

**EFFECTS OF INTENSIVE AGRICULTURE ON SMALL MAMMAL
COMMUNITIES IN AND ADJACENT TO CONSERVATION AREAS IN
SWAZILAND**

A Thesis

by

ZACHARY MATTHEW HURST

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

December 2010

Major Subject: Wildlife and Fisheries Sciences

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December 2010

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ABSTRACT

The Effect of Intensive Agriculture on Small Mammal Communities in and Adjacent to
Conservation Areas in Swaziland. (December 2010)

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Co-Chairs of Advisory Committee: Dr. Robert A. McCleery
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I examined the effect of sugarcane plantations on small mammal communities at 3 sites in the Lowveld of Swaziland during the dry and wet seasons of 2008. I evaluated changes in species abundance and community parameters in relation to distance to the interface, as well as the relationship between small mammal communities and environmental variables. I used pitfall arrays and Sherman live traps to sample small mammals along 9 traplines at the land-use interface and on a gradient extending 375 m into each land-use. I used point-centered-quarter, range pole, and line-transect sampling to characterize plant community structure.

Two generalist small mammal species had increased abundance as distance into the sugarcane increased. Two species with wide geographic ranges appeared to select areas within 75 m of the interface. Four species with restricted habitat tolerances or diets were negatively affected by sugarcane, as was 1 species that selects for low ground cover. Two species may have avoided the interface. For the majority of species in the Lowveld, sugarcane does not provide habitat. Sugarcane monocultures > 375 m in width may form a barrier to movement of small mammal species.

Species richness and diversity significantly decreased at the interface of 2 sites, however, 1 site had increased diversity associated with the interface. My analysis indicated a difference in community composition between the 2 land-uses and differences between the farthest interior conservation area (375 m)-interface (0 m) and the farthest interior sugarcane (375 m). There was no difference in community composition between seasons or distances within the conservation area. The farthest interior sugarcane trapline had distinctness from other traplines within the sugarcane, and may be of importance for minimizing the effects of habitat fragmentation in lowveld savanna.

The effects of sugarcane did not extend into adjoining natural vegetation. My results indicated grass biomass, litter depth and shrub density played important roles in structuring the communities. Between sites, variation in community structure attributable to the sugarcane interface varied. The site with poorest vegetative cover had the highest relative importance of distance to the interface. One species (*Steatomys pratensis*) was negatively affected by distance to the interface.

DEDICATION

To Mom and Dad, whose love and support allowed me to go places that I never
thought I would.

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I would like to thank all of the people that helped to make this project possible. I would particularly like to thank the land managers at all of my sites: J. Ndlovu and the staff of Royal Swazi Sugar Company (Simunye and Mhlume Estates), E. Ehrlendssen, M. Jamieson and the staff of Crookes Brothers Plantations, G. White and the staff of Tongaat-Hulett Sugar Company, and M. Reilly and the staff of Hlane National Park, . I would especially like to thank M. McGinn and the staff of Mbuluzi Game Reserve and T. Minnie and the staff of Nisela Farms, without whose help I may still be wandering around in the bush. I would also like to thank K. Roques, Mduduzi and the staff of All-Out Africa for assistance in the field, help with logistics, as well as, for the good company. I would like to thank Cliff and Thea for their assistance, conversation, and occasional taste of home.

I am indebted to my numerous field assistants who helped dig many holes for the crazy American. I am especially indebted to L. Twala and S. Nandalandze, who showed good humor dealing with the snakes and “lions” and were willing to put in long hours out in the field without complaint.

I would like to thank the faculty and staff at WFSC for their assistance and for making my time at Texas A&M a great experience. I would also like to thank my friends and lab mates, especially M. Licon, K. Adamek, A. Sutton, J. Schmidt, P. McGee, and A. Dedrickson who helped me learn and kept me sane. I would

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CHAPTER I

INTRODUCTION

Agriculture is the dominant cause of land conversion on the planet and is responsible for fragmentation of habitats worldwide (Ramankutty and Foley 1998). Anthropogenic fragmentation has created ecotones with abrupt changes between land-use types. These abrupt changes in land use can have profound effects on wildlife populations, favoring some species at the cost of reduced productivity or exclusion of others (Burel et al. 1998, Fagan et al. 1999). The magnitude and implications of the joining or interfacing land-uses on animal communities' abundance, species richness, and demographic parameters are complex and poorly understood (Yahner 1988, Murcia 1995). Interface-related changes in a focal parameter are generally known as edge effects (Murcia 1995).

Despite extensive studies examining wildlife populations associated with anthropogenic land-use interfaces, there is a lack of consensus as to whether effects associated with abrupt land-use interfaces have emergent properties (Murcia 1995, Ries and Sisk 2004). Several different models have been proposed to explain effects of land-

use interfaces on the distribution and demography of populations (Duelli et al. 1990, Lidicker 1999, Ries and Sisk 2004). These models place differing emphasis on the roles of vegetative structure, resource availability, interspecies interactions, and permeability. Results of empirical studies examining these factors are often conflicting attributing both positive and negative edge abundance relationships to species (Ries and Sisk 2004). Conflicting results highlight the complexity of edge effects, and the need for further study (Ries and Sisk 2004).

Additionally, studies of the effect of land-use interfaces have occurred within a limited geographic area. Sisk and Battin (2002) found there has been a geographical bias in edge studies. Furthermore, species level responses may vary across geographic regions, thus limiting generalizations that can be drawn from individual edge studies (Sisk and Battin 2002).

The land-use matrix in the Lowveld of Swaziland provides an opportunity to examine some of the underlying variables that account for changes in abundance and diversity of small mammal communities while also increasing the geographic scope of edge effect studies. Protected areas, high intensity agriculture, and grazing account for most (~80%) of the lands in the semi-arid lowlands, or Lowveld, of Swaziland (Roques 2002, Monadjem and Garcelon 2005). The interfaces formed between land-use types created interfaces of differing abruptness in regard to water availability and vegetative structure. The Lowveld's land-use mosaic is expected to persist, or increase, into the foreseeable future due to initiatives promoting small farms, as well as, Swazi grazing culture (Doran et al. 1979, Lankford 2001, Terry and Ryder 2007). Currently, Swaziland

is undergoing a shift from subsistence farming to small landholder communal cash cropping, with a corresponding increase in the intensity of land-use (UNCTAD 2000, Lankford 2001, Terry and Ryder 2007).

Small mammals are excellent subjects to study the effects of land-use interfaces on density and diversity. Small mammals have been shown to be susceptible to deleterious edge effects, such as predation, and species have exhibited different affinities for interface habitat (Andren 1994). Furthermore, small mammals are integral to ecosystem processes. Small mammals are important food sources for avian, reptile, and mammalian species. Through seed predation and herbivory small mammals have been shown to greatly influence plant communities, having effects on both invasion and composition of plant communities (Weltzin et al. 1997, Manson et al. 2001, Goheen et al. 2004). Small mammals also have small home ranges, occupy a variety of niches, have differing degrees of specialization, and are relatively easy to sample (Wilson et al. 1996, Skinner and Chimimba 2005). Small mammal populations are highly dynamic, and quick to respond to changes in their environment (Anderson et al. 2003).

By examining the effect of intensive land-use interfaces on abundance and community structure of small mammals my study provides information that will aid management and conservation of small mammal species, while also expanding knowledge about the underlying mechanisms of these changes. Conceptually, my analysis of the dynamics of the conservation-agriculture land-use interface in regards to small mammal populations and habitat associations helps to elucidate functioning of sugarcane-conservation interfaces as either noninteractive or interactive. Noninteractive

effects are categorized by an abrupt change in a response variable as the interface is crossed, while interactive effects are categorized as exhibiting emergent properties across the interface (Lidicker 1999). Therefore, with an interactive response type, variables can't be predicted purely by the land-use characteristics (Lidicker 1999). My study also indicates potential reductions in the effective area of protected areas in the Lowveld of Swaziland for small mammal species and the impacts of sugarcane plantations throughout the region.

RESEARCH GOAL AND OBJECTIVES

I evaluated the effects of intensive agriculture-conservation land-use interfaces on small mammal communities. In order to accomplish this, I: (1) examined differences in small mammal species abundances across agriculture-conservation area land-use interfaces, (2) examined differences in small mammal community structure across agriculture-conservation area land-use interfaces, and (3) examined spatial and environmental factors that contributed to differences in small mammal community structure and species abundances across the agriculture-conservation area land-use interface.

CHAPTER II

SMALL MAMMAL POPULATION RESPONSES TO INTENSIVE AGRICULTURE ADJOINING CONSERVATION AREAS IN SWAZILAND

SYNOPSIS

Land conversion to high intensity agriculture is widespread throughout southern Africa. In the Lowveld of Swaziland, sugarcane production has converted native savanna to agricultural monocultures. Land conversion creates abrupt transitions between land-uses, potentially impacting wildlife populations. I examined the effect of abrupt land-use transitions on small mammal abundance and distribution on a gradient extending into conservation and sugarcane land-uses. I found 2 generalist species (*Lemniscomys rosalia*, *Mastomys natalensis*) increased abundance as distance into the sugarcane increased. Widespread species, such as *Mus minutoides*, *Crocidura hirta*, appeared to select areas within 75 m of the land-use interface. Species with restricted habitat tolerances (*Aethomys ineptus*, *Elephantulus brachyrhynchus*, *Steatomys pratensis*, *Saccostomys campestris*, *Gerbilliscus leucogaster*) or diets (*Steatomys pratensis*, *Saccostomys campestris*) were excluded from, or had lower abundance in the sugarcane. Two species (*Aethomys ineptus* and *Steatomys pratensis*) may have avoided the interface and thus are potentially more susceptible to the effects of sugarcane-induced habitat fragmentation. Species (*Gerbilliscus leucogaster*) that select for low ground cover were negatively affected by the sugarcane. For the majority of species in

the Lowveld, sugarcane does not provide habitat. Sugarcane monocultures > 375 m in width may form a barrier to movement of small mammal species.

INTRODUCTION

Agriculture is the dominant land-use on the planet, replacing and fragmenting habitats on a massive scale (Ramankutty and Foley 1999, Ellis and Ramankutty 2008, Ramankutty et al. 2008). As human populations grow, more land is expected to be converted to agricultural uses (Foley et al. 2005). The conversion of native vegetation to intensive agricultural can have profound impacts on native wildlife through the loss and fragmentation of habitats (Sala et al. 2000, DeFries et al. 2004). Habitat fragmentation can isolate wildlife populations within remnant patches, reduce population viability and gene flow, and increase susceptibility to stochastic events (Saunders et al. 1991, Andren 1994, Merriam 1995, Begon et al. 2006).

Anthropogenic fragmentation can create ecotones with abrupt changes between land-use types (Lidicker 1999). Abrupt changes in land-use can favor some wildlife species and/or reduce or exclude others (Fagan et al. 1999, Lidicker 1999). Implications of edge effects, land-use interfaces and habitat fragmentation are complex and often poorly understood (Yahner 1988, Murcia 1995, Ries et al. 2004).

Despite the integral role of small mammals within savanna ecosystems as herbivores, seed predators, and prey items, relatively little research has been conducted on the impact of land-use interfaces on small mammal populations (Weltzin et al. 1997, Manson et al. 2001, Ries et al. 2004); particularly small mammal populations found in African savannas (Goheen et al. 2004).

Small mammals are well suited for studying the impacts of land-use interfaces on animal populations. Small mammals generally have small home ranges, occupy a variety of niches, have differing degrees of specialization, and are relatively easy to sample (Skinner and Chimimba 2005). Additionally, small mammal populations are dynamic and quick to manifest changes in the local environment (Anderson et al. 2003, Monadjem and Perrin 2003). Furthermore, small mammals have been shown to be susceptible to deleterious edge effects (e.g. predation) and have exhibited different responses to land-use interfaces (Lidicker 1999, Keesing 2000, Ries et al. 2004). Small mammals have been used as indicators of vegetation condition (Avenant and Cavallini 2007), and Laurance (1991) found mammal extinction proneness could be indicated by abundance in the matrix.

In Swaziland, and throughout southern Africa, the Lowveld is a mosaic landscape, wherein conservation areas, sugarcane (*Saccharum spp.*) plantations, commercial cattle ranches, subsistence farmlands, and range areas are interspersed (Roques 2002, Lankford 2007). In the Lowveld landscape, sugarcane monocultures are a unique vegetation type with high water availability and little vegetative complexity. The effect of sugarcane land-use on small mammals in lowveld savanna is unknown despite the potential for conversion more land to sugarcane cultivation (UNCTAD 2000, Bigman 2001, Lankford 2007).

Due to the lack of habitat fragmentation studies conducted within southern African lowveld savanna (Monadjem 1999, Mahlaba and Perrin 2003), the effects of sugarcane on small mammals remain speculative. In other regions, generalists persisted

in sugarcane despite loss of diversity, and insectivores may be present because of the higher insect densities found in the moist sugarcane environment (Hood et al. 1971). Alternatively, more specialized species can be detrimentally affected by sugarcane and other highly modified lands (Laurance 1991).

I examined the effects of the land-use interface on abundance and distribution of small mammal species. I determined spatial extent of edge response for different small mammals across the land-use gradient, and identified species and traits which were susceptible to habitat fragmentation. I provide management recommendations that may help reduce impacts of habitat fragmentation in the Lowveld of Swaziland and throughout Southern Africa.

STUDY AREA

My study was conducted in the Lowveld of Swaziland, the low-lying region between the northern Drakensburg Escarpment to the west and the Lubombo Mountains to the east (Fig. 2.1). The Lowveld lies in the eastern half of the country and is Swaziland's lowest, warmest, and driest region. The Lowveld's elevation ranged between 150–400 m above sea level, with annual precipitation between 550–725 mm (Matondo et al. 2005). Mean average temperature was 22°C with mean monthly temperatures of 26°C in January and 18°C in July (Monadjem 1999). Swaziland has a subtropical climate, and exhibits distinct wet (October–March) and dry (April–September) seasons, 75% and 25% of rains fall during these respective seasons (Matondo et al. 2004). The Lowveld is prone to droughts due to the combination of erratic rain events and high summer temperatures (Matondo et al. 2004). Vegetation in

the Lowveld is characterized as lowveld savanna, with 3 distinct broad-scale vegetation types: *Acacia* savanna, broadleaved woodland, and riverine forest (Mucina and Rutherford 2006).

I sampled at 3 sites with conservation lands directly adjoined large-scale sugarcane plantations (Figs. 2.1, 2.2). In my study, the conservation lands were identified as lands that were managed with the explicit goal of wildlife conservation, including private cattle ranches, private game reserves and national parks. Hlane-Mbuluzi included lands administered by Hlane Royal National Park, Mbuluzi Game Reserve, Tongaat Hulett Sugar (Tabankulu Estate), and Royal Swazi Sugar Corporation (Simunye and Mhlume Estates). Hlane Royal National Park and Mbuluzi Game Reserve were managed with the explicit goal of wildlife conservation and had excluded cattle grazing and conducted prescribed burning. Agricultural lands used flood, overhead sprinkler, and drip irrigation, with similar sugarcane varieties cultivated. Dirt and gravel access roads and a 2-m high fence separated the conservation areas and sugarcane, restricting movements of medium to large sized mammals.

