{-at}$$

Under the assumption that patch depletion only occurs through the predator's harvest (no behavioral resource depression), the predator's instantaneous harvest rate, *h*, is also equivalent to the instantaneous rate of decline of prey items within the patch. Therefore,

$$h = -\frac{dN_t}{dt}$$

The predator's average harvest rate, *H*, includes both the time spent harvesting a patch, *t*, and the time taken to travel to the patch, *T*. *H*, at time *t*, can be expressed as the number of prey items consumed (the number of initial prey items minus those remaining at time *t*), divided by the elapsed time (*t* plus the time taken to get to the patch, *T*).

$$H = \frac{N_0 - N_t}{t + T}$$

To maximize its average harvest rate, the predator should quit the patch when the instantaneous harvest rate equals the average harvest rate for the entire area; that is, when *h* = *H*. This time we call t^*.

The MVT states that a predator should quit a patch when:

$$h = -\frac{dN_{t^*}}{dt} = \frac{N_0 - N_{t^*}}{t^* + T} = H$$

Note that we have not actually solved for t^*. The best we can get is a fairly uninformative transcendental equation. Remember that N_t is a function of *t* and therefore must not be treated as a constant.

$$t^* = \frac{N_0 - N_{t^*}}{aN_{t^*}} - T$$

We now derive the MVT mathematically. The first step (first order necessary condition) for finding the t^* that maximizes H is taking the derivative of H with respect to t and setting the equation to zero. This yields:

$$\frac{dH}{dt} = \frac{-\frac{dN_{t^*}}{dt}(t^* + T) - (N_0 - N_{t^*})}{(t^* + T)^2} = 0$$

Rather than solving for t^*, we solve for $-dN_t/dt$, which, as defined above, is equivalent to h. In this case, it is not the actual quitting time that is of interest, but the relationship of other variables at this time.

Simplifying leads to

$$-\frac{dN_{t^*}}{dt} = \frac{N_0 - N_{t^*}}{t^* + T}$$

and as we saw above,

$$h = -\frac{dN_{t^*}}{dt} = \frac{N_0 - N_{t^*}}{t^* + T} = H$$

Which is the Marginal Value Theorem (MVT). In this formulation we have assumed that all patches begin with the same quality. The MVT can be extended quite easily to include a variety of different patch types that vary in initial prey abundance. Each patch will have a unique t^* that increases with increasing N_0, but the first order necessary condition remains: Leave each patch when $aN_t = H$. This means that if the encounter probability is the same for all patches, then all patches will be left at the same final density of prey N^*. This N^* is known as the giving-up density (Brown 1988).

The MVT, as stated, is incredibly simple and, like any simple model, makes many unrealistic simplifying assumptions. However, it has been shown to be surprisingly robust as it is

and can be readily modified to include some more realistic assumptions (e.g., Pyke 1978, 1984; Zimmerman 1981; Cibula and Zimmerman 1984; Pleasants 1989; Kelly 1990; Brown 1992; Brown et al 1992; Wajnberg et al. 2000; Nonacs 2001; Hayden et al 2011). More recently, much work has been informed by Bayes' Theorem (e.g., McNamara et al 2006), but the MVT remains a good basis for considering optimal behavior.

What happens to the MVT model when including behavioral resource depression and the slow regeneration of resources? We shall form our model in two stages: first by considering BRD only, then adding in a regeneration time component. Other assumptions of the original MVT remain. This is a general model, but for ease of language we shall think of our predator as a solitary predator who moves from patch to patch of prey, and that prey are individuals who are able to hide from the predator but remain within the patch.

C. The model Stage 1: behavioral resource depression

As with the basic MVT, assume a system with one forager and numerous prey distributed in patches. We still have just one patch type. The forager consumes prey until their average harvest rate, H, declines to some value; again, at this point dH/dt will be zero.

However, now the prey has some behavior which renders them unavailable to the forager, whether by hiding, initiating chemical defenses, or something else. Let this rate of "decay" be a constant, z. Assume that prey will depress their availability to the predator immediately upon the predator's entry into the patch, and continue to do so until the predator leaves. Therefore, throughout the foraging bout, the number of available prey will decline due to both being eaten and their own behavior. Table XII provides all variables used at this point.

TABLE XII
VARIABLES USED IN STAGE 1

Variable	Definition
h	instantaneous harvest rate
H	average harvest rate
a	attack rate
z	behavioral depression rate
t	time
T	time to travel between patches
$t*$	patch quitting time
N_0	initial number of prey
N_t	number of prey at t

The rate at which prey are consumed (h) is now affected by both the attack rate (a) and the BRD rate (z). This harvest rate is now a linear ratio of the predation rate to the total resource depletion rate ($a/(a+z)$). N_t is the number of prey available to the predator, which in this scenario is less than the total number of prey alive; N_t decreases exponentially as before, now at a rate of $(a+z)$. To avoid introducing more variables, we can call the total number of prey unavailable to the predator ($N_0 - N_t$). The fraction of prey unavailable to the forager due to BRD is $z/(a+z)$ and the fraction of those unavailable due to having already being eaten is $a/(a+z)$.

Number of prey consumed:

$$\frac{a}{a+z}(N_0 - N_t)$$

Number of prey hidden (alive but unavailable):

$$\frac{z}{a+z}(N_0 - N_t)$$

So

$$h = \frac{a}{a+z}N_t$$

and

$$H = \frac{a}{a+z}\frac{N_0 - N_t}{t+T}$$

where

$$N_t = N_0 e^{-(a+z)t}$$

Once again, to find the relationship of the parameters at the time at which a forager should leave the patch (t^*), we take the derivative of H with respect to t and set the equation to zero. As before, we leave dN_t/dt alone for now.

Rearrange H:

$$H = \frac{aN_0 - aN_t}{(a+z)(t+T)}$$

Differentiate with respect to t (t^* here because we are ultimately looking for t^*):

$$\frac{dH}{dt} = \frac{(a+z)(t^*+T)\left(-a\frac{dN_{t^*}}{dt}\right) - (aN_0 - aN_{t^*})(a+z)}{(a+z)(t^*+T)(a+z)(t^*+T)}$$

Simplify:

$$\frac{dH}{dt} = \frac{\left(-a\frac{dN_{t^*}}{dt}\right)}{(a+z)(t^*+T)} - \frac{-(aN_0 - aN_{t^*})}{(a+z)(t^*+T)(t^*+T)} = \frac{\left(-a\frac{dN_{t^*}}{dt}\right)}{(a+z)(t^*+T)} - \frac{H}{(t^*+T)}$$

$$H = -\frac{dN_{t^*}}{dt}\left(\frac{a}{a+z}\right)$$

$$-\frac{dN_{t^*}}{dt} = \frac{H(a+z)}{a} = \frac{N_0 - N_{t^*}}{t^*+T}$$

To find the actual patch quitting time, we substitute for -dN_t/dt:

$$\frac{dN_{t^*}}{dt} = -N_0(a+z)(e^{-(a+z)t^*})$$

Simplify to isolate t^*. This equation is transcendental because N_t contains t, so it cannot be solved analytically.

$$t^* = \frac{N_0 - N_0 e^{-(a+z)t^*}}{(a+z)N_0 e^{-(a+z)t^*}} - T$$

$$t^* = \frac{N_0 - N_{t^*}}{N_{t^*}(a+z)} - T$$

We can use a spreadsheet to find close approximations for t^* under various scenarios. Using the same values, we can compare to the MVT. Figure 35 is a general graph of prey consumed, still available, and in hiding over time, under both the MVT and our Stage 1 model. The exact shapes of the curves vary with the values used, but this is the general form.