Crookes included lands managed by Crookes Brothers Plantation and Bar J Cattle Ranch (Figs. 2.1, 2.2). Conservation lands fell within the Big Bend Conservancy and were managed for wildlife conservation. Sustainable stocking rates, rotational

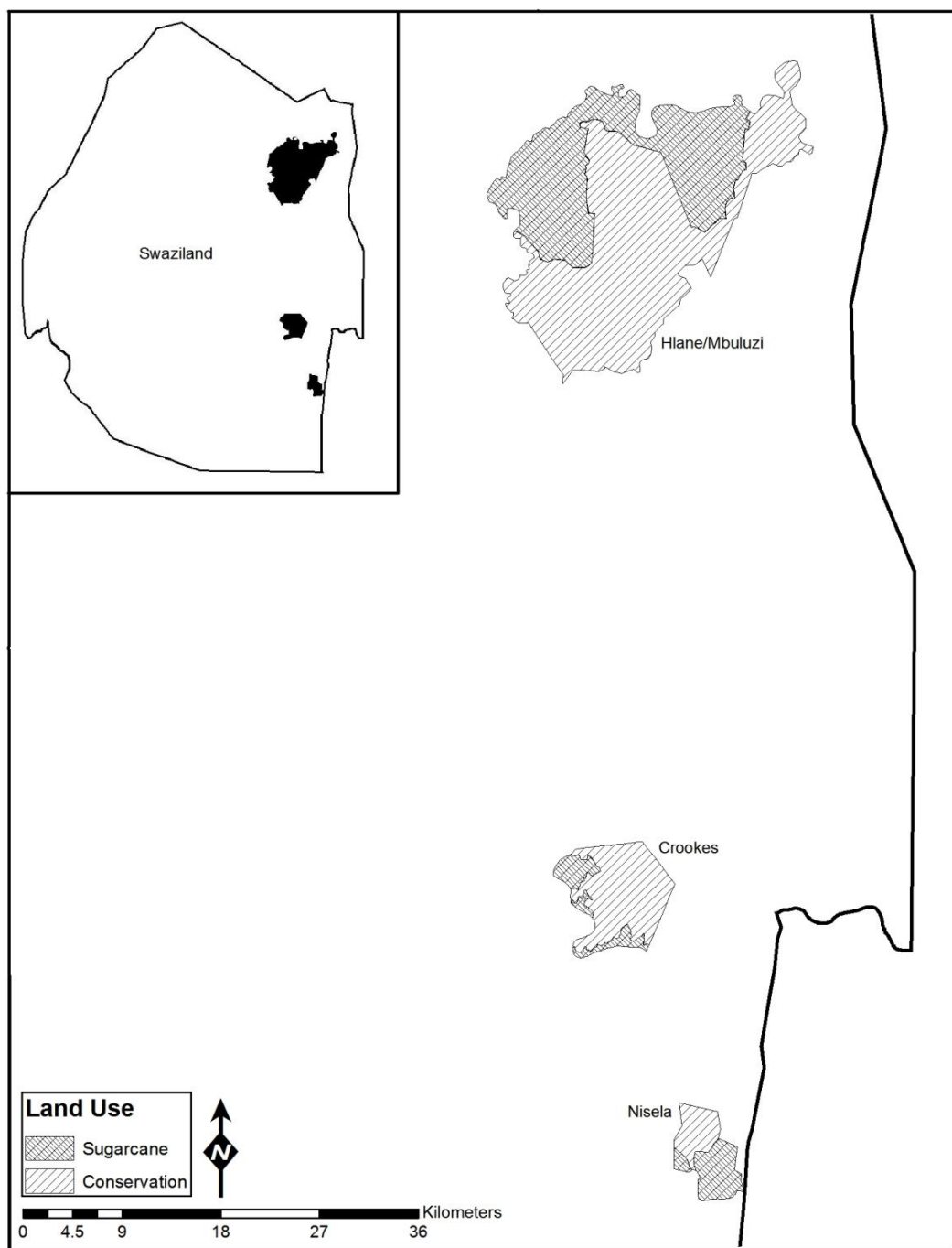


Figure 2.1. Map of the 3 study sites used to examine the effects of intensive agriculture on small mammal communities in the Lowveld region of Swaziland. Interfaces are denoted by the difference between land-uses. Inset: map of Swaziland showing the locations of the 3 sites.

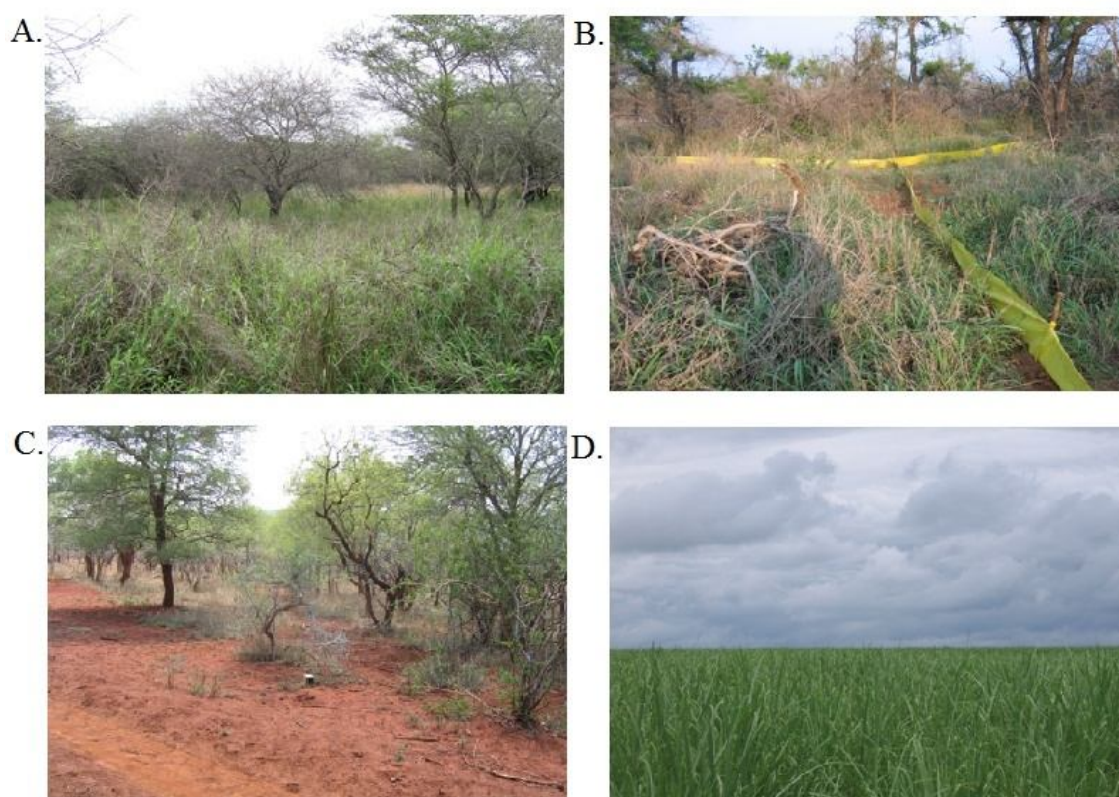


Figure 2.2. Representative photographs of conservation land-use at Hlane-Mbuluzi (A), Crookes (B), and Nisela (C), as well as, the agriculture land-use (D). Pitfall array and Sherman trap placement are shown in the Crookes and Nisela pictures, respectively. All pictures were taken during November 2008 (wet season).

grazing, and prescribed burning were practiced on conservation lands. There were abrupt differences in substrate at the land-use interface, with more productive, less rocky soils found in the sugarcane. Dirt access roads and low, barbed wire fences separated the 2 land-uses and restricted the movement of cattle. Irrigation was conducted using flood, overhead sprinkler, and center pivot irrigation, with similar sugarcane varieties cultivated.

Nisela was overseen by Nisela Farms; conservation lands were managed for wildlife viewing, conservation, and grazing. Prescribed burning and free-range grazing were practiced on the conservation lands. Edaphic discontinuities between land-uses were relatively minimal. Access roads, railroad tracks, and an electrified 2-m fence separated the 2 land-uses. The site used center pivot irrigation and it had 2 structurally different varieties of sugarcane.

METHODS

Sampling Design

Using ground-truthed aerial photographs, Landsat images and a GIS (ArcGIS 9.3, ESRI, Redlands, California), I randomly placed 4 transects at each site along the conservation-agriculture interface. I placed transects perpendicular to the interface using handheld GPS and compass bearings. Transects extended 375 m into each land-use type, the fence line between land-uses was identified as 0-m distance (Fig. 2.3). Along each transect, I placed traplines at: 0, 75, 150, 225, and 375 m into each land-use type, paralleling the interface (Fig. 2.3). Traplines consisted of a pitfall array and 20 Sherman live traps spaced 10 m apart. A total of 180 traps was placed along the entire transect. I

spaced traplines 75-m apart and transects at least 400-m apart to ensure independence of sampling units based upon expected small mammal home ranges (Monadjem and Perrin 1998a). However, at Nisela a limited amount of conservation-agriculture interface required transects to be placed 300-m apart. The farthest interior trapline, (375 m) served as a reference as the influence of land-use edges is usually within 250 m of the interface (Ries et al. 2004).

Along each transect, I placed pitfall arrays at each trapline origin to sample for insectivores (Jones et al. 1996; Fig. 2.3). Pitfall arrays consisted of 7 total buckets using a central bucket with 3 10-m long, radiating drift fences set 120 degrees apart. Additional buckets were placed along each drift fence at 5 m and at each terminus. Drift fences were comprised of 30 cm tall plastic sheeting, staked vertically with the bottom buried; buckets were at least 40 cm deep to eliminate the chance of escape and were flush with the ground (Jones et al. 1996). I used a total of 63 buckets for each transect.

Sherman traps were offset from each pitfall by 50 m. Deploying traps in a transect design yields high levels of area surveyed per trap, and the relatively close spacing of traps ensured adequate sampling for species richness (Jones et al. 1996, Pearson and Ruggiero 2003). I placed each trap within 2 m of the assigned point in an area that would provide increased potential for capture and reduce weather exposure.

During the wet and dry seasons, I trapped each entire transect for 4 consecutive nights to allow for adequate sampling (Jones et al. 1996).

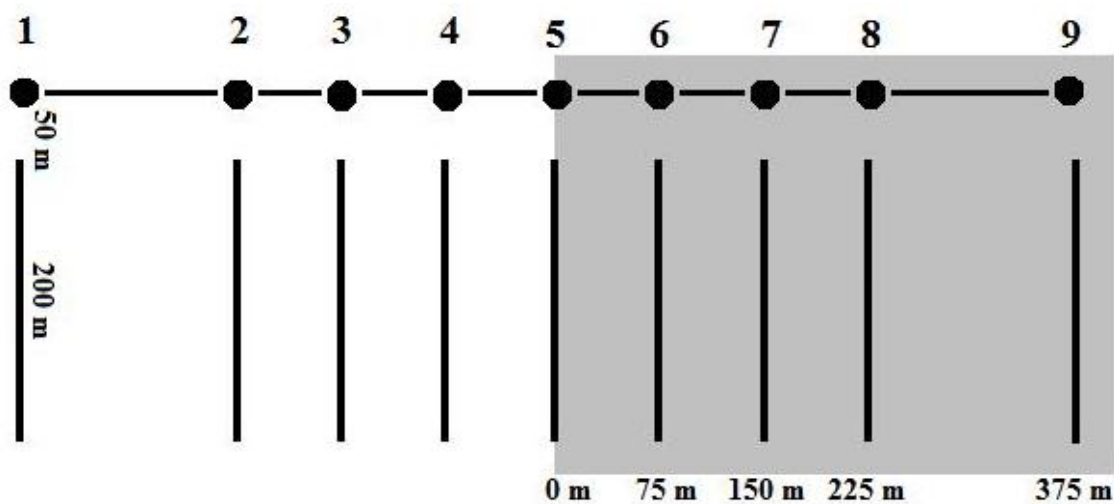


Figure 2.3. Schematic representation of the sampling protocol for small mammals. Transects extended from conservation areas into sugarcane agriculture (gray shading). Sherman traps were placed along traplines (20 traps, 10-m apart; vertical lines), traplines were offset 50 m from the main transect. Pitfalls were located along the transect (circles). Traplines and pitfalls were placed at 0, 75, 150, 225, and 375 m into each land-use and were numbered from 1 to 9, with 1 being the farthest interior conservation trapline.

Traps were baited with a combination of oats and peanut butter and were checked every morning. For each captured individual, I recorded species, age, sex, reproductive condition, ectoparasite presence, body length, hind foot length, and mass (Kunz et al. 1996, Skinner and Chimimba 2005). I gave each individual weighing > 15 g a unique ear tag identifier (1005-1, National Band Co., Newport, Kentucky, USA), smaller individuals and *Mus minutoides* were given ear punches (INS500075-5, Kent Scientific, Torrington, Connecticut, USA). Individuals that received ear punches were uniquely identified using a combination of measurements, including: mass, tail length, body length, and hind foot length, as well as, initial capture location.

All captured insectivores (*Crociodura spp.* and *Suncus spp.*) were collected for later identification (Peter Taylor, Curator of Mammals, Durban Natural Science Museum, Durban, South Africa). Additionally, at least one voucher specimen from each site was deposited in the collections of the Durban Natural Science Museum. I performed captures and data collection following guidelines outlined by the American Society of Mammalogists (Gannon and Sikes 2009) and my study was conducted under Texas A&M University's Animal Use Protocol (permit number 2008-98).

Capture-recapture Analysis

I used mark-recapture analysis for species with >50 individual captures such that I would be able to adequately parameterize closed capture models using program MARK (White 2007). For this analysis, I eliminated individuals captured in pitfalls from analysis due to potential differences in trap response, capture probability and survey effort. I used an information-theoretic approach for model selection (White and

Burnham 1999, Burnham and Anderson 2002). First, I evaluated trap response using models outlined in Otis et al. (1978) for each species (Table 2.1). Once the appropriate trap response model was determined, I modeled the effects of the land-use gradient using *a priori* hypotheses (Table 2.2) and the appropriate trap response model. I derived species abundance estimates for each trapline by site for each season using the best fitting model and its resulting maximum likelihood estimates. I used 95% confidence intervals to determine statistically significant differences of abundance estimates between traplines.

Occupancy Analysis

In order to limit potential overparameterization caused by data paucity typically encountered with small mammal studies, I used presence/absence modeling for species with < 40 individuals captured (White and Burnham 1999, MacKenzie et al. 2002). I estimated distribution across the land-use gradient and among the sites using program PRESENCE (Hines 2006). I evaluated the influence of moon phase, temperature, moon presence (> 6 hours during nighttime), and precipitation on the probability of detection because of their potential to impact small mammal activity (Hughes et al. 1994) (Table 2.3). Once an appropriate detection model was selected, I incorporated the detection model into subsequent occupancy models (Table 2.2). I used occupancy estimates derived from the best fitting model and I evaluated 95% confidence intervals to determine statistically significant differences in occurrence between traplines.

Table 2.1. Notation and descriptions of *a priori* trap heterogeneity models for *Aethomys ineptus*, *Lemniscomys rosalia*, *Mastomys natalensis*, *Mus minutoides*, and *Steatomys pratensis* in the Lowveld of Swaziland (adapted from Otis et al. (1978)). The abbreviated notation includes the capture (p_1 – p_4), and recapture probabilities (c_1 – c_3) for each survey night.

Model notation	Description of detection covariates and models	Abbreviated notation
M_0	constant trap response across all surveys	$p_1=p_2=p_3=p_4=c_1=c_2=c_3$
M_t	time varying trap response	$p_1 \neq p_2 = c_1 \neq p_3 = c_2 \neq p_4 = c_3$
M_b	behavioral trap response	$p_1 = p_2 = p_3 = p_4 \neq c_1 = c_2 = c_3$
M_{tb}	time varying, behavioral trap response	$p_1 \neq p_2 \neq p_3 \neq p_4 \neq c_1 \neq c_2 \neq c_3$

Table 2.2. Models evaluated during capture–recapture (*Aethomys ineptus*, *Lemniscomys rosalia*, *Mastomys natalensis*, *Mus minutoides*, and *Steatomys pratensis*) and occupancy (*Crocidura hirta*, *Elephantulus brachyrhynchus*, *Suncus lixus*, *Gerbilliscus leucogaster* and *Saccostomys campestris*) analysis in the Lowveld of Swaziland. The X's denote a covariate grouping that was included in the model. Traplines span the land-use gradient (1 = 375 m into the conservation area, 5 = interface (0 m), and 9 = 375 m into the sugarcane).

Model name	Season		Site		Trapline						
	all equal	wet≠dry	Hlane/Mbuluzi≠ Crookes≠Nisela	Hlane/Mbuluzi= Crookes =Nisela	1=2=3= 4=5=6= 7=8=9	1≠2≠3≠ 4≠5≠6≠ 7≠8≠9	1=2=3≠ 4=5=6≠ 7=8=9	1≠2=3= 4≠5=6= 7=8≠9	1=2=3= 4≠5=6= 7=8=9	1=2=3= 4≠5≠6= 7=8=9	1≠2≠3≠ 4≠5≠6= 7=8=9
(.)	X										
(season)		X									
(site)			X								
(Hl/Cr)				X							
(cane)					X						
(dist)						X					
(3cane,3mid)							X				
(int,mid,edge)								X			
(4res)									X		
(4res,edge)										X	
(dist,cane)											X
(site;cane)			X		X						
(site;dist)			X			X					
(site;3cane,3mid)			X				X				
(site;int,mid,edge)			X					X			

Table 2.2. continued

Model Name	Season		Site		Trapline						
	all equal	wet≠dry	Hlane/Mbuluzi≠ Crookes≠Nisela	Hlane/Mbuluzi= Crookes ≠Nisela	1=2=3=4 =5≠6=7= 8=9	1≠2≠3≠ 4≠5≠6≠ 7≠8≠9	1=2=3≠ 4=5=6≠ 7=8=9	1≠2=3= 4≠5≠6= 7=8≠9	1=2=3= 4≠5=6= 7=8=9	1=2=3= 4≠5≠6= 7=8=9	1≠2≠3≠ 4≠5≠6= 7=8=9
(site;4res)			X						X		
(site;4res,edge)			X							X	
(site;dist,cane)			X								X
(Hl/Cr;cane)				X	X						
(Hl/Cr;dist)				X		X					
(Hl/Cr;3cane,3mid)				X			X				
(Hl/Cr;int,mid,edge)				X				X			
(Hl/Cr;4res)				X					X		
(Hl/Cr;4res,edge)				X						X	
(Hl/Cr;dist,cane)				X							X
(site;season;cane)		X	X		X						
(site;season;dist)		X	X			X					
(site; season;3cane,3mid)		X	X				X				
(site; season;int,mid,edge)		X	X					X			
(site;season;4res)		X	X						X		
(site; season;4res,edge)		X	X							X	
(site; season;dist,cane)		X	X								X
(Hl/Cr;season;cane)		X		X	X						
(Hl/Cr;season;dist)				X		X					
(Hl/Cr; season;3cane,3mid)		X		X			X				
(Hl/Cr; season;int,mid,edge)		X		X				X			

Table 2.2. continued

Model Name	Season		Site		Trapline						
	all equal	wet≠dry	Hlane/Mbuluzi≠ Crookes≠Nisela	Hlane/Mbuluzi= Crookes ≠Nisela	1=2=3= 4=5≠6= 7=8=9	1≠2≠3≠ 4≠5≠6≠ 7≠8≠9	1=2=3≠ 4=5=6≠ 7=8=9	1≠2=3= 4≠5≠6= 7=8≠9	1=2=3= 4≠5=6= 7=8=9	1=2=3= 4≠5≠6= 7=8=9	1≠2≠3≠ 4≠5≠6= 7=8=9
(Hl/Cr;season;4res)		X		X					X		
(Hl/Cr; season;4res,edge)		X		X						X	
(Hl/Cr; season;dist,cane)		X		X							X

Table 2.3. Notation and descriptions of *a priori* detection models for *Crocidura hirta*, *Elephantulus brachyrhynchus*, *Suncus lixus*, *Gerbilliscus leucogaster* and *Saccostomys campestris* in the Lowveld of Swaziland.

Model notation	Description of detection covariates and models
p(.)	constant detection across all surveys
p(T)	temperature at dawn
p(MP)	moon phase ($<1/4$, $1/4$, $1/2$, $1/2-3/4$, $>3/4$)
p(MO)	moon present for >6 hours during survey night
p(IP)	irrigation or precipitation within 24 hours of survey
p(MOMP)	moon phase and moon present for >6 hours during survey night
p(TMP)	temperature at dawn and moon phase
p(TMO)	temperature at dawn and moon present >6 hours during survey night
p(TIP)	temperature at dawn and irrigation or precipitation within 24 hours of survey
p(TMOMP)	temperature at dawn and moon phase and moon present for >6 hours during survey night
p(MOMPIP)	moon phase and moon present for >6 hours during survey night and irrigation or precipitation within 24 hours of survey

Minimum Number Alive

For the remaining species that had too few individuals (≤ 8) captured to allow for model-based analysis, I calculated minimum number alive (MNA) estimates for each trapline per site per season. I surveyed each site once per season. MNA was the total number of unique individuals captured at each trapline within each site. MNA provided an index of population size while allowing for a comparison of metrics across sites, traplines, and seasons (Slade and Blair 2000, Cramer and Willig 2005).

For each species captured, I summarized its responses as positive, negative, neutral, or absent for each site. I summarized responses by conservation and sugarcane land-uses and the interface by averaging species' responses relative to each other for every site. For species with captures that only allowed for analysis across the entire study, I summarized response for each land-use and the interface.

RESULTS

I trapped during the dry season from 5 July–13 October 2008 and wet season from 28 October 2008–10 January 2009, for 21,564 trap nights (dry season = 9,648 trap nights [8,640 Sherman trap; 1,008 pitfall] and wet season = 11,916 trap nights [8,640 Sherman trap; 3,276 pitfall]). During the dry season pitfall trapping was restricted to 1 site (Hlane/Mbuluzi).

I captured 1,725 unique individuals of 13 species (Table 2.4). I evaluated responses to the gradient for 5 species (*Aethomys ineptus*, *Lemniscomys rosalia*, *Mastomys natalensis*, *Mus minutoides*, *Steatomys pratensis*) using capture–recapture analysis and for 5 species (*Crocidura hirta*, *Elephantulus brachyrhynchus*, *Suncus lixus*,

Table 2.4. Total number of small mammal individuals by species captured at each trapline with distance (m) in parentheses, from 5 July 2008–10 January 2009 in the Lowveld of Swaziland.

Species	Trapline (distance)									Totals
	1(+375)	2 (+225)	3 (+150)	4 (+75)	5 (0)	6 (-75)	7 (-150)	8 (-225)	9 (-375)	
<i>Aethomys ineptus</i>	23	16	15	36	21	4	2	9	0	126
<i>Dendromus mystacalis</i>	0	0	1	0	0	0	0	0	1	2
<i>Elephantulus brachyrhynchus</i>	3	2	0	5	0	0	0	0	0	10
<i>Lemniscomys rosalia</i>	6	21	28	17	13	26	19	19	41	190
<i>Mastomys natalensis</i>	61	71	69	70	68	121	107	135	174	876
<i>Mus minutoides</i>	25	25	25	30	37	45	36	33	25	281
<i>Saccostomys campestris</i>	8	6	4	7	13	1	2	1	0	42
<i>Steatomys pratensis</i>	16	17	15	19	5	0	0	0	0	72
<i>Gerbilliscus leucogaster</i>	4	8	8	2	6	5	2	0	0	35
<i>Crocidura fuscomurina</i>	0	3	0	0	1	3	1	2	3	13
<i>Crocidura hirta</i>	5	10	6	9	11	4	1	4	2	52
<i>Crocidura silacea</i>	0	0	0	0	0	1	0	0	1	2
<i>Suncus lixus</i>	6	0	1	3	1	1	0	0	0	12
<i>Crocidura sp.</i>	3	0	1	5	1	1	0	0	1	12
Total Individuals Captured	160	179	173	203	177	212	170	203	248	1725

Gerbilliscus leucogaster, *Saccostomys campestris*) using occupancy analysis. Although more individuals of *Crocidura hirta* were captured than individuals of *Saccostomys campestris*, distribution of captures didn't allow for capture-recapture analysis. In addition, it was possible to conduct occupancy modeling on some species only during the dry (*Elephantulus brachyrhynchus*) and wet (*Crocidura hirta*, and *Suncus lixus*) seasons due to differences in number of captures between seasons.

Capture-recapture

My analysis indicated that trap response varied between species (Table 2.5). *Aethomys ineptus* and *Steatomys pratensis* shared a time dependent trap response (M_t), the probability of capture (p) increased with time (trap nights: 1–4) for *Steatomys pratensis* ($p_1 = 0.08$, SE = 0.03; $p_4 = 0.18$, SE = 0.07; Tables 2.5, A-5). The probability of capture for *Aethomys ineptus* varied across sites without a clear pattern (Table A-3). *Lemniscomys rosalia* had a time-varying behavioral probability (M_{tb}) where probability of capture increased with time, while the probability of recapture decreased ($p_1 = 0.10$, SE = 0.02, $p_4 = 0.46$, SE = 0.04; $c_1 = 0.54$, SE = 0.1; $c_2 = 0.33$, SE = 0.05; Tables 2.5, A-5). *Mastomys natalensis* had an increase in recapture probability, or a trap happy response (M_b) across all distance groupings and sites (Tables 2.5, A-3). *Mus minutoides* showed no variation in trap response (M_o ; Hlane/Mbuluzi: $p = 0.07$, SE = 0.02; Crookes: $p = 0.13$, SE = 0.03; Nisela: $p = 0.03$, SE = 0.02; Tables 2.5, A-3).

I combined the resultant trap response models with site heterogeneity models to yield best fitting models of differing complexity (Table 2.6). For *Aethomys ineptus*, *Mastomys natalensis*, and *Mus minutoides* the capture-recapture models indicated that

site was an important factor for explaining the variability in capture probability (best fitting model: *Aethomys ineptus* = site, *Mastomys natalensis* = site, 3cane, 3mid; *Mus minutoides* = site; Table 2.6). The models for *Steatomys pratensis*, *Mus minutoides*, and *Mastomys natalensis* showed additional variability that could be attributed to the spatial location of the trapline (*Steatomys pratensis*: cane $\Delta AIC_C = 0.28$, *Mus minutoides*: site, cane $\Delta AIC_C = 0.59$; Table 2.6). Trends for the effect of sugarcane on capture probability were variable for *Steatomys pratensis*, *Mus minutoides*, and *Mastomys natalensis* and varied among sites. *Steatomys pratensis* was the only species whose best fitting model showed an influence of season on capture probability ($\Delta AIC_C = 0.03$) and *Lemniscomys rosalia* (best fitting model = [.]) explained all variability through the trap response models (Table 2.6).

Using the resulting best fitting model, I derived the abundances (\hat{N}) of each species for each trapline per site per season (Figs. 2.4–2.8). Abundance estimates showed differing patterns for most species. *Mastomys natalensis* and *Lemniscomys rosalia* exhibited a similar trend in abundance (Figs. 2.4, 2.5). Both species showed increased abundance with distance into the sugarcane at both Hlane/Mbuluzi and Nisela. However, at Crookes they showed slightly different trends,

Table 2.5. Number of parameters (k), AIC_c, and ΔAIC_c values for *a priori* trap heterogeneity models of *Mastomys natalensis* (MANA), *Mus minutoides* (MUMI), *Lemniscomys rosalia* (LERO), *Aethomys ineptus* (AEIN), and *Steatomys pratensis* (STPR) in the Lowveld of Swaziland. Best fitting models are in bold.

Trap heterogeneity model ^{a,c}	Species														
	MANA			AEIN			LERO			MUMI			STPR ^b		
	k	AIC _c	ΔAIC _c	k	AIC _c	ΔAIC _c	k	AIC _c	ΔAIC _c	k	AIC _c	ΔAIC _c	k	AIC _c	ΔAIC _c
M ₀	1	4801.91	21.73	1	664.19	1.71	1	881.38	78.62	1	757.20	0	1	212.21	12.31
M _t	4	4802.98	22.80	4	662.48	0	4	806.16	3.40	4	758.95	1.76	4	199.90	0
M _b	2	4780.17	0	2	665.36	2.89	2	878.04	75.28	2	758.70	1.51	2	214.02	14.12
M _{tb}	6	4783.56	3.38	6	666.16	3.69	6	802.76	0	6	760.72	3.53	5		

^a Parameter abbreviations: (0) constant trap response, (t) time varying trap response, (b) behavioral trap response, and (tb) time varying, behavioral trap response.

^b Blank indicates model with overdispersed data

^c -2log likelihood for top models: MANA = 4776.17, AEIN = 654.4, LERO = 790.64, MUMI = 755.19, STPR = 191.71.

Table 2.6. Number of parameters (k), AIC_c, and Δ AIC_c values for the top (Δ AIC_c < 2) *a priori* site heterogeneity models of *Mastomys natalensis* (MANA), *Mus minutoides* (MUMI), *Lemniscomys rosalia* (LERO), *Aethomys ineptus* (AEIN), and *Steatomys pratensis* (STPR) in the Lowveld of Swaziland. Best fitting models are in bold.

Species	Site heterogeneity model ^a	k	AIC _c ^b	Δ AIC _c
MANA	(site;3cane,3mid)	18	4770.44	0
MUMI	(site)	3	753.37	0
	(site;cane)	6	753.96	0.59
	(HI/Cr)	2	754.17	0.80
	(HI/Cr;season)	4	755.20	1.83
	(site;season)	6	755.24	1.87
LERO	(.)	6	802.76	0
AEIN	(site)	12	657.76	0
STPR	(.)	4	199.90	0
	(season)	8	200.18	0.03
	(cane)	8	200.18	0.28

^aParameter abbreviations: (.) constant, (site) site location, (season) wet or dry, (HI/Cr) site grouping by vegetation condition, (cane) landuse type, (3 cane, 3 mid) grouping of traplines: 3 sugarcane (6–9), 3 middle (4–6), and 3 conservation landuse (1–3).

^b-2logLikelihood for top models: MANA = 4734.25, MUMI = 747.34, LERO = 790.64, AEIN = 633.13, STPR = 191.71.

where *Lemniscomys rosalia* was more abundant farthest into the sugarcane (375 m; dry season: $\hat{N} = 6.57$, SE = 1.48, wet season: $\hat{N} = 7.88$, SE = 1.63) than within the remainder of the sugarcane. There was a significant peak in abundance 150–75 m ($\hat{N} = 9.2$, SE = 1.77) into the conservation lands during the dry season (Fig. 2.5). At Crookes, *Mastomys natalensis* exhibited different trends across seasons with a decrease in abundance with increased distance into the sugarcane during the dry season and the opposite of this trend during the wet season (Fig. 2.4). Changes in abundance across the gradient were less at Crookes than for the other sites.

Aethomys ineptus had significantly lower abundances in the sugarcane (average difference between traplines 5 and 6 = 4.12) than in conservation lands and was not present farthest into the sugarcane (375 m; Fig. 2.6). Additionally, there was a peak in abundance at 75 m (trapline 4) within each conservation area (Hlane: dry, $\hat{N} = 9.97$, SE = 1.07; wet, $\hat{N} = 11.08$, SE = 1.13; Crookes: dry, $\hat{N} = 8.48$, SE = 2.07; wet, $\hat{N} = 12.72$ SE = 2.64; Nisela: dry, $\hat{N} = 7.01$, SE = 3.74; wet, $\hat{N} = 0$, SE = 0). Abundances also varied between sites, the average abundance was lowest at Nisela Farms (Hlane: dry, $\bar{x} = 4.43$, wet, $\bar{x} = 5.29$; Crookes: dry, $\bar{x} = 2.82$, wet, $\bar{x} = 3.61$; Nisela: dry, $\bar{x} = 0.98$, wet, $\bar{x} = 0.39$). Abundance trends were similar across seasons.

Generally, it can be noted that *Mus minutoides* was present at all distances, and persisted to the farthest sugarcane (375-m) trapline (Fig. 2.7; appendix). At Crookes, the species exhibited highest abundance near the interior edge (75–150 m into the

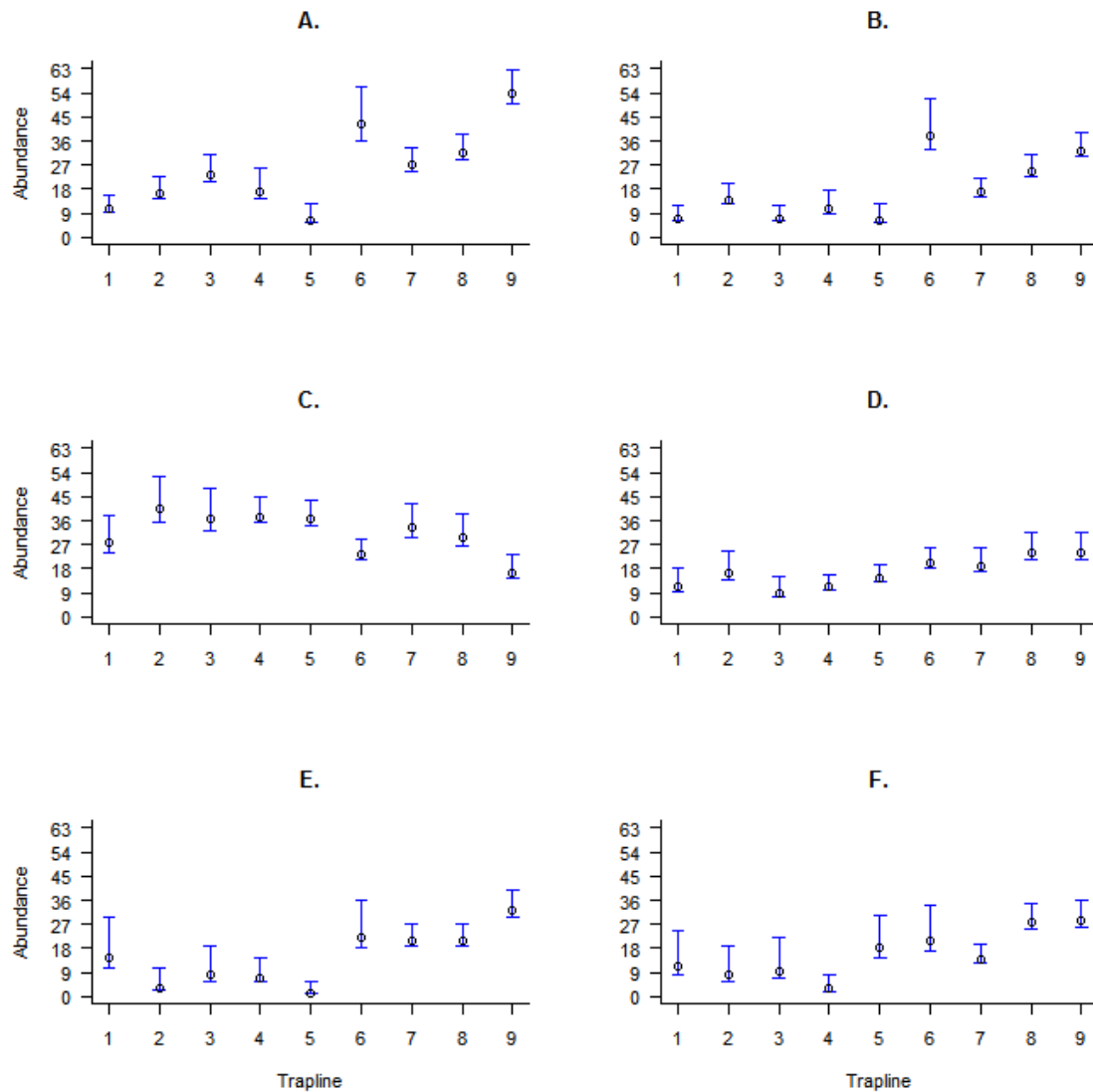


Figure 2.4. Derived abundance estimates (\hat{N}) with 95% confidence limits at each trapline for *Mastomys natalensis* in the Lowveld of Swaziland. Abundance estimates are for the 2008 dry (A, C, E) and 2008 wet (B, D, F) seasons in Hlane-Mbuluzi (A, B), Crookes (C, D), and Nisela (E, F). Traplines span the land-use gradient (1 = 375 m, 2 = 225 m, 3 = 150 m, 4 = 75 m into the conservation area, 5 = interface [0 m], and 6 = 75 m, 7 = 150, 8 = 225 m, 9 = 375 m into the sugarcane).