Figure 35   General form of the changes in prey number over time using the Marginal Value Theorem (MVT) and Stage 1 Behavioral Resource Depression (BRD).
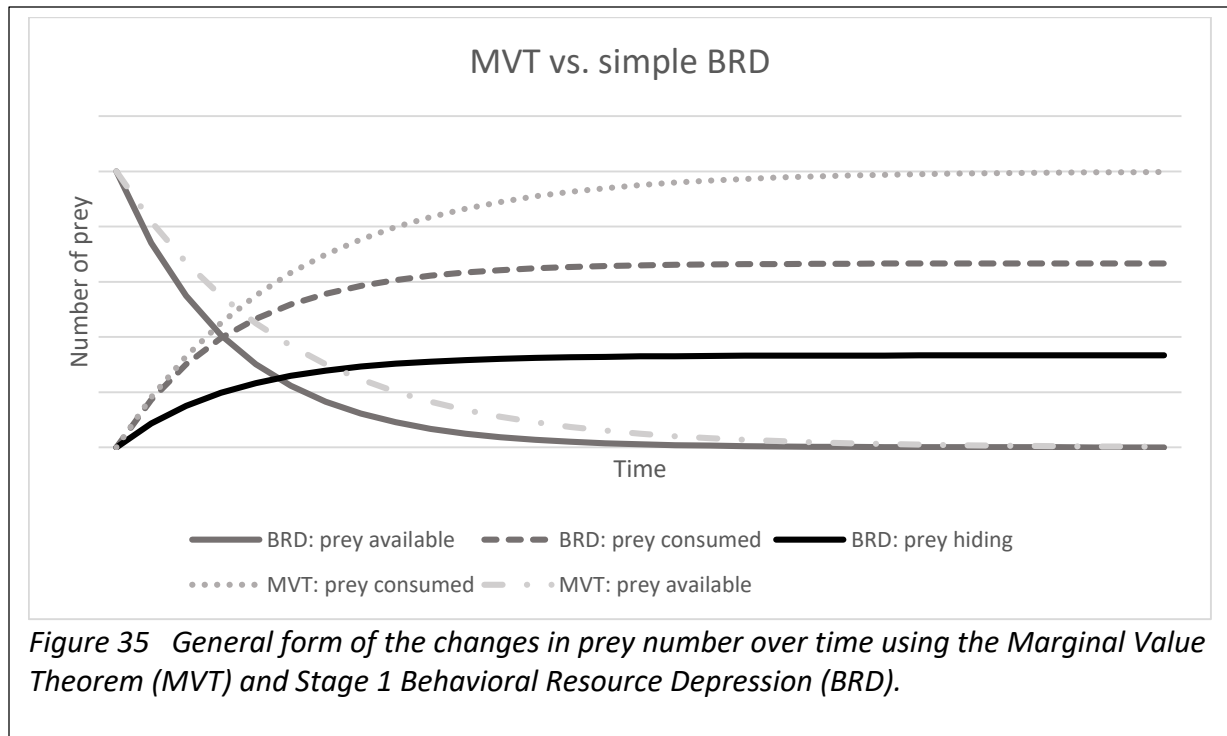
Both the MVT and our Stage 1 BRD model predict a simple exponential decay in the number of prey available, and an exponential increase in the number of prey consumed. The BRD adds another exponential curve, the number of prey alive but unavailable (hiding).

In general, the number of prey consumed under BRD is less than the number predicted by the MVT. Similarly, the time spent in a patch is also less under BRD than predicted by MVT. This remains to be tested empirically, but it makes sense: if prey are actively leaving the patch, their available population will more rapidly decrease the predator's harvest rate to the quitting point.

D. The model Stage 2: behavioral resource depression with slowly regenerating resources, infinite patches

Stage 1 only covered what happens in a single patch during a single bout of foraging. However, foragers do not just use one patch, and patches do not just get visited once. While the forager moves on to a new patch, the recently exploited patch begins to recover. In most cases, this recovery happens much more slowly. A foraging bout may last minutes or hours, but recovery may take weeks or months. Therefore, the next stage of building our model is a patch recovery time. The patch recovers in two ways: some of the prey that were unavailable return to availability, and new prey are born or grown.

At the time the predator is done with the patch, t^*, there are N_{t*} prey remaining available to the predator. Because we are now considering time beyond that spent in the patch along with the number of prey available at foraging's end, let us now call this N^*.

The actual prey population size is N^* plus the quantity of prey alive but unavailable to the forager due to hiding.

$$N = N^* + \frac{z}{a + z}(N_0 - N^*)$$

What happens to the populations both available for foraging and in hiding as time passes? Assume that during foraging, the prey can either be eaten or go into hiding. Once the forager leaves the patch, the prey stop going into hiding ($z = 0$) and begin to return to being available at some rate. Let r be the rate at which the prey return from hiding; They also begin reproducing at a rate we shall call b. Let f represent the time since t^*, and N_f be the number of prey potentially available to predators at time f.

Assume that the forager moves between patches in a regular pattern; that is, the time between visits to any given patch will be the same as for all other patches. Previous variables and assumptions about patch quality hold. Variables are presented in Table XIII.

Variable	Definition
h	instantaneous harvest rate
H	average harvest rate
a	attack rate
z	behavioral depression rate
t	time
T	time to travel between patches
t^*	patch quitting time
N_0	initial number of prey
N_t	number of prey at t
N^*	available prey at t^*
N_f	available prey at f
M	prey in hiding; same subscripts as N
$M^\dagger$	equilibrium prey in hiding
b	prey birth rate
r	prey return rate
f	fallow time (time after predation)

TABLE XIII
VARIABLES USED IN STAGES 2 AND 3

The number of prey items available at any time between the end of foraging and being ready for the next round is the number available at the end of foraging (N^*), plus those which have hidden and then returned from hiding, plus new prey born:

$$N_f = N^* + \frac{z}{a+z}(N_0 - N^*)(1 - e^{-rf}) + bf$$

Each patch has two "pools" of prey: those available to the forager, and those hidden. Assume that at time 0, the patch has N_0 prey in the available pool, and 0 hidden. As the forager visits, N will decrease based on both attack rate a and BRD rate z, as described above. At time t^* the predator leaves to find another patch. At this time, there are N^* prey available in the first patch. Let M be the number of prey in hiding, with subscripts indicating the time as with N. Assume that prey in hiding are non-reproductive.

At time t^*:

$$M_{t^*} = (N_0 - N_t)\left(\frac{z}{a+z}\right)$$

As soon as the predator leaves the patch, prey regeneration begins. This happens in two parts: some of the hidden prey come out of hiding (rate r), and reproduction resumes (b births per time step). The rate at which prey in hiding return to the available pool is constant at rf. This means that the number of prey returning from hiding will increase exponentially. Let the number of new prey born per time step remain constant; therefore, the number of prey added to the available pool will be bf.

Let N_r be the number of prey returning to the available pool from hiding, where:

$$N_r = M^*(1 - e^{-rf})$$

The number of prey still in hiding at time f is the number in hiding at time t^* minus the number that have returned to availability:

$$M_f = M^* - N_r$$

The number of prey available to the predator at time f is the number available at t^*, plus the number which have returned from hiding, plus the number born.

$$N_f = N^* + N_r + bf$$

Note that in the above equation, N_f contains itself, making the equation again transcendental and not solvable by analytical methods.

$$N_f = N^* + \frac{z}{a+z}(N_f - N^*) + bf$$

Consider the limiting case where at the end of fallow time, f, all hidden prey have returned and are once again available. That is, as f goes to infinity. In this case, $N_f = N_0$ when the forager returns and therefore subsequent visits will start with the same conditions as Stage 1 and all we have done is to track the patch recovery.

To show that a sufficiently long f will result in the same situation as with infinite patches, we solve for N_f:

$$N_f = N^* + \frac{bf}{1 - \dfrac{z}{a+z}}$$

The time it takes to make the rounds of all available patches is the time to use each patch plus the time travelling between them times the number of patches (minus the focal one): $(t^* + T)(n-1)$. This equals the fallow time for a given patch.

$$f = (t^* + T)(n - 1)$$

So now the harvest rate is

$$H = \frac{a}{(a+z)}\left(\frac{(N_f - N^*)}{(t^* + T)}\right)$$

As before, we can take the derivative with respect to t to find t^*. And again we can

instead solve for dN_f/dt to find the conditions for t^*

$$\frac{dH}{dt} = \frac{a}{a+z}\left(\frac{\frac{dN_f}{dt} - (N_f - N^*)}{t^* + T}\right) = 0$$

and

$$\frac{dN_f}{dt} = \frac{N_f - N^*}{t^* + T} = \frac{a+z}{a}H$$

This is the same as Stage 1 as expected, confirming that with this model, sufficiently

long fallow time due to a large number of patches is effectively the same as having infinite

patches. Note that this formulation allows for some individual prey to remain in hiding

indefinitely so long as the birth rate is sufficiently high. Figure 36 is a general representation of

prey numbers under this Stage 2 model.

Figure 36   General form of the prey numbers under behavioral resource depression (BRD) with slowly regenerating resources (SRR).
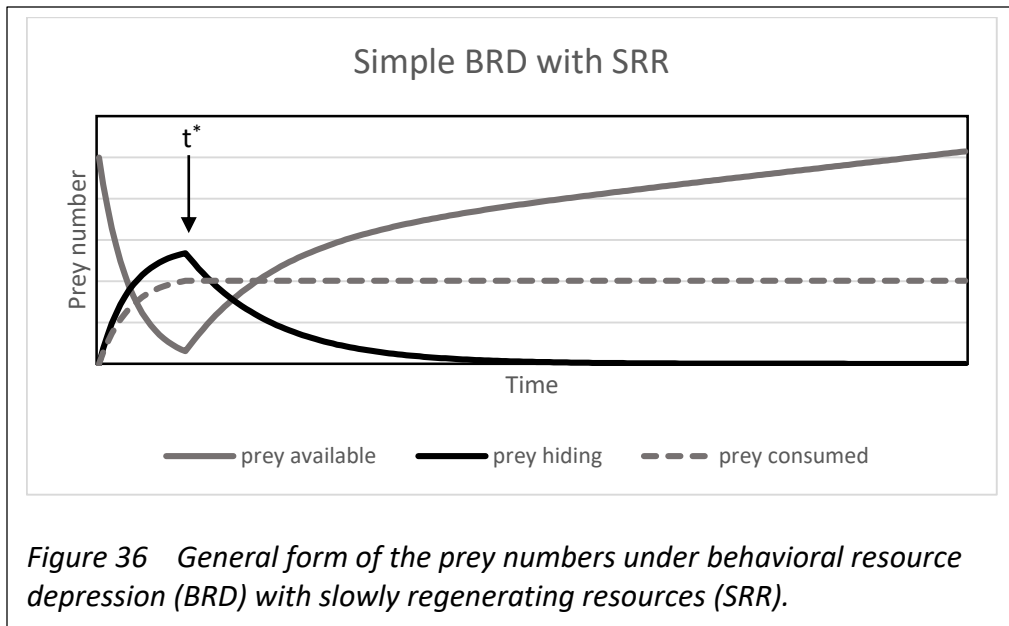
As seen in Fig. 36, the number of prey consumed remains exactly the same as in Stage 1.