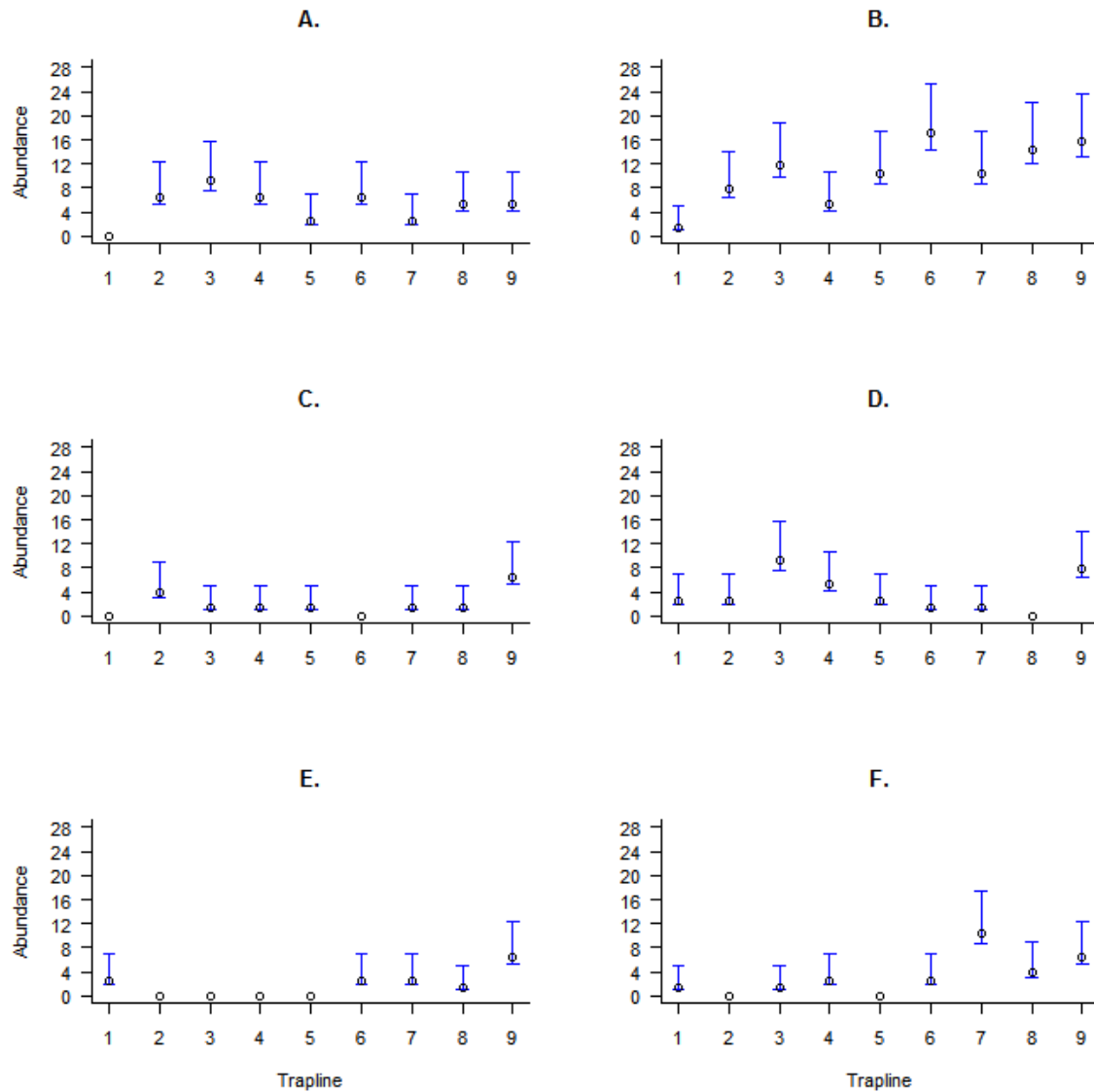


Figure 2.5. Derived abundance estimates (\hat{N}) with 95% confidence limits at each trapline for *Lemniscomys rosalia* in the Lowveld of Swaziland. Abundance estimates are for the 2008 dry (A, C, E) and 2008 wet (B, D, F) seasons in Hlane-Mbuluzi (A, B), Crookes (C, D), and Nisela (E, F). Traplines span the land-use gradient (1 = 375 m, 2 = 225 m, 3 = 150 m, 4 = 75 m into the conservation area, 5 = interface [0 m], and 6 = 75 m, 7 = 150, 8 = 225 m, 9 = 375 m into the sugarcane).

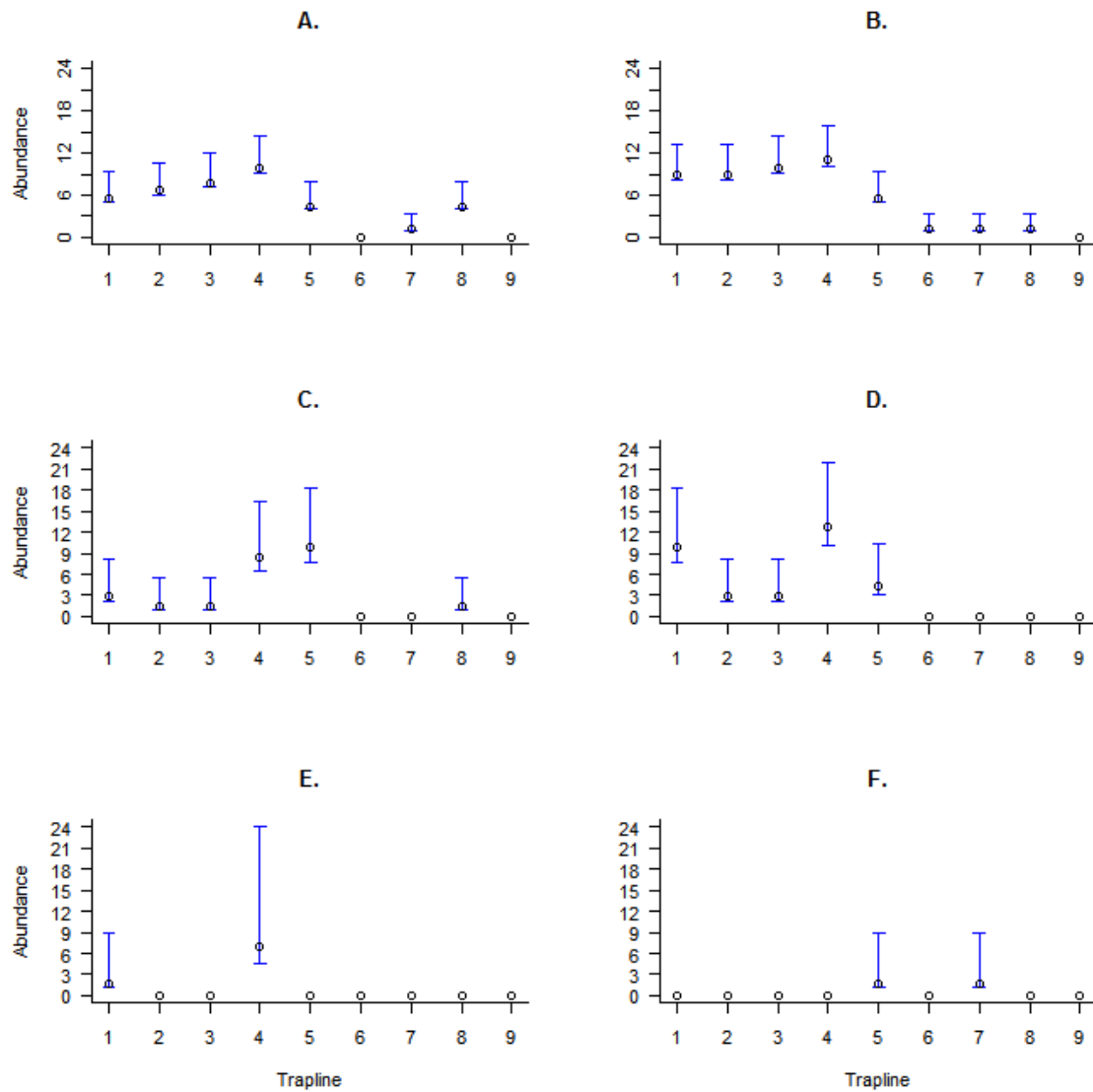


Figure 2.6. Derived abundance estimates (\hat{N}) with 95% confidence limits at each trapline for *Aethomys ineptus* in the Lowveld of Swaziland. Abundance estimates are for the 2008 dry (A, C, E) and 2008 wet (B, D, F) seasons in Hlane-Mbuluzi (A, B), Crookes (C, D), and Nisela (E, F). Traplines span the land-use gradient (1 = 375 m, 2 = 225 m, 3 = 150 m, 4 = 75 m into the conservation area, 5 = interface [0 m], and 6 = 75 m, 7 = 150, 8 = 225 m, 9 = 375 m into the sugarcane).

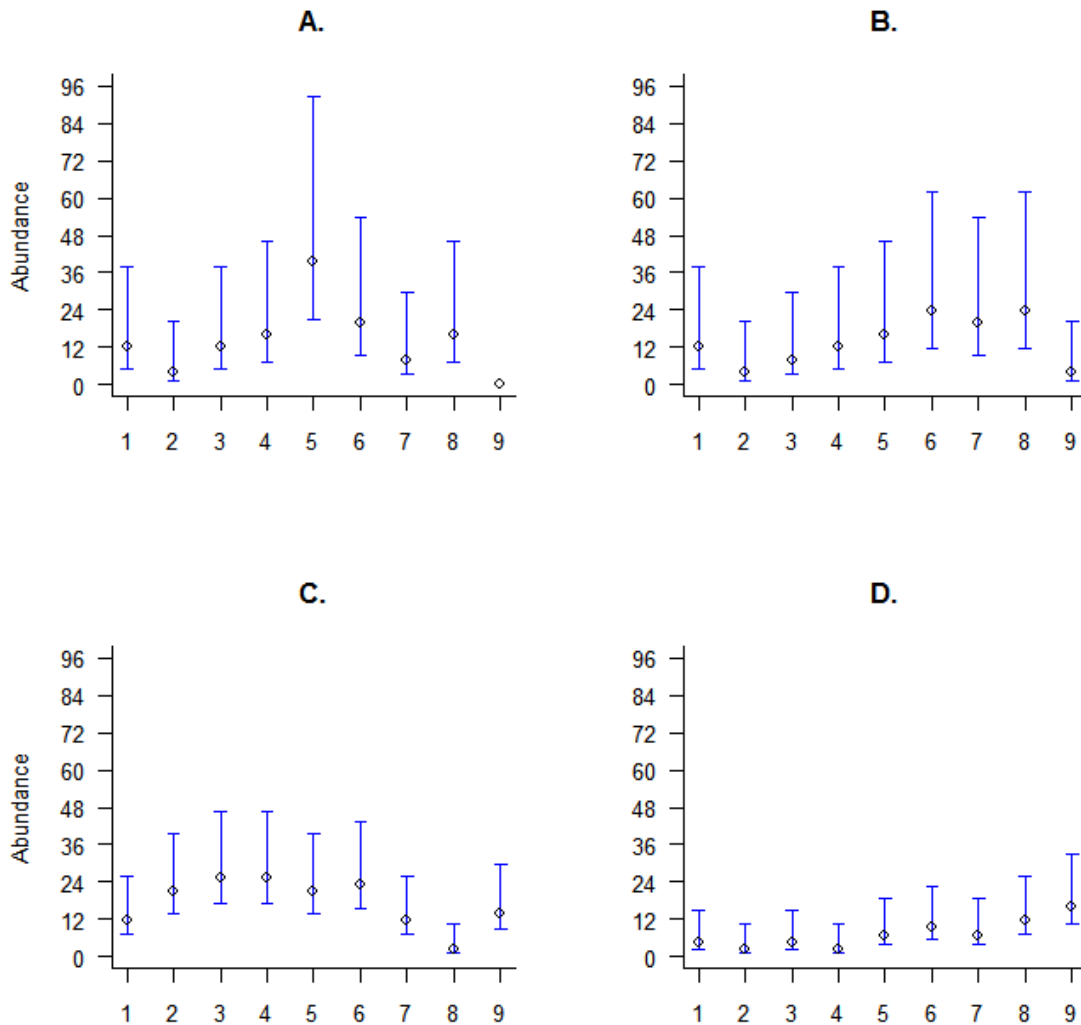


Figure 2.7. Derived abundance estimates (\hat{N}) with 95% confidence limits at each trapline for *Mus minutoides* in the Lowveld of Swaziland. Abundance estimates are for the 2008 dry (A, C) and 2008 wet (B, D) seasons in Hlane-Mbuluzi (A, B) and Crookes (C, D). Traplines span the land-use gradient (1 = 375 m, 2 = 225 m, 3 = 150 m, 4 = 75 m into the conservation area, 5 = interface [0 m], and 6 = 75 m, 7 = 150, 8 = 225 m, 9 = 375 m into the sugarcane). Nisela was omitted due large confidence intervals.

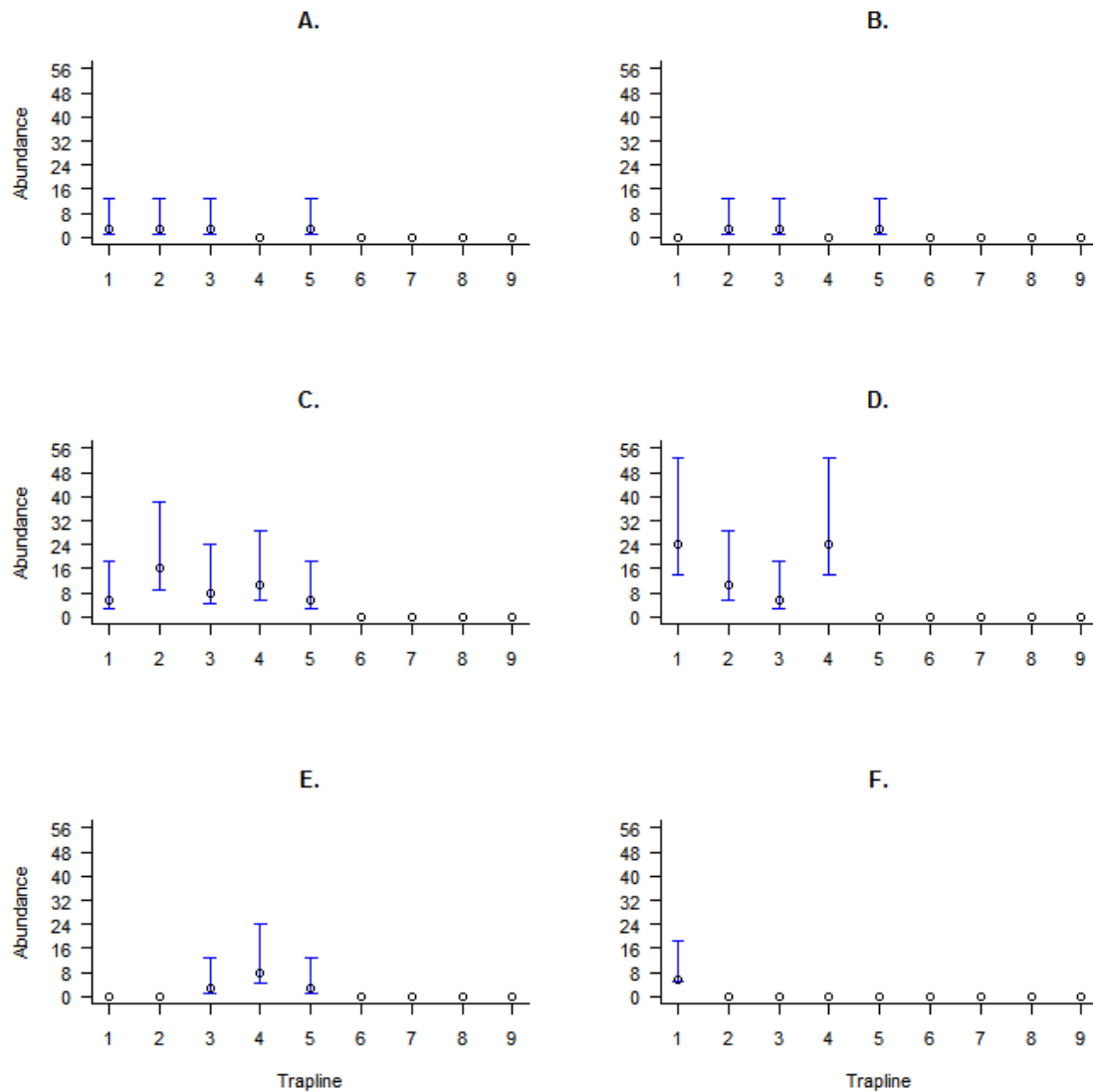


Figure 2.8. Derived abundance estimates (\hat{N}) with 95% confidence limits at each trapline for *Steatomys pratensis* in the Lowveld of Swaziland. Abundance estimates are for the 2008 dry (A, C, E) and 2008 wet (B, D, F) seasons in Hlane-Mbuluzi (A, B), Crookes (C, D), and Nisela (E, F). Traplines span the land-use gradient (1 = 375 m, 2 = 225 m, 3 = 150 m, 4 = 75 m into the conservation area, 5 = interface [0 m], and 6 = 75 m, 7 = 150, 8 = 225 m, 9 = 375 m into the sugarcane).

conservation land-use) during the dry season ($\hat{N} = 25.46$, SE = 6.99). During the wet season, abundance increased with distance into the sugarcane. At Hlane, highest abundance of *Mus minutoides* was associated with the interface (0 m) during the dry season ($\hat{N} = 39.76$, SE = 16.64), and during the wet season increased from 75–225 m with lowest abundance farthest into the sugarcane ($\hat{N} = 3.98$, SE = 3.66).