During foraging, prey available and prey hiding change exponentially, again as in Stage 1. It is at

time t^* that things change. At this point, the trends of prey available and prey in hiding reverse:

prey in hiding decrease exponentially as individuals return to availability, and prey available

increase by not just that number but also by the birth rate. Eventually, if left undisturbed long

enough, the patch will return to its pre-foraged state (or better). When the forager does return,

the cycle begins anew. With infinite patches, there is no real effect of slow regeneration as far

as the forager is concerned—there is always another patch to exploit. But in reality, patches are

not infinite, and the time it takes for resources to regenerate becomes significant.

E. The model Stage 3: behavioral resource depression with slowly regenerating resources, limited patches

A slightly more realistic, and therefore complex, situation is one in which the amount of time the patch takes to recover to its initial population is longer than the fallow time—that when the patch is foraged again there may be prey still in hiding, an insufficient number of births, or both. In keeping with our stepwise approach, we maintain all previous assumptions, except we now limit the number of available patches so that the fallow time between visits is less than the time required for all prey to come out from hiding and the population to fully recover. Because this gets very complicated very quickly, we shall describe the Stage 3 model without attempting to explicitly solve it.

This iteration of the model begins as in Stage 2. However, we now allow f to be sufficiently small that $N_f < N_0$. At some threshold N, the prey numbers are again sufficiently high for the predator to return. Despite the patch being less-populated than at the first visit, there are enough prey, and too few patches, available, so the patch will be preyed upon before it has fully recovered. Predation and recovery proceed as before, though predation will be completed in less time because the starting prey number is lower, but the quitting number is presumably similar to the first round. Figure 37 is a general graph for Stage 3.

Figure 37   General graph of behavioral resource depression (BRD) and slowly regenerating resources (SRR) with a limited number of patches.
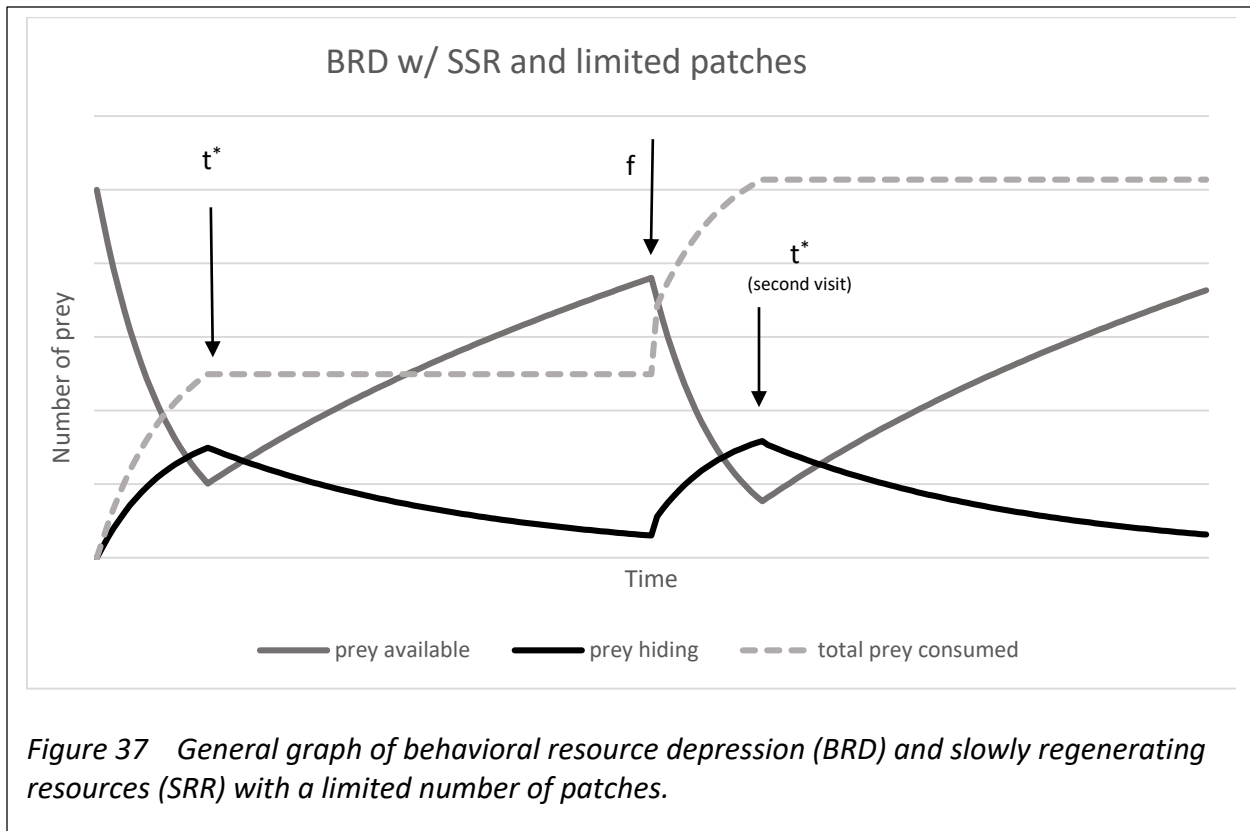
Initially, prey numbers change as before: exponential increases in the number consumed and in hiding, and an exponential decrease in the number available. At t^*, recovery begins as in Stage 2. At time f, the cycle begins again. In the example in Fig. 3, the patch had not completely recovered before the second visit (otherwise it would collapse to the earlier-stage models) and the forager exploits the patch to a lower number of available prey than in the first round. Then, at the second t^*, recovery begins again. As long as the patch is not foraged too low to recover, and is allowed to recover sufficiently between foraging bouts, this can go on indefinitely.

At some point, the system should reach an equilibrium, which will include an equilibrium M, which we call $M^\dagger$. That is, over time the patch will vary in available prey numbers but the addition of new prey to the "hidden" pool will be balanced by those going back to the "available" pool. As with all other outcomes, the number of rounds this will take will depend upon all parameters.

Figure 38 is a simplified schematic of the prey pools at various times.

Available
Hidden

$t = 0$

N_0

0

Available
Hidden

$t = t^*$

N^*

M_{t^*}

Predation

Available
Hidden

z

a

$t = f$

Available
Hidden

N_f

M_f

Recovery

Available
Hidden
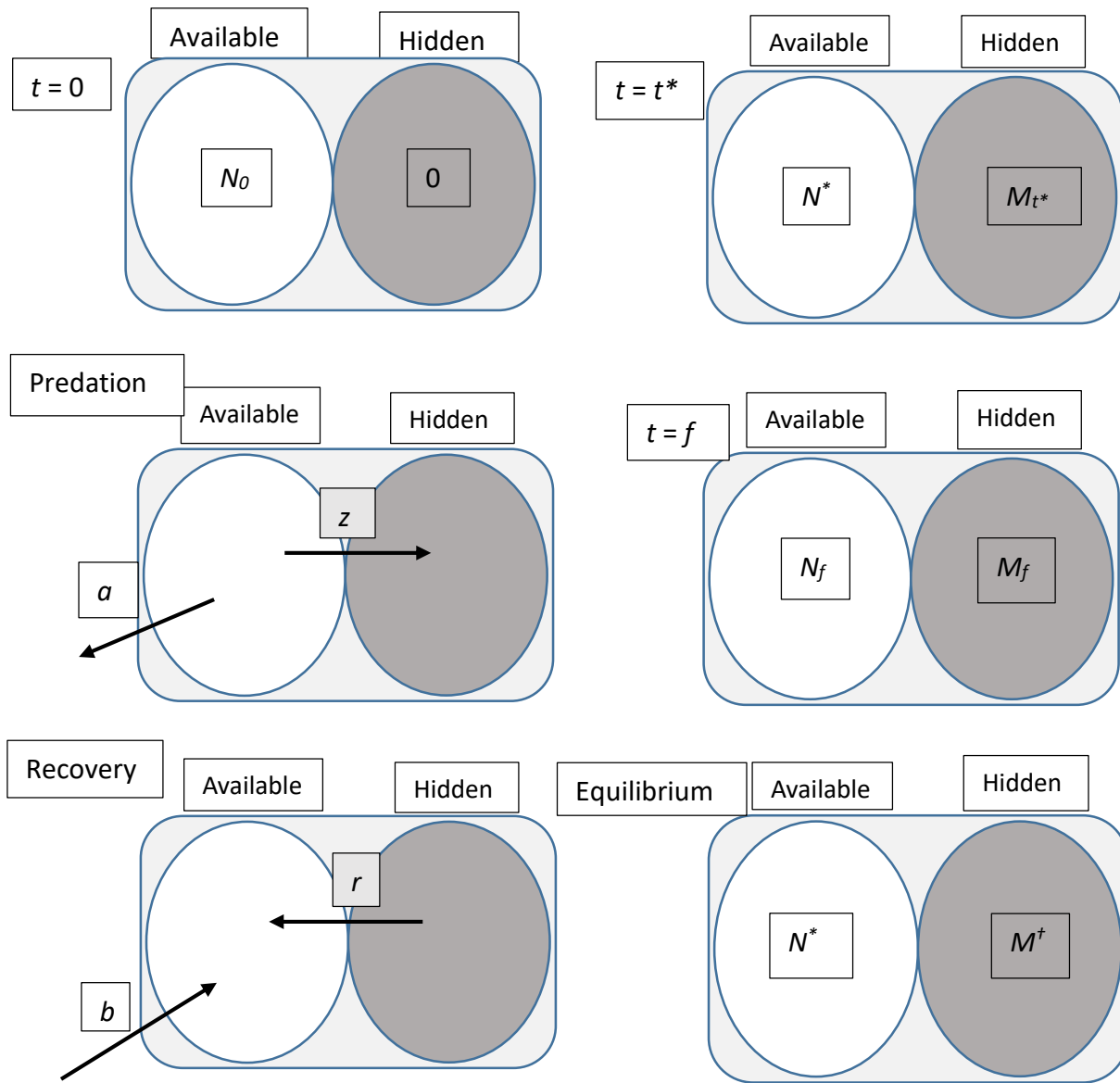
r

b

Equilibrium

Available
Hidden

N^*

$M^\dagger$

Figure 38   Summary schematic of prey numbers and movement between "available" and "hidden" pools. t = time; t* = patch quitting time; f = fallow time; N = available prey number; M = hidden prey number; a = predation rate; z = behavioral depression rate; b = prey birth rate; r = prey return rate.

F. Discussion and Conclusion

Our models, based on simple additions to the Marginal Value Theorem, are a first-round attempt at modelling the very complex system of foraging or predating in a patchy environment where the prey actively make themselves unavailable or less desirable to the predator, then take time to return to the previous state. These models assume that food patches do recover from predation at a slow but predictable rate. Though it is not part of the model, there is also the assumption that when the predator leaves the patch, there are enough remaining prey to recover from predation; future expansion of the model should include this threshold population explicitly.

The models presented here represent a very simplified idea of how behavioral resource depression, coupled with slowly regenerating resources, can affect a foraging animal. There are unlimited ways in which these models can be expanded. However, before creating more-complex models and working through them, we should perform some empirical tests to see if the above models generally hold. We can make numbers do anything, but prey is much more difficult. This model was inspired by the system of aardvarks preying upon ants and termites. The prey can both hide in deeper areas of the nest and replace some individuals with toxin-laden soldiers. These soldiers are presumably a lower-quality food and thus the patch quality is decreased. Once the aardvark leaves, the nest begins to return to normal. The recovery process is much slower than the predation. Aardvark predation on ants lasts at most a few minutes (Taylor et al. 2002), but ant nest recovery takes considerably longer. The figures generated here compress the recovery time. In reality, f should be several orders of magnitude larger than t.

Along with a thorough exploration of the scenario presented in Stage 3, one could create a dynamical game in which the prey modulates its behavioral depression, return from hiding, or both, depending on the aggressiveness of the forager, and in which the forager modulates its aggressiveness in response to prey behavior. One may also consider multiple prey or patch types. Eventually, any good model must drop the assumption of optimality so as to better reflect a world where no one is omniscient. This can be done using Bayes' Theorem, in which probabilities depend on previous observations rather than some external "true" probabilities (McNamara et al 2006).

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VI. THE ROLE OF HUNGER IN A PREDATOR-PREY FORAGING GAME

A. Introduction

1. Foraging

Few things are as important to an animal as food. Another is to avoid becoming food. Foragers must constantly assess their situation, considering their own state (whether energy or hunger), the potential for being preyed upon, the direct and indirect energetic and missed opportunity costs of searching for and eating food, and the benefits of consuming the food. What appears to be a simple decision—should I go eat something?—is actually complex, though this complexity is not conscious (Sih 1980, Lima et al. 1985, Brown et al. 1999, Stephens 2008, McArthur et al. 2014). Researchers have been investigating how costs and benefits play into a forager's decisions of when, where, and how to forage, and for what and how long, with both theoretical and empirical approaches (Stephens et al. 2007).

Theoretical approaches to foraging questions include mathematical models. Traditional models begin with the optimization of a single factor, then build to include more complexity. Generally, this means that all factors except the one under study remain static. Even when multiple factors are considered, the model may remain static; that is, the values of each factor do not change over the time covered.

Foraging, however, is not done in a vacuum. When a forager goes out in search of food, it is not the only individual making decisions. The forager's decisions and outcomes are influenced by actions of other individuals—their prey, predators, or both. Foraging in fact is a game with multiple players, each with multiple possible strategies; each player's best strategy is

influenced by the strategies of the others, and strategies can change over time (see Vincent and Brown 2005). Among the many factors that go into foraging decisions is hunger. Simply put, hungry individuals will take greater risks than those who do not need to eat any time soon (Lima and Valone 1986). Hunger can strongly affect immediate foraging decisions (e.g., Whitham and Mathis 2000) and even future decisions by affecting learning ability (Marsh et al. 2004).

Game theory allows us to develop and explore many ideas about how individuals and populations may interact while making their own foraging decisions. As with traditional models, one must begin with a very simple situation.

We developed a two-player game exploring how hunger affects immediate foraging decisions made by a forager and its predator. We rely on simple assumptions to greatly simplify the game and to permit analytic, generalizable results. As our model system, we use a real, well-studied foraging game played every night—that between gerbils searching for seeds and owls hunting for gerbils.

2. The real-world inspiration

In the deserts of the Middle East, foraging games in which gerbils forage for seeds and both owls and snakes hunt for gerbils unfold every night (Brown et al. 2001). The gerbils are safe in their burrows, but face danger from owls when foraging out in the open, and snakes when foraging under bushes. The two predators essentially help one another: when gerbils hide from owls, they are in snake territory, and when running from snakes they end up out in the open, where owls can easily spot and capture them.

This game of predator facilitation (Kotler et al. 1992, 1993) has been explored for many years, notably by Brown et al. (2001) who modeled a game between gerbils and their predators with a focus on the pulsed (regularly renewed *en masse*) gerbil food. Bouskila (2001) explored habitat selection of kangaroo rats facing the risk of predation by both owls and snakes. These two papers followed a tradition of predator–prey games begun by Brown and Vincent (1992) and Hugie and Dill (1993). The first predator–prey models were created in the early 20th century by AJ Lotka and V Volterra; game theory was first applied to evolutionary biology in 1961 by Lewontin, and Maynard Smith (1974) neatly outlined evolutionary game theory and thus paved the way for these dynamic models, in which the players actively influence one another.

In our real-world example, gerbils who are not hungry will stay in the burrow, but hungry gerbils must take the risk of foraging (e.g., Lima et al. 1985). In turn, the owls and snakes expend energy and take risks in hunting gerbils, and have no reason to do so unless a) there are gerbils to hunt, and b) they are sufficiently hungry so as to be willing to take the risks. As implied by b), this is a state-dependent game, as the energetic state (hunger level) determines the players' motivation to forage and the payoffs associated with acquiring food (predator) or suffering mortality (prey).

We created, from scratch, a model of the effects of hunger on foraging decisions. We asked how the hunger level of foragers (prey gerbils and predator owls) dictate each other's foraging outcomes and fitness. While the game played in the gerbil–owl system has been the basis for both practical and theoretical work, we chose to use this game as inspiration for a more general foraging game in which the hunger state of the players is the primary driver of foraging strategy decisions.

B. The models

Stage 1: The matrix

For this model, we assume a one-predator–one-prey system. For simplicity of terminology, we have chosen to use owls as our example predator and gerbils as our example prey. However, this model is not meant to apply specifically to this system, and is thus kept general in form. For this game, payoffs are measured as net change in hunger state. Evolutionary games generally have fitness, a measure of reproductive success, as the ultimate payoff, but here we chose the more immediate payoff of survival until the next day.

We built our model one step at a time, beginning with no state-dependence. For this stage, we used a two-player binary non-zero-sum matrix game. That is, there are two players (owl and gerbil), each with two possible strategies (forage or do not forage), the sum of the payoffs to each is variable, and the game can be described mathematically using a matrix.