Steatomys pratensis was not present in the sugarcane at any of the sites (Fig. 2.8). Additionally, abundance varied widely between sites (Hlane, dry, $\bar{x} = 2.15$, wet $\bar{x} = 1.61$; Crookes, dry, $\bar{x} = 9.13$, wet, $\bar{x} = 12.89$; Nisela: dry, $\bar{x} = 2.69$, wet, $\bar{x} = 1.07$) and across the gradient. Abundance at the land-use interface (Crookes, dry, $\hat{N} = 5.37$, SE = 3.29; wet $\hat{N} = 0$, SE = 0; Nisela, dry, $\hat{N} = 2.68$, SE = 2.23; wet, $\hat{N} = 0$, SE = 0) was lower than 75 m into the conservation lands.

Occupancy Modeling

Dry Season.— I conducted dry season occupancy modeling for 2 species (*Saccostomys campestris*, *Elephantulus brachyrhynchus*). The best detection model for both species was the constant detection model (Table 2.7). Subsequent occupancy models indicated an effect of site and land-use interface on the distribution of the 2 species (best models: *Saccostomys campestris* = [site; 4res, edge]; *Elephantulus brachyrhynchus* = [site; 4res]; Table 2.8). *Elephantulus brachyrhynchus* was absent from the interface and sugarcane, as well as, the Nisela site (Table 2.9). *Saccostomys campestris* had the highest probability of presence (ψ) at the interface (0 m) of each site (Hlane/Mbuluzi: $\psi = 0.79$, SE = 0.24; Crookes: $\psi = 0.42$, SE = 0.3; Nisela: $\psi = 0.22$, SE = 0.22), with higher probability of presence in the conservation lands than the sugarcane,

Table 2.7. The number of parameters (k), AIC_c, and Δ AIC_c values for *a priori* detection models of *Saccostomys campestris* (SACA) and *Elephantulus brachyrhynchus* (ELBR) in the Lowveld of Swaziland during the 2008 dry (April-September) season. Best fitting models are in bold.

Detection model ^{a, b}	Species					
	SACA			ELBR		
	k	AIC _c	Δ AIC _c	k	AIC _c	Δ AIC _c
p(.)	2	110.52	0	2	69.68	0
p(T)	3	111.54	1.02	3	71.75	2.07
p(MP)	3	110.98	0.46	3	71.74	2.06
p(MO)	3	111.46	0.94	3	71.76	2.08
p(IP)	3	111.55	1.03	3	71.71	2.03
p(MOMP)	4	112.12	1.6	4	73.89	4.21
p(TMP)	4	111.94	1.42	4	73.9	4.22
p(TMO)	4	113.58	3.06	4	73.91	4.23
p(TIP)	4	113.7	3.18	4	73.66	3.98
p(TMOMP)	5	113.98	3.46	5	76.09	6.41
p(MOMPIP)	5	114.26	3.74	5	75.91	6.23

^a Parameter abbreviations: (.) constant detection, (T) temperature at dawn, (MP) moon phase, (MO) moon present >6 hours of night, and (IP) irrigation or precipitation within 24 hours of survey.

^b -2logLikelihood of top models: SACA = 105.23, ELBR = 65.57.

Table 2.8. The number of parameters (k), AIC_c, and Δ AIC_c values for the top (Δ AIC_c < 2) *a priori* occupancy models of *Saccostomys campestris* (SACA), *Elephantulus brachyrhynchus* (ELBR), *Crocidura hirta* (CRHI), *Suncus lixus* (SULI), and *Gerbilliscus leucogaster* (GELE) in the Lowveld of Swaziland during the 2008 wet (October–March) and 2008 dry (April–September) seasons. Best fitting models are in bold.

Species	Season							
	Dry				Wet			
	Occupancy model ^{a,b}	k	AIC _c	Δ AIC _c	Occupancy model ^{a,b}	k	AIC _c	Δ AIC _c
SACA	$\psi(\text{site}+4\text{res},\text{edge})$	6	105.73	0	$\psi(\text{site}+\text{cane})$	5	156.3	0
	$\psi(\text{site}+3\text{cane},3\text{mid})$	6	105.75	0.02	$\psi(\text{site}+4\text{res},\text{edge})$	6	158.18	1.88
	$\psi(\text{HI}/\text{Cr}+3\text{cane},3\text{mid})$	5	105.97	0.24				
	$\psi(\text{HI}/\text{Cr}+4\text{res},\text{edge})$	5	106.32	0.59				
	$\psi(3\text{cane},3\text{mid})$	4	106.59	0.86				
	$\psi(4\text{res},\text{edge})$	4	107.19	1.46				
ELBR	$\psi(\text{site}+4\text{res})$	5	63.16	0				
	$\psi(\text{HI}/\text{Cr}+4\text{res})$	4	61.2	1.96				
CRHI					$\psi(3\text{cane},3\text{mid})$	4	170.28	0
					$\psi(\text{cane})$	3	171.35	1.07
					$\psi(\text{HI}/\text{Cr}+3\text{cane},3\text{mid})$	5	171.44	1.16
					$\psi(4\text{res})$	3	171.58	1.3
					$\psi(.)$	3	171.86	1.58
SULI					$\psi(\text{cane})$	3	81.06	0
					$\psi(.)$	2	81.14	0.08
					$\psi(4\text{res})$	3	81.99	0.93
GELE					$\psi(\text{cane})$	3	130.85	0
					$\psi(3\text{cane},3\text{mid})$	4	132.35	1.5
					$\psi(\text{site}+\text{cane})$	5	132.58	1.73
					$\psi(4\text{res})$	3	132.77	1.92
					$\psi(\text{HI}/\text{Cr}+\text{cane})$	4	132.8	1.95

^a Parameter abbreviations: (.) constant occupancy, (site) site location, (HI/Cr) site grouping by vegetation condition, (cane) landuse type, (3cane, 3 mid) grouping of traplines: 3 sugarcane, 3 middle, and 3 conservation landuse, (4res) grouping of traplines: 4 interior conservation area, edge/sugarcane, and (4res,edge) grouping of traplines: 4 interior conservation area, edge, and sugarcane.

^b -2logLikelihood of top models: Dry; SACA = 95.39, ELBR = 52.57, Wet; SACA = 146.3, CRHI = 162.28, SULI = 74.83, GELE = 123.25.

however this trend was not statistically significant (Table 2.9). Probability of presence varied between sites, the highest probability was at Hlane/Mbuluzi and lowest at Nisela.

Wet Season.—For wet season occupancy modeling, I included 2 shrew species (*Crocidura hirta*, *Suncus lixus*), as well as 2 rodents (*Gerbilliscus leucogaster*, *Saccostomys campestris*). As with the dry season, the best detection model for all species was the constant detection model (Table 2.10). Occupancy models varied by species, but all indicated that sugarcane affected their distributions (Table 2.8). *Crocidura hirta* had its highest probability of presence within 75 m of the interface (traplines 4–6, $\psi = 0.42$, SE = 0.18) in addition, the occupancy estimate was higher in the conservation areas than in the sugarcane, however, these were not statistically significant (conservation, $\psi = 0.37$, 95% CL = 0.13–0.70; sugarcane, $\psi = 0.11$, 95% CL = 0.02–0.38; Table 2.11). Occupancy models for *Crocidura hirta* attributed little variation to site differences. *Suncus lixus* had highest estimated probability of presence within the conservation land-use, and lower estimates in the sugarcane although these were not significant (conservation: $\psi = 0.10$, 95% CL = 0.04–0.24; sugarcane, $\psi = 0.03$, 95% CL = 0–0.17; Table 2.11). As with *Crocidura hirta*, *Suncus lixus* models attributed little variation to site differences (Table 2.11). *Gerbilliscus leucogaster* occupancy models also showed little influence of site on occupancy. However, there was a difference between land-use with occupancy estimates higher within the conservation lands than in the sugarcane although these were not statistically significant (conservation, $\psi = 0.15$, 95% CL = 0.08–0.27; sugarcane, $\psi = 0.04$, 95% CL = 0.01–0.15; Table 2.11).

Table 2.9. Maximum likelihood real estimates (MLE) of occupancy (ψ) probability with upper ($\uparrow 95\%$) and lower ($\downarrow 95\%$) 95% confidence intervals for the derived parameters of the top ranked model for each of *Saccostomys campestris* (SACA) and *Elephantulus brachyrhynchus* (ELBR) in the Lowveld of Swaziland during the 2008 dry (April–September) season. Traplines span the land-use gradient (1 = 375 m, 2 = 225 m, 3 = 150 m, 4 = 75 m into the conservation area, 5 = interface (0 m), and 6 = 75 m, 7 = 150, 8 = 225 m, 9 = 375 m into the sugarcane).

Site	Trapline	Species			
		SACA		ELBR	
		ψ		ψ	
		MLE	$\uparrow 95\%$	MLE	$\uparrow 95\%$
Hlane/ Mbuluzi	1-4	0.19	0.52	0.24	0.59
			0.05		0.07
			0.99		0.00
	5	0.79	0.18	0	0
			0.45		0.00
			0.03		0
	6-9	0.13	0.27	0	0.50
			0.01		0.04
			0.89		0.00
Crookes	1-4	0.04	0.06	0	0
			0.22		0.00
			0.00		0
	5	0.42	0.21	0	0.00
			0.00		0
			0.77		0.00
	6-9	0.03	0.02	0	0
			0.16		0.00
			0.00		0
Nisela	1-4	0.02	0.00	0	0
			0.77		0.00
			0.02		0
	5	0.22	0.16	0	0.00
			0.02		0
			0.16		0.00
	6-9	0.01	0.00	0	0
			0.00		0
			0.00		0

Table 2.10. The number of parameters (k), AIC_c, and Δ AIC_c values for *a priori* detection models of *Crocidura hirta* (CRHI), *Suncus lixus* (SULI), *Saccostomys campestris* (SACA), and *Gerbilliscus leucogaster* (GELE) in the Lowveld of Swaziland during the 2008 wet (October–March) season. Best fitting models are in bold.

Detection model ^{a,b}	Species											
	CRHI			SULI			SACA			GELE		
	k	AIC _c	Δ AIC _c	k	AIC _c	Δ AIC _c	k	AIC _c	Δ AIC _c	k	AIC _c	Δ AIC _c
p(.)	2	171.37	0	2	81.03	0	2	170.97	0	2	132.47	0
p(T)	3	172.69	1.32	3	82.99	1.96	3	172.9	1.93	3	134.59	2.12
p(MP)	3	171.65	0.28	3	83.84	2.81	3	172.55	1.58	3	134.5	2.02
p(MO)	3	172.09	0.72	3	82.94	1.91	3	172.61	1.64	3	134.46	1.99
p(IP)	3	172.46	1.09	3	82.62	1.59	3	172.52	1.55	3	134.49	2.02
p(MOMP)	4	172.86	1.49	4	84.06	3.03	4	174.71	3.74	4	136.61	4.14
p(TMP)	4	171.65	0.28	4	84.68	3.65	4	174.41	3.44	4	136.28	3.81
p(TMO)	4	173.46	2.09	4	83.08	2.77	4	174.12	3.26	4	135.99	3.52
p(TIP)	4	174.42	3.05	4	81.49	0.046	4	173.64	2.67	4	135.82	3.35
p(TMOMP)	5	173.44	2.07	5	85.48	4.45	5	176.59	5.62	5	138.18	5.71
p(MOMPIP)	5	173.43	2.06	5	82.79	1.76	5	176.82	5.85	5	138.75	6.28

^a Parameter abbreviations: (.) constant detection, (T) temperature at dawn, (MP) moon phase, (MO) moon present >6 hrs of night, and (IP) irrigation or precipitation within 24 h of survey.

^b -2logLikelihood for top models: CRHI = 167.26, SULI = 77.03, SACA = 166.86, GELE = 128.36.

Table 2.11. Maximum likelihood real estimates (MLE) of occupancy (ψ) and detection (p) probability with upper ($\uparrow 95\%$) and lower ($\downarrow 95\%$) 95% confidence intervals for the derived parameters of the top ranked model for each of *Crocidura hirta* (CRHI), *Suncus lixus* (SULI), *Saccostomys campestris* (SACA), and *Gerbilliscus leucogaster* (GELE) in the Lowveld of Swaziland during the 2008 wet (October–March) season. Traplines span the land-use gradient (1 = 375 m, 2 = 225 m, 3 = 150 m, 4 = 75 m into the conservation area, 5 = interface (0 m), and 6 = 75 m, 7 = 150, 8 = 225 m, 9 = 375 m into the sugarcane).

Site	Trapline	Species ^a							
		CRHI		SULI		SACA		GELE	
		ψ		ψ		ψ		ψ	
		MLE	$\uparrow 95\%$	MLE	$\uparrow 95\%$	MLE	$\uparrow 95\%$	MLE	$\uparrow 95\%$
			$\downarrow 95\%$		$\downarrow 95\%$		$\downarrow 95\%$		$\downarrow 95\%$
Hlane/Mbuluzi	1-3	0.37	0.7	0.1	0.24	0.54	0.76	0.15	0.27
			0.13		0.04		0.29		0.08
			0.75		0.24		0.76		0.27
	4	0.42		0.1		0.54		0.15	
			0.15		0.04		0.29		0.08
			0.75		0.24		0.76		0.27
	5	0.42		0.1		0.54		0.15	
			0.15		0.04		0.29		0.08
			0.75		0.24		0.76		0.27
	6	0.42		0.03		0.12		0.04	
			0.15		0.04		0.29		0.08
			0.75		0.18		0.37		0.16
	7-9	0.11		0.03		0.12		0.04	
			0.15		0		0.03		0.01
			0.38		0.18		0.37		0.16
			0.02		0		0.03		0.01

Table 2.11 continued.

Site	Trapline	Species ^a							
		CRHI		SULI		SACA		GELE	
		ψ		ψ		ψ		ψ	
		MLE	↑95%	MLE	↑95%	MLE	↑95%	MLE	↑95%
			↓95%		↓95%		↓95%		↓95%
Crookes	1-3	0.37	0.7	0.1	0.24	0.1	0.34	0.15	0.27
			0.13		0.04		0.03		0.08
			0.75		0.24		0.34		0.27
	4	0.42	0.1	0.1	0.1	0.1	0.15	0.15	0.08
			0.15		0.04		0.03		0.08
			0.75		0.24		0.34		0.27
	5	0.42	0.1	0.1	0.1	0.1	0.15	0.15	0.08
			0.15		0.04		0.03		0.08
			0.75		0.17		0.1		0.16
	6	0.42	0.03	0.01	0.01	0.01	0.04	0.04	0.01
			0.15		0		0		0.01
			0.38		0.17		0.1		0.16
Nisela	7-9	0.11	0.03	0.013	0.013	0.013	0.04	0.04	0.01
			0.02		0		0		0.01
			0.7		0.24		0.34		0.27
	1-3	0.37	0.1	0.1	0.1	0.1	0.15	0.15	0.08
			0.13		0.04		0.03		0.08
			0.75		0.24		0.34		0.27
	4	0.42	0.1	0.1	0.1	0.1	0.15	0.15	0.08
			0.15		0.04		0.03		0.08
			0.75		0.24		0.34		0.27

Table 2.11. continued

Site	Trapline	Species ^a							
		CRHI		SULI		SACA		GELE	
		ψ		ψ		ψ		ψ	
		MLE	↑95%	MLE	↑95%	MLE	↑95%	MLE	↑95%
			↓95%		↓95%		↓95%		↓95%
Nisela	5	0.42		0.1		0.1		0.15	
			0.15		0.04		0.03		0.08
			0.75		0.17		0.1		0.16
	6	0.42		0.03		0.01		0.04	
			0.15		0		0		0.01
			0.38		0.17		0.1		0.16
	7-9	0.11		0.03		0.01		0.04	
			0.02		0		0		0.01

Saccostomys campestris models showed an influence of both site and land-use (Table 2.8). At all sites, occupancy estimates were higher in the conservation lands than in the sugarcane, but this trend was not significant (Hlane-Mbuluzi, conservation, $\psi = 0.54$, 95% $CL = 0.29\text{--}0.76$, sugarcane, $\psi = 0.12$, 95% $CL = 0.03\text{--}0.37$; Crookes and Nisela, conservation, $\psi = 0.10$, 95% $CL = 0.03\text{--}0.34$, sugarcane: $\psi = 0.01$, 95% $CL = 0\text{--}0.10$; Table 2.11). Additionally, the estimated occupancy probability in the conservation lands at Hlane-Mbuluzi was higher ($\psi = 0.54$, 95% $CL = 0.29\text{--}0.76$) than at the other sites; which had the same derived occupancy estimates ($\psi = 0.1$, 95% $CL = 0.04\text{--}0.24$; Table 2.11).