Variables (see Table XIV for definitions) were not assigned variables or even ranges of variables, with the exception of any probability variables, which were constrained between zero and one (inclusive or exclusive depending on the variable). All other variables were assigned values for simulations as needed to meet the assumptions of the model or the conditions of the simulation; some values were chosen to create a representative graph of the expected outcome.

TABLE XIV
VARIABLES USED IN STAGE 1

Variable	Definition
k	cost of foraging
f	gain from foraging
d	probability owl will kill gerbil
p	probability gerbils forage
q	probability owls hunt
λ	net payoff
T	time at game termination (i.e., number of iterations)
Subscript g	variable applies to gerbil
Subscript b	variable applies to owl

The players are populations of gerbils and owls. Each can decide whether or not to forage (or hunt), and face some probability of success as well as some costs of foraging. With predators on the hunt, it seems gerbils would prefer to stay in their dens. However, gerbils are generally unable to store much food, and so must venture out into their dangerous world to avoid starvation. For our model, we assumed that no food is cached. Those who do not forage incur no foraging costs, but do experience a decline in their health state. The choice of whether to forage or not is influenced by the player's own state, the probability of success, and the costs of foraging. The optimal strategy for each may be pure (always forage or never forage) or mixed (forage sometimes). A pure strategy is when every player does the same thing every iteration of the game. For our gerbils, that means always forage ($p = 1$) or never forage ($p = 0$). A mixed

strategy is when the player sometimes forages and sometimes does not, which means any value of $0 < p < 1$. A mixed strategy is represented by the proportion of time an individual plays each of its available strategies. A mixed strategy can also be the proportion of a group of players on the same "team" that are playing each strategy. In our scenario, gerbils and owls can also be thought of as playing as teams; as long as each team divides its players in the right proportions the game works the same way. This is because it's not really players we are concerned with but strategies. If the ESS requires that the gerbils be at $p = 0.3$, then gerbils must, as a whole, forage 30% of the time. While it certainly matters for real gerbils, mathematically it makes no difference whether 30% of individuals forage all the time and the rest never forage, each individual forages 30% of the time, or something else. Because food is needed by each individual, we can assume that in this model the mixed strategy applies to each individual.

The net gain or loss is known as a payoff. To explore the game, we can construct a payoff matrix with both players' payoffs for each possible strategy. Here we use two matrices, one with the payoffs to the gerbil, the other with the payoffs to the owl. The entry for each cell of the matrix contains the payoff to the given player if the gerbil plays the row strategy and the owl plays the column strategy. Therefore, the payoff to the gerbil when it does not forage and the owl does not hunt is 0 (Fig. 39).

(a)		Owl strategy	
		Do not hunt	Hunt
Gerbil strategy	Do not forage	0	0
	Forage	$f_g - k_g$	$f_g - k_g - d_g$

(b)		Owl strategy	
		Do not hunt	Hunt
Gerbil strategy	Do not forage	0	$-k_b$
	Forage	0	$f_b - k_b$

Figure 39   Payoff matrix for Stage 1 game. (a) Payoff to the owl; (b) payoff to the gerbil. Variables are as defined in Table XIV.

The expected payoff is the sum of the payoffs in each possible scenario (gerbil foraging, owl not hunting; gerbil foraging, owl hunting; etc.) at the proportions of time at which each occurs. Each player wants to maximize its own payoff, but their options are limited by what the other player is doing. If the owls are hunting, the gerbils cannot get the payoff they would if owls were not hunting.

The set of strategies at which the model will settle over time is known as the evolutionarily stable strategy (ESS). When the system is at an ESS, neither player (or team) will change their strategy; any slight change in strategy will lead to a poorer outcome. The set of strategies at an ESS are said to be un-invadable, as a newcomer with a different strategy will be unable to successfully invade the system (Vincent and Brown 2005).

ESS always involve both players—gerbil strategies are influenced by owl strategies and owl strategies are influenced by gerbil strategies. A strategy cannot be an ESS if the player (team) could benefit by changing its strategy, assuming the opposing team doesn't also change strategies. An evolutionarily stable strategy is one that cannot be successfully invaded by a slightly different strategy. If the gerbils would have a better payoff by foraging slightly more often, then they were not at an ESS. When the system is at an ESS, gerbils foraging have the same payoff as gerbils not foraging, and owls hunting have the same payoff as owls not hunting.

Assume that gerbils that forage will do so successfully except when killed by an owl (that is, there is always food available for the gerbils and they will find it). Owls are successful in hunting at a rate of d as long as there are gerbils to be caught (that is, if the probability of gerbils foraging is > 0). Assume that animals not out foraging or hunting have no gains or losses. Owls that hunt when gerbils are all in hiding will bear the cost of foraging but no gain, as they cannot catch what is not there. Gerbils have a probability of foraging of p, and therefore a probability of not foraging of (1-p). Owls similarly have a hunting probability of q and a not-hunting probability of (1-q). We assume an effectively infinite population.

If the gerbils do not forage, they have a payoff of zero regardless of the owl's strategy, as they remain in safety (no cost) but do not forage (no gain) (Table 6.2a). If they forage but the owls are not hunting, the gerbil's payoff is a simple gain of f_g, minus the cost of foraging of k_g. If the gerbils forage and the owls hunt, the gerbils' net payoff is the same as when the owls are not hunting, minus the possibility of being killed by the owls. We assume this probability as an

overall probability for the population of gerbils—if an individual is killed, it has a payoff of death.

As for the owls, they similarly have a payoff of zero if they do not hunt. Here we assume that hunting has some risks, such as the energy exerted in swooping down on what it hopes to be a gerbil. An owl that hunts when there are no gerbils to be hunted expends that energy, $-k_b$. If they hunt when there are gerbils to be caught, we assume that they are successful, and thus gain at f_b while still bearing the cost of $-k_b$ (Table 6.2b)

This game is not just played once. Let the game be played in distinct iterations; to keep with our gerbil–owl example, one iteration is one night. For each iteration, an individual decides whether to forage or not. This is not an endlessly iterated game. The game is played nightly throughout the gerbil's lifetime, but the important part, evolutionarily speaking, is reproduction. Assume that the game terminates once the gerbil realizes its fitness (that is, it has reproduced for the season). For now, we will not explicitly consider time. Rather, the iterative aspect allows our players to have mixed strategies and for this to truly be a game.

Do our owls and gerbils have pure-strategy ESS? We can deduce this logically. First, we must make a few assumptions about the relative values of the variables. Assume that for both players, the gain from foraging successfully is much greater than the cost of foraging; that is,

$$f_g \gg k_g$$

and

$$f_b \gg k_b$$

If the gerbils' net gain from foraging (gain minus the cost) is greater than the expected loss due to being eaten by an owl (probability of being eaten):

$$f_g - k_g \geq d_g$$

Note that d_g is a probability, such that

$$0 \leq d \leq 1$$

and because the costs and benefits of foraging are mathematically defined relative to d_g, all values of f and k must also be between 0 and 1.

If both $p = 0$ and $q = 0$, both gerbil and owl have payoffs of 0. Either could increase their payoffs by foraging or hunting even a little, so (0,0) cannot be an ESS. Note that in reality, never finding food would actually result in starving to death, which is in fact quite stable. But the moment an individual decides to eat (i.e., changing the strategy slightly), they'd have a better payoff (i.e., not dying). If $p = 0$ and $q = 1$, the gerbils could improve by sometimes taking the risk of foraging, and the owls could improve by not foraging unless there are some gerbils around to hunt, so (0, 1) is also not an ESS. If $p = 1$ and $q = 0$, the gerbils would be happy at first, but the owls could improve their payoff by hunting. (1, 0) is not an ESS. Finally, if $p = 1$ and $q = 1$, the gerbils forage all the time, and because their payoff for foraging is always greater than their payoff from not foraging, regardless of the owls' activities, foraging is a dominating strategy here. The owls have a positive payoff when hunting, and that would only decrease if they skipped a hunt. Therefore, (1, 1) is an ESS. This is known as a "bottom-up" strategy; the gerbils' activity influences the owls', but the owls' activity does not influence the gerbils'. The player lower on the food chain drives the system. However, if the risk of death is high enough that foraging is truly risky (as it is in the real world), that is

$$f_g - k_g < d_g$$

then the ESS must be a mixed strategy, where the gerbils forage sometimes and owls hunt

sometimes. This is a "top-down" scenario, because the primary driver of how frequently gerbils

forage is the lethality of the owls. To find this mixed-strategy ESS, we first calculate the average

expected payoff to each player. This is the payoff they get in each of the four possible situations

(gerbils foraging or not, owls hunting or not), each multiplied by the probability of that situation

(the probability of the gerbils' behavior multiplied by the probability of the owls' behavior).