Minimum Number Alive.—MNA estimates were calculated for the remaining 3 species (*Crocidura silacea*, *Crocidura fuscomurina*, and *Dendromus mystacalis*; Table 2.4). *Dendromus mystacalis* was present in the farthest interior sugarcane (375 m) trapline in a natural strip of vegetation, as well as, trapline 3 (150 m). Both of the shrew species were found within the sugarcane. *Crocidura silacea* was only captured within the sugarcane, and *Crocidura fuscomurina* had a higher average number of individuals found at each trapline within the sugarcane (conservation, $\bar{x} = 0.8$; sugarcane, $\bar{x} = 2.25$).

DISCUSSION

My study shows various effects of sugarcane cultivation on small mammal abundances and distributions (Table 2.12). Five (*Crocidura silacea*, *Crocidura fuscomurina*, *Mastomys natalensis*, *Mus minutoides* and *Lemniscomys rosalia*) of the 13

Table 2.12. Summary of species' generalized responses (positive [+], negative [-], neutral [=], absent [0]) by site (Hlane/Mbuluzi, Crookes, Nisela) to conservation and sugarcane land-uses and the subsequent interface in the Lowveld of Swaziland during the 2008 wet and dry seasons. The responses are averaged across seasons, relative to each other, and include the results of capture-recapture, occupancy, and minimum number alive analysis. For species with low number of captures, overall trends for all sites are given. Due to low number of individual captures, *Dendromys mystacalus* and *Crocidura silacea* are not presented.

Species	Relative response								
	Land-use								
	Conservation			Interface (0 m)			Sugarcane		
	Hlane/Mbuluzi	Crookes	Nisela	Hlane/Mbuluzi	Crookes	Nisela	Hlane/Mbuluzi	Crookes	Nisela
<i>Aethomys ineptus</i>	+	+	+	-	=	-	-	0	=
<i>Elephantulus brachyrhynchus</i>	+	+	0	0	0	0	0	0	0
<i>Lemniscomys rosalia</i>	-	+	-	=	=	-	+	-	+
<i>Mastomys natalensis</i>	-	=	-	-	=	=	+	=	+
<i>Mus minutoides</i>	-	+	-	+	+	=	+	=	+
<i>Saccostomys campestris</i>	+ (overall)			+ (overall)			- (overall)		
<i>Steatomys pratensis</i>	+	+	+	=	-	-	0	0	0
<i>Gerbilliscus leucogaster</i>	+ (overall)			= (overall)			- (overall)		
<i>Crocidura fuscomurina</i>	- (overall)			- (overall)			+ (overall)		
<i>Crocidura hirta</i>	+ (overall)			+ (overall)			- (overall)		
<i>Suncus lixus</i>	+ (overall)			= (overall)			- (overall)		

species encountered during my study were more abundant within sugarcane than in conservation lands at, in the least, one site or during one season (Table 2.12). Only 2 (*Crocidura silacea*, *Crocidura fuscomurina*) species were restricted to, or were more abundant, within the sugarcane at all sites.

Both *Crocidura silacea* and *Crocidura fuscomurina* are insectivores and the artificially moist environment of the sugarcane may increase the abundance of potential insect prey items. These shrew species also may benefit from competitive release they encounter by being able to persist within the sugarcane (Larsen 1986, Hughes et al. 1994). The most abundant shrew species (*Crocidura hirta*), and presumably dominant competitor of *Crocidura silacea* and *Crocidura fuscomurina*, had fewer individuals captured within the sugarcane. Although small sample sizes for these 2 shrew species limited the inferences that could be drawn, at minimum, sugarcane does not restrict the distribution of these insectivorous species and it is possible that sugarcane may provide favorable environmental conditions for these species within the Lowveld.

Generalists such as *Mastomys natalensis* and *Lemniscomys rosalia*, that opportunistically inhabit areas with favorable food availability and avoid areas with low grass cover (Monadjem 1997a, Monadjem and Perrin 1997;1998a;b, Yarnell et al. 2007) had similar responses to the land-use gradient. Abundance of *Mastomys natalensis* and *Lemniscomys rosalia* increased with distance into the sugarcane at both Hlane/Mbuluzi and Nisela (Table 2.12). It appears that sugarcane may be selected for when the adjoining lands have low grass cover due to brush encroachment (Hlane-Mbuluzi), or overutilization (Nisela).

Furthermore, the continued increase of *Lemniscomys rosalia* and *Mastomys natalensis* abundance with distance into the sugarcane monoculture at Hlane-Mbuluzi and Nisela for all traplines indicates that interface related changes may extend farther into patches than has previously been described for small mammals and other taxa (Ries et al. 2004).

Widespread species (Taylor 1998, Skinner and Chimimba 2005), such as *Mus minutoides* and *Crocidura hirta*, appeared to select areas within 75 m of the land-use interface. Wide-ranging species generally can exploit many different vegetation types and may have highest abundances near the interface due to complementary resources found near the interface, a scenario that was first described by Leopold (1933). Furthermore, neither *Mus minutoides*, an omnivore with a low proportion of seeds in its diet (Monadjem 1997a, Taylor 1998) nor *Crocidura hirta*, predominantly an insectivore (Taylor 1998) rely on seeds in their diet. Insects and herbaceous material are likely more prevalent in sugarcane than seeds due to weed control measures. In areas bordering agricultural systems, it appears that species with wide tolerances of vegetation types and a low proportion of seeds in their diet may increase abundance along the land-use interface.

Species (*Aethomys ineptus*, *Elephantulus brachyrhynchus*, *Steatomys pratensis*, *Saccostomys campestris*, *Gerbilliscus leucogaster*) with restricted environmental tolerances or diets were excluded from, or had reduced abundances in the sugarcane. Even for widespread species sugarcane may not provide analogous environmental features. For *Aethomys ineptus*, despite being omnivorous (Monadjem 1997b) and

tolerant of a wide range of vegetation types (Linzey and Kesner 1997, Monadjem 1997a, Fitzherbert et al. 2007), sugarcane may not provide features approximating shrubs, trees or rocky substrates. Furthermore, sugarcane may not be conducive to fossorial and semi-fossorial mammals. The exclusion of *Steatomys pratensis* from sugarcane, despite its use of cultivated lands in other parts of its range (Taylor 1998), may be attributable to its use of excavated burrows (De Graaff and Nel 1992) which may be subject to flooding, or other adverse effects from the high soil moisture found within the sugarcane. Species (*Steatomys pratensis*, *Saccostomys campestris*) that had a high proportion of seeds in their diet (Kerley 1992, Miller 1994, Monadjem 1997b) also were detrimentally affected by sugarcane. Sugarcane lacks large seeds, especially *Acacia spp.*, which have been shown to be selected for in the diet of *Saccostomys campestris* (Kerley 1989). Species (*Gerbilliscus leucogaster*) that select for low ground cover (Monadjem 1997) also were negatively affected by the sugarcane.

Despite varying responses from negatively affected species (*Aethomys ineptus*, *Elephantulus brachyrhynchus*, *Steatomys pratensis*, *Saccostomys campestris*, *Gerbilliscus leucogaster*), all were absent at 375 m into the sugarcane, suggesting that sugarcane might be impermeable to a large number of small mammal species. Currently, there is likely limited connectivity and hindered dispersal ability for small mammal populations that inhabit conservation areas separated by the expanses of sugarcane that cover a considerable portion (~8%) of Swaziland's lowveld savanna, and other areas throughout the region (Lankford 2007). Furthermore, the low presence of *Aethomys ineptus*, *Elephantulus brachyrhynchus*, *Steatomys pratensis*, *Saccostomys*

campestris and *Gerbilliscus leucogaster* in the matrix indicates that they may be more prone to expatriation (Laurance 1991).

Only *Aethomys ineptus* and *Steatomys pratensis* had reduced abundance at the interface (0 m), which is a seemingly deleterious edge effect for these species. The interface associated reduction in abundance could hinder conservation by decreasing the effective area of conservation for small mammal species and increase their susceptibility to the effects of habitat fragmentation (Sisk et al. 1997, Ewers et al. 2007). This edge effect could be due to predator activity, edge avoidance behavior, or management practices (Hughes et al. 1994, Lidicker 1999, Dijak and Thompson 2000). Increased predator activity may also explain the trend of increasing abundance with distance into the sugarcane for both *Lemniscomys rosalia* and *Mastomys natalensis*. Management practices at all of the sites included maintenance of access roads or mowed firebreaks, which reduced available habitat at the interface. Edge avoidance may have combined with decreased permeability of the interface to create a “fence effect”, producing higher abundances at the interior (75 m) traplines from decreased dispersal potential (Gaines and McClenaghan 1980, Stamps et al. 1987).

Overall, there were few changes between seasons for different species, which may be due to the wet season characteristics during my study. The 2008–2009 wet season was marked by late arrival of significant rains. Other factors, such as sugarcane harvesting, may be more important in explaining the minor changes in abundance trends between seasons. During the harvest, fields are burned and then the biomass is completely removed, leaving bare ground.

The interplay between sugarcane plantations and different land-uses is highly complex. The implications for wildlife populations need to be examined further; describing the effects of sugarcane matrices represents a first step toward adequate understanding of this system and mitigating the effects of sugarcane-induced habitat fragmentation.

CHAPTER III

EFFECTS OF INTENSIVE AGRICULTURE ON SMALL MAMMAL COMMUNITIES IN AND ADJACENT TO CONSERVATION AREAS IN THE LOWVELD OF SWAZILAND

SYNOPSIS

Throughout southern Africa, land conversion due to sugar production is responsible for widespread fragmentation of native vegetation. I studied the effect of sugarcane (*Saccharum* spp.) plantations and their interfaces on small mammal communities along a gradient extending 375 m from the interface into agriculture and conservation land-uses. I trapped small mammals at 3 sites during dry and wet seasons using Sherman live-traps. Species richness and diversity significantly decreased at the interface of 2 land-uses at 2 of my sites, while there was increased diversity associated with the interface at 1 site. An Analysis of Similarity indicated a difference in community composition between the 2 land-uses and a large difference between the farthest interior conservation area (375 m)/interface (0 m) and the farthest interior sugarcane (375 m). Additionally, there was no difference in community composition (species proportions) between seasons or across distances within the conservation area. However, the farthest interior sugarcane trapline had increased divergence from other traplines within the sugarcane land-use. The farthest sugarcane distance (375 m) may be

of importance for conservation areas that seek to minimize the effects of habitat fragmentation in lowveld savanna throughout Southern Africa.

INTRODUCTION

Worldwide agriculture is the dominant land-use, responsible for land conversion and habitat fragmentation on a massive scale (Ramankutty and Foley 1999, Ellis and Ramankutty 2008, Ramankutty et al. 2008). Furthermore, agriculture-induced fragmentation is expected to continue for at least the next 50 years (Tilman et al. 2001, Foley et al. 2005). In agricultural landscapes, patches of intact native vegetation are often surrounded by a matrix of croplands, which may have implications for biodiversity (Tilman et al. 2001, Donald and Evans 2006). Isolated wildlife populations have shown reduced viability and gene flow and increased susceptibility to stochastic events (Saunders et al. 1991, Andren 1994, Begon et al. 2006). Despite the prevalence of the agricultural land-use matrix, relatively few studies have evaluated the agriculture land-use matrix's effects on wildlife communities, and small mammals in particular (Prevedello and Vieira 2010). Moreover, most fragmentation studies have not incorporated edge effects in their designs, even though edge effects are integral to understanding landscape processes (Laurance 2008).

Within the lowveld areas of Swaziland and throughout southern Africa, areas of native vegetation have been converted into sugar production (Hackel 1993, Lankford 2007). In the Swazi lowveld, all major sugarcane (*Saccharum* spp.) plantations adjoin areas managed for wildlife conservation, sustainable grazing, or wildlife viewing, all of which can be thought of as *de facto* conservation areas (Monadjem and Garcelon 2005).

There have been no studies examining how wildlife responds to intensive agriculture bordering these *de facto* conservation areas in Swaziland, or within Southern Africa. Moreover, no studies examined the spatial extent, and temporal variation of interface-related changes on wildlife communities.

Small mammals play an important role in most ecosystems, including lowveld savanna *Acacia* communities found in southern and east Africa (Peterson 2006). Through herbivory and seed predation small mammals can drastically affect vegetative communities (Keesing 2000, Manson et al. 2001). Small mammals also play a role as prey items for a wide array of species, are nest predators, and occupy a range of niches (Skinner and Chimimba 2005). Additionally, small mammal communities are correlated with vegetation variables making them useful indicators of rangeland health; an incomplete assemblage of small mammal species may indicate a decrease in the functioning of ecosystem processes (Avenant and Cavallini 2007). Understanding the response of small mammal communities to the interface of agricultural and conservation land-uses may elicit insights about the extent of changes in both the vegetative and wildlife communities.

In this study, I examined variation in diversity, species richness, and composition of small mammal communities across a conservation-agriculture land-use interface on a gradient extending into each land-use type. I evaluated responses during the wet and dry seasons, and described the spatial extent of changes in community parameters, in relation to the land-use interface.

STUDY AREA

My study was conducted in the Lowveld of Swaziland, the low-lying region between the northern Drakensburg Escarpment to the west and the Lubombo Mountains to the east (Fig. 2.1). The Lowveld lies in the eastern half of the country and is its lowest, warmest, and driest region, elevation is 150–400 m above sea level, with annual precipitation averaging between 550–725 mm (Matondo et al. 2005). The Lowveld's mean average temperature is 22°C with mean monthly temperatures of 26°C in January and 18°C in July (Monadjem 1999). Swaziland has a subtropical climate, and exhibits distinct wet (October–March) and dry (April–September) seasons, 75% and 25% of rains fall during these respective seasons (Matondo et al. 2004). The Lowveld is prone to droughts due to the combination of erratic rain events and high summer temperatures (Matondo et al. 2004). The Lowveld's vegetation is characterized as lowveld savannah, with 3 distinct broad-scale vegetation types: *Acacia* savannah, broadleaved woodland, and riverine forest (Mucina and Rutherford 2006).

I sampled at 3 sites that had conservation lands that directly adjoined large-scale sugarcane plantations (Figs. 2.1, 2.2). In my study, the conservation lands were identified as lands that were managed with explicit goal of wildlife conservation, including: private cattle ranches, private game reserves and national parks. Hlane-Mbuluzi included lands administered by Hlane Royal National Park, Mbuluzi Private Game Reserve, Tongaat Hulett Sugar (Tabankulu Estate), and Royal Swazi Sugar Corporation (Simunye and Mhlume Estates). The conservation areas (Hlane Royal National Park and Mbuluzi Game Reserve) at Hlane-Mbuluzi site were managed with

the explicit goal of wildlife conservation and had excluded cattle grazing and conducted prescribed burning. Irrigation was conducted using flood, overhead sprinkler, and drip irrigation, with similar sugarcane varieties cultivated. Dirt and graveled access roads and 2-m high fence separated the conservation areas and sugarcane, restricting the movements of medium- to large-sized mammals.

Crookes included lands managed by Crookes Brothers Plantation and Bar J Cattle Ranch (Figs. 2.1, 2.2). Conservation lands fell within the Big Bend Conservancy and were managed for wildlife conservation. Sustainable stocking rates, rotational grazing, and prescribed burning were practiced on these lands. There were abrupt differences in substrate at the land-use interface; dirt access roads and low, barbed wire fences separated the 2 land-uses and restricted the movement of cattle. Irrigation was conducted using flood, overhead sprinkler, and center pivot irrigation, with similar sugarcane varieties cultivated.

Nisela was overseen by Nisela Farms; conservation lands were managed for wildlife viewing, conservation, and grazing (Figs 2.1, 2.2). Prescribed burning and free-range grazing were practiced on these lands. There were no appreciable edaphic discontinuities between land-uses. Access roads, railroad tracks, and an electrified 2-m fence separated the 2 land-uses. Nisela used center pivot irrigation and it had 2 structurally different varieties of sugarcane.

METHODS

Sampling Design

I evaluated the changes in small mammal composition across a conservation-agriculture interface during wet and dry seasons. Using ground-truthed aerial photographs, Landsat images and a GIS (ArcGIS 9.3, ESRI, Redlands, California), I randomly placed 4 transects at each site along the identified conservation/agriculture interface. I placed transects perpendicular to the interface using handheld GPS and compass bearings; transects extended 375 m into each land-use type with the fence line between land-uses identified as 0 m distance (Fig. 3.1). Along each transect, I placed traplines at: 0, 75, 150, 225, and 375 m into each land-use, paralleling the interface (Fig. 3.1). Traplines consisted of 20 Sherman live traps spaced 10 m apart. A total of 180 traps was placed along the entire transect. I spaced the traplines 75-m apart and transects at least 400 m apart to ensure independence of sampling units based upon estimated small mammal ranges (Monadjem and Perrin 1998). The farthest interior trapline, (375 m) served as a “reference” (sensu Ries et al. 2004), depth of edge influence was expected to be within 250 m for most taxa. At Nisela, a limited amount of conservation/agriculture interface required transects to be placed 300-m apart.

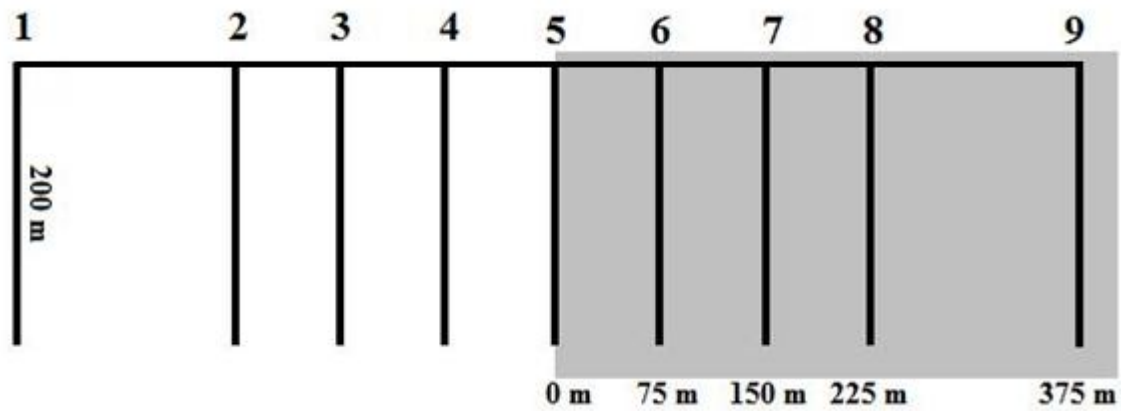


Figure 3.1. Schematic representation of the sampling protocol for small mammals without pitfalls. Transects extended from conservation areas into sugarcane agriculture (gray shading). Sherman traps were placed along traplines (20 traps, 10-m apart; vertical lines). Traplines were placed at 0, 75, 150, 225, and 375 m into each land-use and were numbered from 1 to 9, with 1 being the farthest interior conservation trapline.

Deploying traps in a transect design yields high levels of area surveyed per trap, and the relatively close spacing of traps ensured adequate sampling for species richness (Jones et al. 1996, Pearson and Ruggiero 2003). I placed each trap within 2 m of the assigned point in an area that would provide increased potential for capture and reduce weather exposure.

During each survey, I trapped each entire transect for 4 consecutive nights to allow for adequate sampling (Jones et al. 1996). Traps were baited with a combination of oats and peanut butter, and were checked every morning. For each captured individual, I recorded species, age, sex, and reproductive condition (Kunz et al. 1996, Skinner and Chimimba 2005). I collected additional information of ectoparasite presence, body length, hind foot length, and mass (Skinner and Chimimba 2005). I gave each individual weighing over 15 g a unique ear tag identifier (1005-1, National band Co., Newport, Kentucky, USA), smaller individuals and *Mus minutoides* were given ear punches (INS500075-5, Kent Scientific, Torrington, Connecticut, USA). Individuals that received ear punches were identified using a combination of measurements, including: mass, tail length, body length, and hind foot, as well as, initial capture location.

All captured insectivores (*Crociodura spp.* and *Suncus spp.*) were collected for later identification (Peter Taylor, Curator of Mammals, Durban Natural Science Museum, Durban, South Africa). Additionally, a voucher specimen of each species was collected from each site and deposited in the collections of the Durban Natural Science Museum. I performed captures and data collection following guidelines outlined by the American Society of Mammalogists (Gannon and Sikes 2009) and the study was

conducted under Texas A&M University's Animal Use Protocol (permit number 2008-98).

Data Analysis

To compare small mammal community responses to the land-use interface, I used minimum number known alive (MNA) estimates from each trapline per site per season to calculate community statistics (Krebs 1999). Despite its shortcomings (Slade and Blair 2000), I used MNA because the high variability of individual species capture rates limited the amount of statistical estimation that could be made between species and across traplines. MNA provided an index of population size while allowing for a comparison of metrics across sites, traplines, and seasons (Slade and Blair 2000, Michael and Michael 2005). I surveyed each site once per season. MNA was the total number of unique individuals captured at each trapline within each site, calculated by pooling among transects. Changes in community structure are not easy to encapsulate, examining multiple complementary metrics can aid in understanding changes and their implications. Species richness can provide an indication of absolute species response, which may be overshadowed by other metrics. Diversity complements species richness by incorporating evenness, and it indicates some of the community structure. Cluster analysis and ANOSIM provide a non-subjective means to compare communities, by incorporating species these analyses may cause misleading comparisons between different vegetation types.

Species Richness

I used capture data to record the presence of each species at each trapline per site per season. I calculated species richness for each trapline per site per season, as well as each trapline overall for the entire study. Additionally, I rarefied species richness (Krebs 1999), in order to non-linearly standardize the number of species expected to be encountered for a given sampling effort or number of individuals using species accumulation curves (Gotelli and Colwell 2001). I rarefied by using the trapline with the lowest number of individual captures as my baseline to avoid extrapolation errors, and standardized species to the individuals captured (Gotelli and Colwell 2001). Rarefied species richness is the number of species expected if the same number of individuals had been captured at each trapline. I rarefied for each trapline per site per season; because of potential biases incurred by unequal species evenness between land-uses, I presented both the unmodified and rarefied species richness estimates in tabular form (Weibull et al. 2003).

Diversity

I calculated the number of equally common species (N_1) to evaluate the effects of the land-use gradient on diversity because of its sensitivity to less abundant species (Hill 1973, Krebs 1999). N_1 translates the Shannon diversity index (H') into more easily interpretable units (species), by calculating the number of equally common species needed to produce the corresponding H' value. Calculation of N_1 is done by taking the base of the logarithm that H' was computed with (MacArthur 1965). Thus, N_1 can be thought of as a transformation of H' and is a measure of diversity that maintains

characteristics of H' including evenness (Hill 1973, Peet 1974). Using MNA data, I calculated N_1 with bootstrapped 95% confidence intervals based upon 5,000 iterations for each distance sampled using the computer program, Ecological Methodology (Exeter Software, Setauket, New York, USA). I calculated estimates for each trapline per site per season, as well as, combined site data by trapline by season. I compared N_1 across the land-use gradient, as well as, among sites and between seasons using the derived confidence intervals. I presented my results graphically (Anderson et al. 2001b).

MDS, ANOSIM, and Cluster Analysis

To understand variations in community composition between traplines, sites, and season, I used multi-dimensional scaling (MDS), Analysis of Similarity (ANOSIM), and cluster analysis. I conducted my analysis using programs PRIMER (PRIMER-E Ltd, Lutton, Ivybridge, England, UK) and R packages VEGAN, stats, and cluster (<http://cran.r-project.org>, <http://vegan.r-forge.r-project.org/>, <http://stats.r-forge.r-project.org/>, <http://cluster.r-forge.r-project.org/>).

I first used MNA data to calculate a Bray-Curtis dissimilarity matrix, due to its robust, non-parametric nature, for each trapline per site per season (Bray and Curtis 1957, Faith et al. 1987). The Bray-Curtis matrix is created by dividing the sum of the difference in abundance of each species by the sum of the total abundance of each species for each pair (McCune et al. 2004). I created this matrix using a square root transformation of the capture data, which increased the relative weight of less abundant species while maintaining some of the variability in species abundances (McCune et al. 2002). Using the Bray-Curtis dissimilarity matrix, I first performed MDS for all of the

traplines, with land-use as a factor and 50 restarts to avoid errors from local minima (McCune et al. 2002). I used multi-dimensional scaling to graphically examine the patterns of dissimilarity seen, without any assumption of relationships between the data (Clarke 1993, McCune et al. 2002).

Due to the iterative nature and subjective interpretation of MDS, I next performed one-way ANOSIM R-tests to evaluate differences in composition among sites, season and traplines; both overall and within each land-use (Clarke 1993). I performed global and pairwise tests with *R* values compared to a distribution of *R* values derived from a maximum of 999 permutations of randomly sampled, reordered replicates. ANOSIM is a non-parametric test of differences between multivariate sampling units, and so the data were not constrained to assumptions of normality (Clarke 1993). The ANOSIM test statistic (*R*) ranges from -1 to 1 with the highest degree of similarity equal to -1 and the highest degree of dissimilarity equal to 1 (Clarke 1993). The error rate for pairwise ANOSIM tests is not controlled, in lieu of a Bonferroni type correction; I used the general guidelines outlined by Clarke and Gorley (2001): *R* > 0.75, well separated; *R* > 0.5, clearly different; *R* < 0.25, barely separable.

Finally, I conducted cluster analysis to provide a non-subjective graphical representation of the dissimilarities between traplines within sites and across seasons, as well as for the combined trapline data between seasons. Cluster analysis allowed me to view the MDS results in finer detail, and to reconcile potential shortcomings of the 2 dimensional representation of MDS (Clarke 1993). I constructed hierarchical dendrograms using the flexible beta linkage method with $\beta = -0.25$, which limited the

propensity for chaining, or the sequential joining of sequential samples (a potential artifact of agglomeration linkage methods), and maintained compatibility with the Bray-Curtis dissimilarity matrix (Lance and Williams 1966, McCune et al. 2002).

RESULTS

Species Richness

I trapped during the dry season from 5 July–13 October 2008 and wet season from 28 October 2008–10 January 2009, for 17,280 trap nights (8,640 per season). I captured 1,612 unique individuals of 10 species.

Species richness (n) decreased from the conservation areas to the sugarcane land-use (0 m vs. 75 m) at Hlane-Mbuluzi and Crookes (Table 3.1). At Nisela, species richness did not decrease at the land-use interface (traplines 4–6; 0–75 m), nonetheless species richness was higher within the conservation land-use than the sugarcane (Nisela peak species richness: conservation: $n = 7$; sugarcane: $n = 6$; Table 3.1). For all of the sites during both seasons, a trapline with the lowest species richness was found within the sugarcane, and a trapline with the highest species richness was between 150–0 m from the interface (Table 3.1). No single trapline contained the total assemblage of species trapped during the study. Crookes ($n = 10$) did have the entire assemblage of species, as well as, higher overall species richness than Hlane-Mbuluzi ($n = 9$) or Nisela ($n = 8$; Table 3.1).

Table 3.1. Small mammal species richness (n) for traplines and their corresponding distance (m) across an agriculture/conservation land-use gradient at 3 sites (Hlane-Mbuluzi, Crookes, Nisela, and overall for the entire study) in the Lowveld of Swaziland during the dry (May–September), wet (October–March), and combined seasons of 2008.

		n									
		Trapline (distance)									
Site	Season	1(375)	2 (225)	3 (150)	4 (75)	5 (0)	6 (75)	7 (150)	8 (225)	9 (375)	Total
Hlane/											
Mbuluzi	dry	6	7	5	7	8	4	3	4	2	9
	wet	5	7	7	6	7	5	5	5	3	8
	combined	7	8	7	7	8	6	5	5	3	9
Crookes	dry	6	7	7	5	7	2	4	4	3	9
	wet	9	8	7	9	6	4	4	3	4	9
	combined	10	9	7	9	8	4	5	4	4	10
Nisela	dry	4	2	2	4	4	4	3	2	4	8
	wet	6	4	7	4	5	6	4	3	4	8
	combined	7	5	7	6	6	6	4	3	4	8
Overall	dry	8	8	7	8	8	5	5	5	4	9
	wet	10	8	8	9	8	7	6	6	4	10
	combined	10	9	8	9	8	7	6	6	4	10

Rarefied species richness analysis (n') showed similar trends to those exhibited by the unmodified species richness (Table 3.2). Estimates of n' were calculated with a baseline of 3 captures. Hlane-Mbuluzi and Crookes both had higher n' in the conservation than in the sugarcane land-use, with the largest contiguous difference between 0 m (trapline 5; Hlane-Mbuluzi: $n' = 2.56$ [dry and wet seasons]; Crookes: $n' = 2.01$ [dry season], $n' = 2.17$ [wet season]) and 75 m (trapline 6, Hlane-Mbuluzi: $n' = 1.76$ [dry season] and $n' = 1.98$ [wet seasons]; Crookes: $n' = 1.74$ [dry season], $n' = 1.77$ [wet season]). Hlane's highest n' was at the interface (0 m), and Crooke's highest n' was within the conservation land-use at 150 m (trapline 3; $n' = 2.09$) during the dry season and at 75 m (trapline 4; $n' = 2.57$) during the wet season. At Nisela, n' did show a slight decrease at the land-use interface (traplines 5–6, 0–75 m) during the dry season (trapline 5: $n' = 2.2$; trapline 6: $n' = 2.13$), but overall had an increase associated within 75 m of the interface. At all of the sites, n' values were lowest at the interior sugarcane traplines (8–9, 225–375 m).

Diversity

The number of equally common species (N_1) showed a significant difference between the conservation and sugarcane land-uses (trapline 5 [0 m] vs. 6 [75 m]) during the dry and wet seasons at Hlane-Mbuluzi (trapline 5: dry season, $N_1 = 5.74$, 95% *CL* [4.41–6.99]; wet season $N_1 = 4.85$, 95% *CL* [3.96–5.59]; trapline 6: dry season, $N_1 = 2.12$, 95% *CL* [1.68–2.55]; wet season $N_1 = 2.55$ 95% *CL* [2.07–3.05]), and during the

Table 3.2. Rarefied small mammal species richness for traplines and their corresponding distance (m) across an agriculture/conservation land-use gradient at 3 sites (Hlane/Mbuluzi, Crookes, Nisela, and overall for the entire study) in the Lowveld of Swaziland during the dry (May–September), wet (October–March) seasons of 2008.

Site	Season	n'								
		Trapline (distance)								
		1(+375)	2 (+225)	3 (+150)	4 (+75)	5 (0)	6 (-75)	7 (-150)	8 (-225)	9 (-375)
Hlane/										
Mbuluzi	dry	2.23	2.35	2.16	2.52	2.56	1.76	1.44	1.89	1.17
	wet	2.36	2.49	2.46	2.38	2.56	1.98	2.12	2.05	1.66
Crookes	dry	2.00	2.08	2.09	2.07	2.01	1.74	1.73	1.36	1.97
	wet	2.46	2.44	2.53	2.57	2.17	1.77	1.97	1.65	2.01
Nisela	dry	1.75	2.00	1.86	2.44	2.20	2.13	1.75	1.27	1.58
	wet	2.40	2.23	2.53	2.40	2.05	2.28	2.11	1.74	1.75
Overall	dry	2.06	2.20	2.16	2.34	2.33	1.88	1.65	1.65	1.53
	wet	2.52	2.56	2.56	2.57	2.42	2.13	2.10	1.89	1.91

dry season at Crookes (trapline 5 [0 m]: $N_1 = 2.94$ 95% *CL* [2.34–3.58]; trapline 6 [75 m]: $N_1 = 1.91$, 95% *CL* [1.57–2]). Conversely, Nisela exhibited a peak in diversity in both land-uses within 75 m (traplines 4–6) of the interface (trapline 5; 0 m) during the dry season ($N_1 = 3.13$; Figs. 3.2, 3.3). During the wet season Nisela had higher diversity within the conservation land-use (Fig. 3.2).

Hlane-Mbuluzi had higher diversity associated with the interface (0 m) during both seasons and had the lowest diversity at the farthest interior sugarcane trapline (9; 375 m) during both seasons (dry: $N_1 = 1.25$; wet: $N_1 = 1.77$; Fig. 3.2). Crookes showed differing patterns within both land-uses. The conservation land-use had less fluctuation in N_1 compared to the other sites; additionally there was a decrease in N_1 at the interface (trapline 5, 0 m) during both seasons (dry: $N_1 = 2.94$; wet: $N_1 = 3.94$). Within the sugarcane, diversity had a decreasing trend from traplines 6–8 (75–225 m), however, diversity increased abruptly at trapline 9 (375 m) during both seasons (trapline 8 [225 m]: dry season, $N_1 = 1.54$; wet season, $N_1 = 1.8$; trapline 9 [375 m]: dry season, $N_1 = 2.46$; wet season, $N_1 = 2.65$; Fig. 3.2).