When payoffs are calculated and simplified, we find that the payoff to gerbils is:

$$\lambda_g = p(f_g - k_g - qd_g)$$

and the payoff to owls is:

$$\lambda_b = q(pf_b - k_b)$$

We need to find the foraging probability that will keep the gerbils' payoff steady

regardless of what they do in a given step, and the hunting probability that will keep the owls'

payoffs steady regardless of their current activity. Because both are to remain stable, we do this

by taking the derivative of one player's payoff, setting it to zero (that is, no change), and solving

for the strategy of the other. For example, to find the owls' stable strategy, we take the

derivative of the gerbils' payoff, set it equal to zero, and solve for the owls' hunting probability,

q. We call this solution q^*:

$$\frac{d\lambda_g}{dp} = f_g - k_g - qd_g \qquad\qquad \text{Eq. 1}$$

$$\frac{d\lambda_g}{dp} = f_g - k_g - q^*d_g = 0$$

$$q^* = \frac{f_g - k_g}{d_g} \qquad\qquad \text{Eq. 2}$$

In words, Equation 2 means that the owls' equilibrium strategy is defined as the gerbils'
net gain from foraging (gain minus cost of foraging) divided by the rate at which gerbils are
killed by owls. This means that if owls kill gerbils frequently (high d_g) they will not hunt as much
(low q^*) as if they kill gerbils less frequently (low d_g), which is logical.

Note that under the previous condition of

$$f_g - k_g \geq d_g$$

q^* would always be at least 1. Because q is also constrained at $0 \leq q \leq 1$, this means that $q^* = 1$
at all times—the owls would have to hunt every possible moment. Only in our later scenario
where the threat of death to gerbils is greater than their net foraging payoff it is possible to
have a q^* less than 1.

Similarly, to find the gerbils' foraging probability, p^*:

$$\frac{d\lambda_b}{dq} = pf_b - k_b$$

$$\frac{d\lambda_b}{dq} = pf_b - k_b$$

$$p^* = \frac{k_b}{f_b} \qquad\qquad \text{Eq. 3}$$

Predator efficiency is the ratio of the predator's gain from foraging (f_b) to their loss from
foraging (k_b); that is, a measure of how good they are at foraging or hunting (Rosenzweig and
MacArthur 1963). In this case, the owl's efficiency is calculated as f_b/k_b. Note that this is the
inverse of p^*. This means that a very efficient predator will lead to a low p^*, and therefore low
available prey numbers and an unstable system. For the system to be stable, the predator must
not be *too* good at hunting.

The model (Stage 1), represented by Equations 1 and 2, reveals the point at which the gerbil payoff crosses zero (q^*) and the point at which the owl payoff crosses zero (p^*). Figure 40 shows an example of how payoffs change depending on foraging probabilities. In general, gerbils' payoffs will be positive as long as owls are hunting at a rate below some threshold, and negative if owls hunt more. The point at which gerbil payoffs are zero is the owl portion of the ESS. Similarly, owl payoffs will be negative when gerbils are foraging below some threshold rate, and positive above this rate. The rate at which gerbil foraging results in an owl payoff of zero is their part of the ESS. In this most simple of games we see the owls and gerbils both foraging quite often, the exact amount depending on what they gain as well as their basic risks.
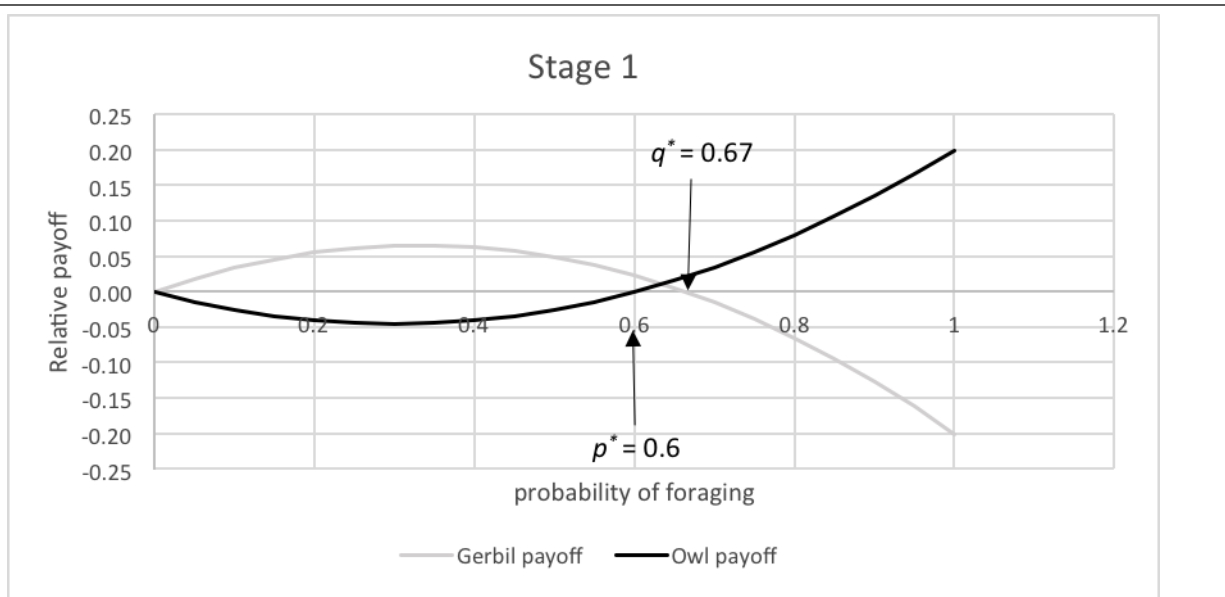
Figure 40   Example of gerbil and owl payoffs under the Stage 1 matrix model. Gerbils have a net positive payoff when owls hunt at a rate of less than 0.67, and a net loss at higher rates. Owls have a net negative payoff at gerbil foraging rates below 0.6 but positive payoffs at higher hunting rates The ESS is when gerbils are foraging at 0.6 and owls are hunting at 0.67. Parameter values: k(g) = 0.2; k(b) = 0.3; f(g) = 0.6; f(b) = 0.5; d = 0.6.

2. Stage 2: state dependence

To introduce hunger into the owl–gerbil game, we include time and the gerbils' energy state. For simplicity, we only consider the gerbils' state; we assume that owls will always hunt if there are adequate gerbils to be hunted. Because this gets complicated quickly, we will use simple equations for the total expected payoff for each player rather than a matrix.

We will now consider the time (T) over which the game is played: the time until gerbil reproduction. We add several more variables in this stage. Table XV summarizes all variables used in Stage 2. The game starts anew after the breeding season.

TABLE XV
VARIABLES USED IN STAGE 2

variable	definition
k	cost of foraging
f	gain from foraging
d	probability owl will kill gerbil
p	probability gerbils forage
q	probability owls hunt
λ	net payoff
T	time at game termination (i.e., number of iterations)
E_0	initial energy state (gerbil)
E_T	terminal energy state (gerbil)
m	metabolic cost of living
α	scaling for effect of hunger state
Subscript g	variable applies to gerbil
Subscript b	variable applies to owl

The gerbil begins at some energy state E_0. In the simplest case, assuming there are no owls and the gerbil forages, the gerbil's energy state at the next time step is

$$E_1 = E_0 + f_g - k_g$$

That is, the gerbils' energy state at time step 1 is their starting energy state at time zero, plus any gains from foraging, minus the cost of foraging. If the individual does not forage, f and k are zero, and $E_1 = E_0$. To find the gerbils' energy state at the termination of a game, time T, we must consider the gain and loss from foraging in each time step.

$$E_T = E_0 + \left(f_g - k_g\right)pT$$

Specifically, energy at time T is equal to starting energy plus the product of the net gain from foraging, the proportion of time spent foraging, and time. In this formulation, there is no penalty for not foraging, and foraging always results in a net energy gain (as defined earlier, $f \gg k$).

This is of course entirely unrealistic; if there were no energy lost by simply living, gerbils would stay in their burrows, never seeing a decrease in energy state and never needing to take the risks of foraging. However, not eating does decrease one's energy state (or in other words, increases one's hunger). Let m be the metabolic cost of living, whether animals are foraging or not. We had not considered m earlier as it is a fixed cost, unlike the variable cost of foraging k. Now that we are considering energy state and the changes in state over time, m begins to affect other variables (m itself is still assumed to be constant).

So now, energy at time T is equal to starting energy plus energy plus the product of the net gain from foraging, the proportion of time spent foraging, and time minus the product of

the energy loss from living, the proportion of time not spent foraging, and time. This assumes the gerbil is alive until time T.

$$E_T = E_0 + (f_g - k_g - m)pT - (1 - p)mT$$

Or more simply:

$$E_T = E_0 + (f_g - k_g)pT - mT$$

This equation describes the energy state of the gerbil at time T without the presence of owls. That is, there is no penalty to going out and foraging (as we previously defined $f \gg k$), but there is a metabolic cost of simply living and they must forage to keep their energy state above zero (death). Therefore, gerbils in this situation always forage unless at some maximum (sated) state, in which case they would simply skip foraging until hungry again. In this case, the payoff to the gerbil, λ_g, is equal to its final energy state E_T. Note that if $E_0 > mT$ (that is, the gerbil's initial energy state is greater than the total energy loss over time), gerbils never have to forage—their initial energy state is sufficient for them to survive until time T without ever eating, assuming that any $E_T > 0$ is an acceptable outcome. If $E_0 < mT$, gerbils must forage or they will starve to death before time T.

Hunger state is not linear. A near-starved individual (E near zero) has more to gain from foraging, and more to lose by not foraging. Conversely, a near-sated individual has little to gain by foraging and little to lose by taking the day off. The balance of these gains and losses depends on the relationship between energy state and expected fitness. If well-fed gerbils have greater expected fitness than poorly fed gerbils, then the benefit to foraging is greater than if the gerbils' expected fitness merely depends on it being alive. Therefore, we add in decreasing returns with higher state, i.e., foraging is more work and food is more important when hungry.

The magnitudes of both k_g and f_g are greater when E is smaller. We add in another variable, α, a scaling factor for the intensity of the effects of energy state.

$$0 < \alpha \leq 1$$

A player for whom hunger state plays a large role will have an α near zero; a player unaffected by state will have α = 1, at which point our model collapses to the non-state-dependent version above. The gerbils' payoff is

$$\lambda_g = E_T{}^\alpha$$

However, this still results in gerbils foraging whenever they feel like it, as there is no penalty for either foraging or not foraging. With no state-dependence or predator, it's just an open buffet. We have to bring the owls back into the game. Recall our assumption that the owls will hunt whenever there are gerbils to hunt. We add in the possibility of the gerbil dying at some point, the one variable in this model that makes foraging truly risky for the gerbil. Each gerbil has some probability of being killed by an owl while out foraging; this probability is the product of owl hunting rate (q), owl success rate (d), and gerbil foraging rate (p), over the entire game.

$$\lambda_g = E_T{}^\alpha - d_g pqT$$

In words, the gerbils' total payoff over time T is equal to the total energy harvested as affected by their starting state minus the product of the probability of being killed when owls are hunting, the probability the owls are hunting, the probability the gerbils are foraging, and time.

Expanded:

$$\lambda_g = [E_0 + (f_g - k_g)pT - mT]^\alpha - d_g pqT$$

Expanded further:

$$\lambda_g = [E_0 + (f_g - k_g - m)pT - m(1-p)T]^\alpha - d_g pqT$$

Because we are not considering the owls' state, their payoff remains as before:

$$\lambda_b = q(pf_b - k_b)$$

As before, we find the mixed-strategy ESS.

$$\frac{d\lambda_g}{dp} = \frac{d}{dp}[E_0 + (f_g - k_g)pT - mT]^\alpha - d_g q^* T$$

$$\frac{d\lambda_g}{dp} = \alpha T(f_g - k_g)[E_0 + (f_g - k_g)pT - mT]^{\alpha-1} - d_g q^* T$$

$$\frac{d\lambda_g}{dp} = \alpha T(f_g - k_g)E_T^{\alpha-1} - d_g q^* T = 0$$

$$q^* = \frac{\alpha(f_g - k_g)E_T^{\alpha-1}}{d_g} \qquad\qquad \text{Eq. 4}$$

Though it appears that q^* could be greater than 1 mathematically, simulations show that this is not true, so long as the conditions for the other values are met. Note that because E_T contains p, q^* depends on p. To be at an ESS, owls must be at q^* and gerbils at p^*. Therefore, to calculate q^* one must first calculate p^*.

Because the owls are not affected by their own hunger state (i.e., their likelihood of foraging is not affected by their own energy state, and they have no metabolic cost of living), the gerbils' optimal strategy is the same as in Stage 1 of our model:

$$\frac{d\lambda_b}{dq} = pf_b - k_b$$

$$\frac{d\lambda_b}{dq} = p^* f_b - k_b = 0$$

$$p^* = \frac{k_b}{f_b} \qquad\qquad \text{Eq. 3}$$

Using Eq. 3 and 4, we can create a graph of the payoffs for different foraging probabilities and find p^* and q^*, as shown in Fig. 41.

Figure 41   Example of a Stage 2 game. Gerbils have a net positive payoff when owls hunt at a rate of less than 0.4, and a net loss at higher rates. Owls have a net negative payoff at gerbil foraging rates below 0.2 but positive payoffs at higher hunting rates (although in this example owl payoff is always very close to zero). The ESS is when gerbils are foraging at 0.2 and owls are hunting at 0.4. Parameter values: k_g = 0.2; k_b = 0.1; f_g = 0.6; f_b = 0.5; d = 0.6; E_0

By changing the value of one variable at a time, we can see how well this model holds up to common sense. Only k_b and f_b have any effect on p^*. As the owls' net gain from foraging goes down (k_b increases, f_b decreases, or both), the gerbil's ESS foraging probability (p^*)

increases. The owls' hunting probability (q^*) increases when either players' foraging gain or the gerbils' metabolic cost of living (f_g, f_b, and m respectively) increase. The last turns out to be a very sensitive measure, and must be close to zero for the model to not fall apart. Increases in k_g, k_b, d, E_0, α, or T lead to a decrease in q^*. If the owls incur a higher cost of foraging (k_b), they will hunt less. A higher kill rate (d) means that owls can get the same net gain while hunting less frequently, and more time (T) has the same effect. A higher foraging cost to the gerbils (k_g) having an effect of decreasing owl hunting probability while not affecting gerbil foraging probability offers no simple explanation. The gerbils' initial energy state (E_0) has only a small effect on owl hunting, and here says that less-hungry gerbils lead to owls hunting more often. Again, given that the model says that gerbil foraging rates are unaffected, this is not easily resolved. Similar problems exist with the remaining variables. For example, as gerbils are more state-dependent (α), they should react more to a change in initial state (E_0), but this is not the case.

There are two ways to resolve these problems. The first is to construct a complex narrative including competing effects that perfectly negate one another. The second, which we invoke, is that the model is simply flawed. While the reasoning behind it may have merit, this model as it stands does not describe reality. Therefore, we shall discontinue this model for the time being.

3. Stage 3: the asset protection principle

Clark (1994) took a somewhat different approach to state-dependence. He treated an individual's potential for future reproduction as an asset to protect. In short, this Asset

Protection Principle holds that when an individual is in a good physiological state, such as having high weight, it has a lot to lose and therefore will be very cautious in its foraging habits. If their state is near zero—that is, death—there is not much to lose but a lot to gain, so they will take just about any risk necessary to attempt to better their state and thus protect their assets. We used these ideas to create a population-level model for our gerbil–owl game, and perhaps avoid the problems we encountered earlier. Many variables and assumptions are as before, with the addition of gerbil and owl population sizes (Table XVI), but the approach to building the model is different.

TABLE XVI
VARIABLES USED FOR STAGE 3

variable	definition
k	cost of foraging
f	gain from foraging
d	probability owl will kill gerbil
p	probability gerbils forage
q	probability owls hunt
λ	net payoff
T	time at game termination (i.e., number of iterations)
G	gerbil population size
B	owl population size
Subscript g	variable applies to gerbil
Subscript b	variable applies to owl

For this model, we reason out the payoff to both the owl and the gerbil. The owl's payoff is simply the product of the population of gerbils, the probability that gerbils are foraging, the probability that owls are hunting, the lethality of the owls, and the owls' gain from eating gerbils minus the owls' cost of foraging times the probability of foraging (cost whether gerbils are out or not). As an equation:

$$\lambda_b = Gpqd_gf_b - k_bq$$

Following the logic outlined in Stage 1, we determine the gerbils' mixed-strategy ESS (recall that the gerbils' optimal strategy depends on the owls' payoff):

$$\frac{d\lambda_b}{dq} = Gp^*d_gf_b - k_b = 0$$

$$p^* = \frac{k_b}{Gd_gf_b} \qquad \text{Eq. 5}$$

Note that this p^* is equivalent to the p^* of Stages 1 and 2, with addition of the population of gerbils and lethality of an owl attack in the denominator. The gerbils should forage at a population-level frequency that minimizes an individual's likelihood of being eaten, which generally means high G, low d, or both. If the product of G and d is 1, this collapses to the single-animal scenario of Stages 1 and 2.

Similarly, the gerbil's payoff is the product of the probability that they are foraging, the net gain from foraging, total time, and an exponential decay function incorporating the probability of exposure to owls, the number of times that exposure occurs, the and lethality of that exposure. This function assumes that the likelihood of surviving until time T diminishes exponentially as T increases.
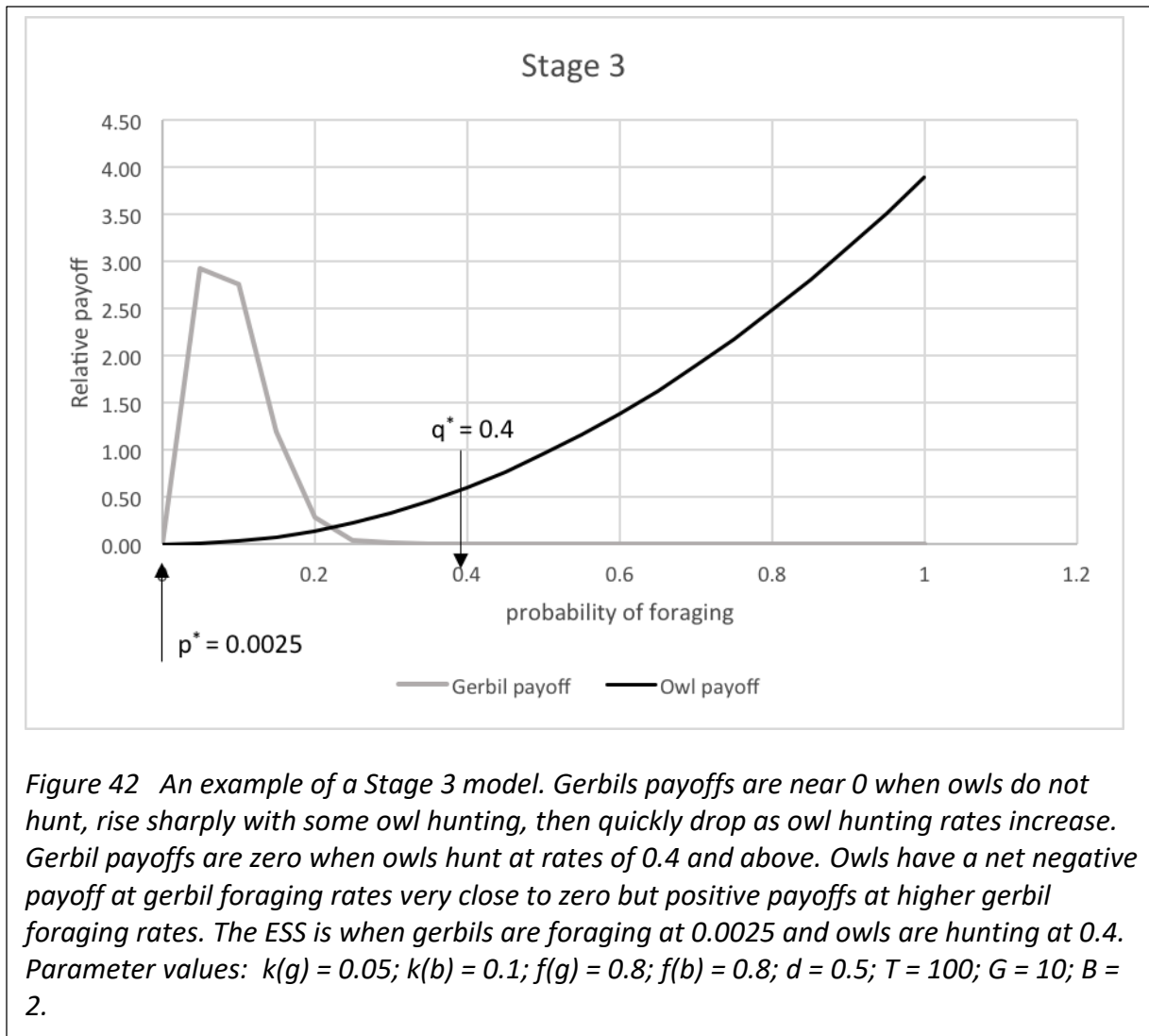
$$\lambda_g = [(f_g - k_g)pT](e^{-pqd_gBT})$$

$$\frac{d\lambda_g}{dp} = \left[(k_g - f_g)pq^*d_gBT^2 + (f_g - k_g)pT\right](e^{-pq^*d_gBT}) = 0$$

Because e^x cannot be zero by definition, the only solution is:

$$q^* = \frac{1}{pd_gTB} \qquad\qquad \text{Eq. 6}$$

As in Stage 2, it is mathematically but not physically possible for $q^* > 1$. Therefore, in those cases we let $q^* = 1$. Owls will hunt at a rate inversely proportional to the product of the proportion of gerbils out, the owl population, the length of the game, and the lethality of any given attack. Equations 5 and 6 show the calculation of equilibrium points for this model. Also as in Stage 2, q^* contains p, so one must calculate p^* first, then q^*. In general, gerbils' payoffs follow a more complex pattern than in Stages 1 and 2. Their payoffs are near zero when owls are not hunting at all, a result that may be due to a flawed model. This payoff increases rapidly until owls hunt more frequently, then drop quickly to zero as the hunting intensity increases. Owl payoffs simply rise as their prey are more active: more prey running around equals more prey eaten. The ESS is thus near zero foraging for the gerbils, and some higher rate for the owls, depending on other parameters chosen. Figure 42 shows a simulation of this model.

Figure 42   An example of a Stage 3 model. Gerbils payoffs are near 0 when owls do not hunt, rise sharply with some owl hunting, then quickly drop as owl hunting rates increase. Gerbil payoffs are zero when owls hunt at rates of 0.4 and above. Owls have a net negative payoff at gerbil foraging rates very close to zero but positive payoffs at higher gerbil foraging rates. The ESS is when gerbils are foraging at 0.0025 and owls are hunting at 0.4. Parameter values: k(g) = 0.05; k(b) = 0.1; f(g) = 0.8; f(b) = 0.8; d = 0.5; T = 100; G = 10; B = 2.

This model does not include hunger state. Rather, it is an alternate approach to the basic foraging question explored with Stage 1. This model shows some promise, but as-is does not result in logical outcomes. The gerbils under this model should forage almost never (p^* is always near 0), and under most simulations the owls should never stop foraging (q^* is often greater than 1).

Furthermore, when exploring the effects of changing single variables as in Stage 2, many had effects that defy easy explanation or appear counterintuitive. For example, increasing the owl population (*B*) has no effect on the gerbil foraging probability and decreases owl foraging probability, which seems counterintuitive (owls should have to hunt more frequently to make up for the increased competition with a stable prey pool).

For these reasons, we did not explore this model further. It is presented here as an example of an alternate approach and thus a hint of the wide variety of models one may create in an attempt to approximate reality.

C. Conclusion

Our models indicate that owls forage based on the gerbils' hunger state (Eq. 4), but that gerbils forage based only on the owls' feeding efficiency (Eq. 3, which shows that gerbils' stable strategy is the inverse of owl predator efficiency; Eq. 5 shows a direct influence of the owls' rate of killing gerbils). While we did not include owl hunger state in these models, it is clear that the owls' hunting behavior is driven by the gerbils' behavior and hunger state, and the gerbils' behavior is driven by the owls' efficiency and effectiveness in hunting. Owl hunger may affect their hunting efficiency, including the rate at which they kill gerbils, and thus drive gerbil behavior. In this game one player's behavior is driven more by the hunger state of the opposing player than their own. That owl hunger should increase their hunting success rate is suggested by studies in which hungry predators as varied as domestic cats, salmon, and jumping spiders increased their attack rate and lethality (Gardner 1966, Biben 1979, Morgan and Ritz 1984, Hall and Bradshaw 1998). Altwegg (2003) found that hungry predators killed both hungry and sated

prey, but that sated predators killed only hungry prey. Much as suggested by our game, the hunger of the opponent was more of a factor than the players' own, except when the players' own hunger was extreme.

Berger-Tal et al. (2010) found, in a vivarium experiment, that owls base their activity on their own hunger state, not the gerbils'; that gerbils responded to the owls' state; and that when they are hungry gerbils will forage no matter what the owls are doing. While our results agree for the gerbils, they disagree when it comes to the owls. However, Embar et al. (2014) conducted a vivarium gerbil–owl foraging game that effectively tested the ideas discussed here, and found that owls can, and in some circumstances do, respond to gerbil energy state. They found that hungry gerbils take more risks when foraging, and the owls focus their hunting efforts on the hungry gerbils. The lack of a similar effect in Berger-Tal et al (2010) was attributed to both the vivarium enclosure and the subtlety of the owls' choices in most of the tested scenarios. Our models show some promise in this outcome. We are confident that they could form the basis of more robust models. These models should include the owls' level of hunger, which we did not consider here. One approach to owl hunger was the model of Brown et al. (2001), which considered the predator's energy state and the relative risk of injury incurred when hunting and could be modified to fit our scenario.

The games played by foraging and hunting animals are complex, and the models explored here do not, as they stand, provide much insight into the games played. However, they do hint at the tradeoffs between the need to forage and the need to avoid being killed. One could combine the above approaches with other models, existing or new, to build a model to further explore the role hunger plays in the foraging game.

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VITA

NAME: Hilary Beth Osborne

EDUCATION: B.S., Biological Sciences, Northeastern University, Boston, Massachusetts, 2000

                 Ph.D., Biological Sciences, University of Illinois at Chicago, Chicago, Illinois, 2016

TEACHING
EXPERIENCE: Department of Biological Sciences, University of Illinois at Chicago, Chicago, Illinois, Teaching Assistant (courses: Introductory Biology for Non-Science Majors; Introductory Ecology; Field Ecology; History of Life; Animal Behavior; Comparative Vertebrate Anatomy; Animal Physiology), 2005–2015

HONORS: Excellence in Teaching Award, 2006

PROFESSIONAL
MEMBERSHIP: Board of Editors in the Life Sciences
                 Council of Science Editors