When data were combined for all of the sites, N_1 showed patterns similar to Crookes, with significant decreases in diversity at the interface; however, lowest overall diversity was 375 m (trapline 9) into the sugarcane (Fig. 3.3). During the dry season,

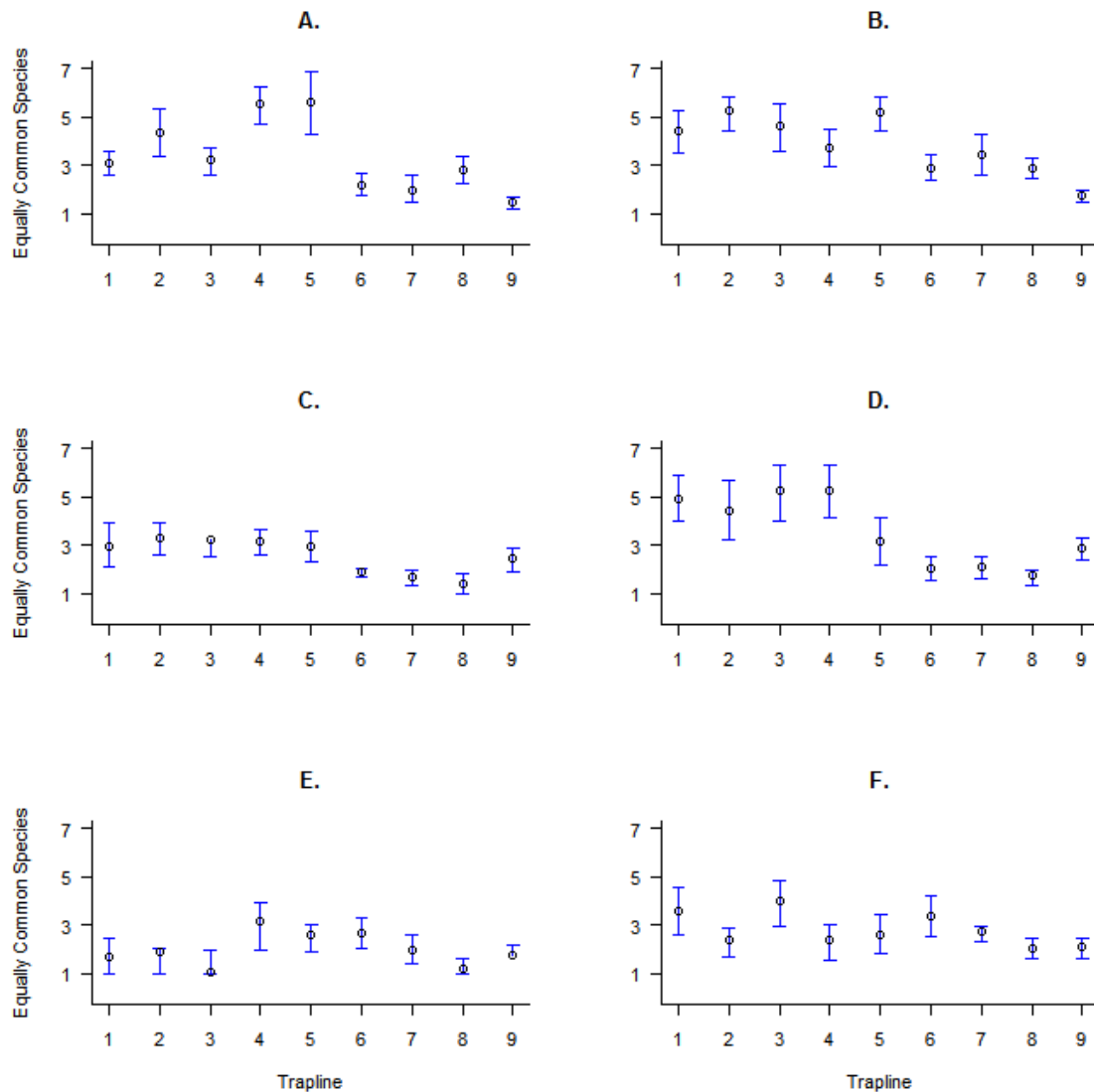


Figure 3.2. Number of equally common species (N_1), and bootstrapped 95% confidence limits, for traplines across an agriculture-conservation land-use gradient at 3 sites in the Lowveld of Swaziland during the dry (May–September), wet (October–March) seasons of 2008. Plots are for each trapline by site by season (Hlane-Mbuluzi: A., B. (dry season, wet season); Crookes: C., D. (dry season, wet season); Nisela: E., F. (dry season, wet season)). Traplines correspond to distances across the gradient (1 = 375 m, 2 = 225 m, 3 = 150 m, 4 = 75 m into the conservation area, 5 = interface [0 m], and 6 = 75 m, 7 = 150, 8 = 225 m, 9 = 375 m into the sugarcane). N_1 was calculated using MNA data.

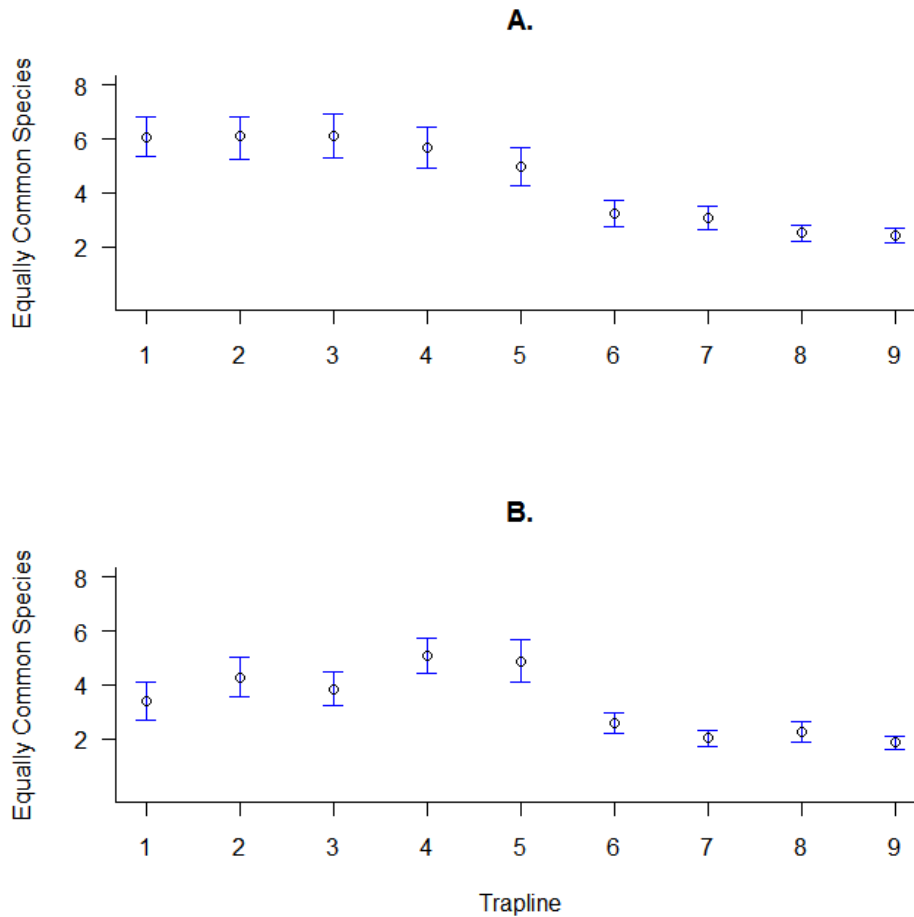


Figure 3.3. Number of equally common species (N_1), and bootstrapped 95% confidence limits, for traplines across an agriculture-conservation land-use gradient in the Lowveld of Swaziland during the dry (May–Sept), wet (October–March) seasons of 2008. Plots are for each trapline by season (A = dry season, B = wet season). Traplines correspond to distances across the gradient (1 = 375 m, 2 = 225 m, 3 = 150 m, 4 = 75 m into the conservation area, 5 = interface [0 m], and 6 = 75 m, 7 = 150, 8 = 225 m, 9 = 375 m into the sugarcane). N_1 was calculated using MNA data from the 3 study sites.

diversity in conservation lands, peaked 75 m from the interface (trapline 4, $N_1 = 4.89$), decreased slightly at the interface (trapline 5, $N_1 = 4.88$, 95% *CL* [4.16–5.64]). There was a significant decrease in diversity in the sugarcane within 75 m of the interface (trapline 6, $N_1 = 2.59$, 95% *CL* [2.23–2.96]). This decrease in diversity continued, with the lowest diversity at the farthest interior sugarcane trapline (trapline 9 [375 m], $N_1 = 1.83$). During the wet season, diversity remained highest and relatively constant within the conservation lands ($N_1 = \sim 6.5$), at trapline 4 (75 m) there was an increase in diversity ($N_1 = 6.64$) with a decrease at the interface (trapline 5, $N_1 = 5.34$, 95% *CL* [4.5–6.2]). There was a significant decrease in diversity 75 m into the sugarcane (trapline 6, $N_1 = 3.74$, 95% *CL* [3.16–4.37]). This decrease continued as distance into the sugarcane increased, diversity was lowest at the farthest interior sugarcane traplines (trapline 8 [225 m]: $N_1 = 2.6$, trapline 9 [375 m]: $N_1 = 2.68$).

MDS, ANOSIM, and Cluster Analysis

Multi-dimensional scaling indicated there was a difference between composition of the small mammal assemblages found within the sugarcane and conservation land-uses (Fig. 3.4). The plot had distinct groupings formed by the 2 land-uses, with marginally acceptable stress level (stress = 0.21) (Clarke 1993). Furthermore, the

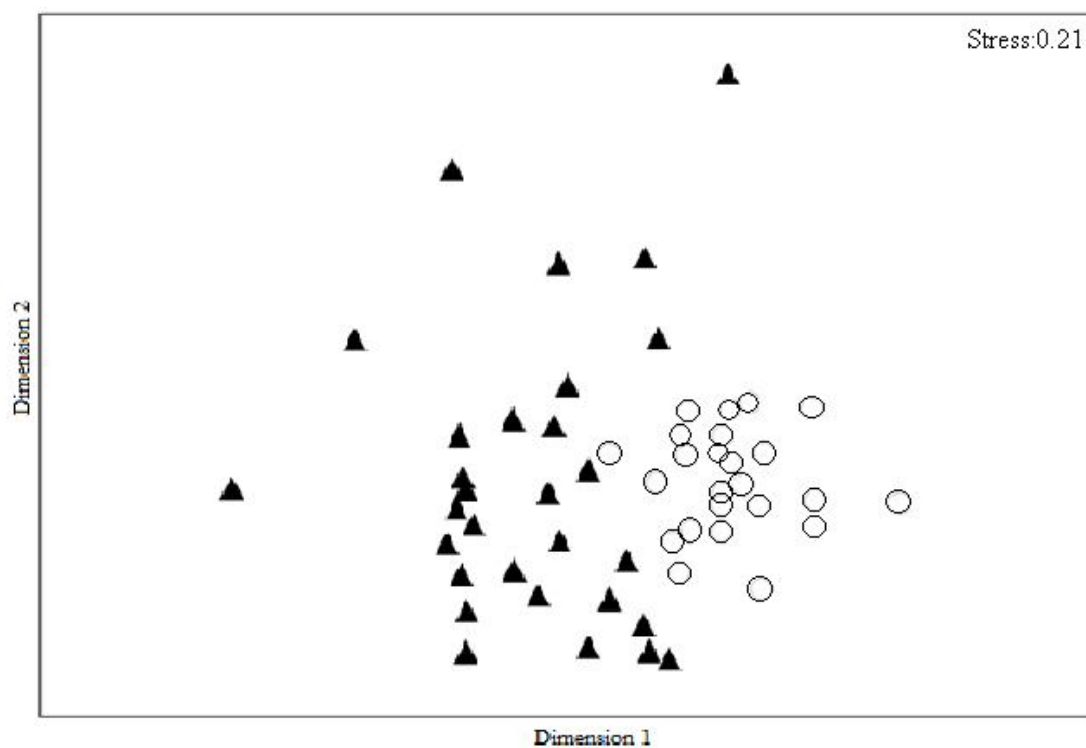


Figure 3.4. Two-dimension multi-dimensional scaling plot with stress of the composition of species found within the conservation (solid triangles) and sugarcane (open circles) land-uses within the Lowveld of Swaziland captured between July 2008 and January 2009. The axes represent the relative similarity between different different traplines. Stress is noted in the upper right.

distribution of the respective land-use points was less dispersed for the sugarcane than for the conservation areas, indicating less variation in the assemblage composition within the sugarcane.

The ANOSIM test for differences between land-use (traplines 1–5 vs. 6–9) corroborated the MDS results ($R = 0.412$, $P = 0.001$). Pairwise tests indicated significant differences in composition among conservation and sugarcane traplines, with the most significant difference between 375 m to 375 m into each land- use (traplines 1 vs. 9: $R = 0.724$, $P = 0.002$) and from 0–375 m into the sugarcane (traplines 5 vs. 9: $R = 0.726$, $P = 0.002$; Table 3.3). With the complete data, the 2-way ANOSIM tests also indicated that there was a significant, but small, difference in composition between sites ($R = 0.189$, $P = 0.001$), and seasons ($R = 0.095$, $P = 0.047$).

ANOSIM tests indicated there was a significant difference in composition between sites in both land-uses (sugarcane: $R = 0.234$, $P = 0.002$; conservation: $R = 0.401$, $P = 0.001$). Pairwise comparisons indicated that Hlane/Mbuluzi and Crookes were significantly different ($R = 0.48$) and Hlane/Mbuluzi vs. Nisela, and Crookes vs. Nisela were highly dissimilar ($R = 0.404$ and 0.433 , respectively) within the conservation land-use. In the sugarcane, Crookes and Hlane/Mbuluzi were shown to be different ($R = 0.54$) and Hlane/Mbuluzi vs. Nisela and Crookes vs. Nisela were very similar ($R = 0.16$ and 0.01 , respectively). Within the sugarcane ANOSIM tests showed no significant change in composition between seasons ($R = 0.093$, $P = 0.068$), while there was a change within the conservation lands ($R = 0.139$, $P = 0.001$). There was no

Table 3.3. ANOSIM results (R value) and significance (P -value) for pairwise trapline comparisons of the dissimilarity between assemblages of small mammals across a conservation-agriculture land-use gradient in the Lowveld of Swaziland. Traplines correspond to distances across the gradient (1 = 375 m into conservation land-use, 5 = 0 m land-use interface, 9 = 375 m into agriculture land-use). Dissimilarity matrices were calculated using square root transformed capture data collected between July 2008 and January 2009. Significant results according to Clarke and Gorley (2001) are highlighted in bold.

Pairwise comparison	R value	P -value
1, 2	-0.091	0.818
1, 3	0.085	0.214
1, 4	-0.176	0.97
1, 5	-0.061	0.675
1, 6	0.483	0.002
1, 7	0.47	0.002
1, 8	0.426	0.006
1, 9	0.724	0.002
2, 3	-0.115	0.952
2, 4	-0.137	0.961
2, 5	-0.03	0.639
2, 6	0.281	0.009
2, 7	0.356	0.002
2, 8	0.346	0.009
2, 9	0.417	0.002

Table 3.3 continued.

Pairwise comparison	<i>R</i> value	<i>P</i> -value
3, 4	-0.009	0.476
3, 5	0.019	0.409
3, 6	0.419	0.002
3, 7	0.57	0.002
3, 8	0.5	0.002
3, 9	0.563	0.002
4, 5	-0.02	0.569
4, 6	0.35	0.004
4, 7	0.452	0.002
4, 8	0.393	0.006
4, 9	0.504	0.002
5, 6	0.389	0.004
5, 7	0.583	0.002
5, 8	0.489	0.002
5, 9	0.726	0.002
6, 7	-0.161	0.911
6, 8	-0.072	0.673
6, 9	0.044	0.271
7, 8	0.061	0.288
7, 9	0.217	0.041
8, 9	0.107	0.173

difference among traplines in either land-use (sugarcane: $R = 0.037$, $P = 0.26$; conservation: $R = -0.048$, $P = 0.84$), but pairwise tests indicated that trapline 9 (375 m) was more distinct than any other trapline (Table 3.3).

Cluster analysis indicated the distinctness of communities between land-uses. During the dry season, both Hlane/Mbuluzi and the combined data had similar patterns, with a cluster break by land-use (traplines 1–5 and 6–9; Figs. 3.5, 3.6). Hlane-Mbuluzi's trapline 8 (225 m) was included in the conservation area cluster (Fig. 3.5). During the wet season, the pattern for the combined capture data, as well as, for Crookes and Hlane-Mbuluzi was for a separation of the traplines at the land-use level at their first grouping, and there was the same cluster structure within the conservation areas (Figs. 3.5, 3.6). Nisela had different composition of the initial grouping; during the dry season, the farthest interior conservation area trapline (1, 375 m; trapline 1) was grouped with the sugarcane traplines (6–9; Fig. 3.5). During the wet season, the traplines were grouped with the farthest interior sugarcane assemblages most alike (traplines 7–9; 150–375 m). Furthermore, the dissimilarity within the initial groupings had more range at Nisela than at the other sites.

Trapline 9 (375 m) had a unique cluster for the majority of site, season plots, including: Hlane/Mbuluzi dry, Crookes wet, Nisela wet, and pooled wet sites (Figs. 3.5, 3.8). Additionally, it was paired with trapline 8 (225 m) at Crookes wet and with the pooled dry sites, making it the most distinct distance from all of the data (Figs. 3.5, 3.6).

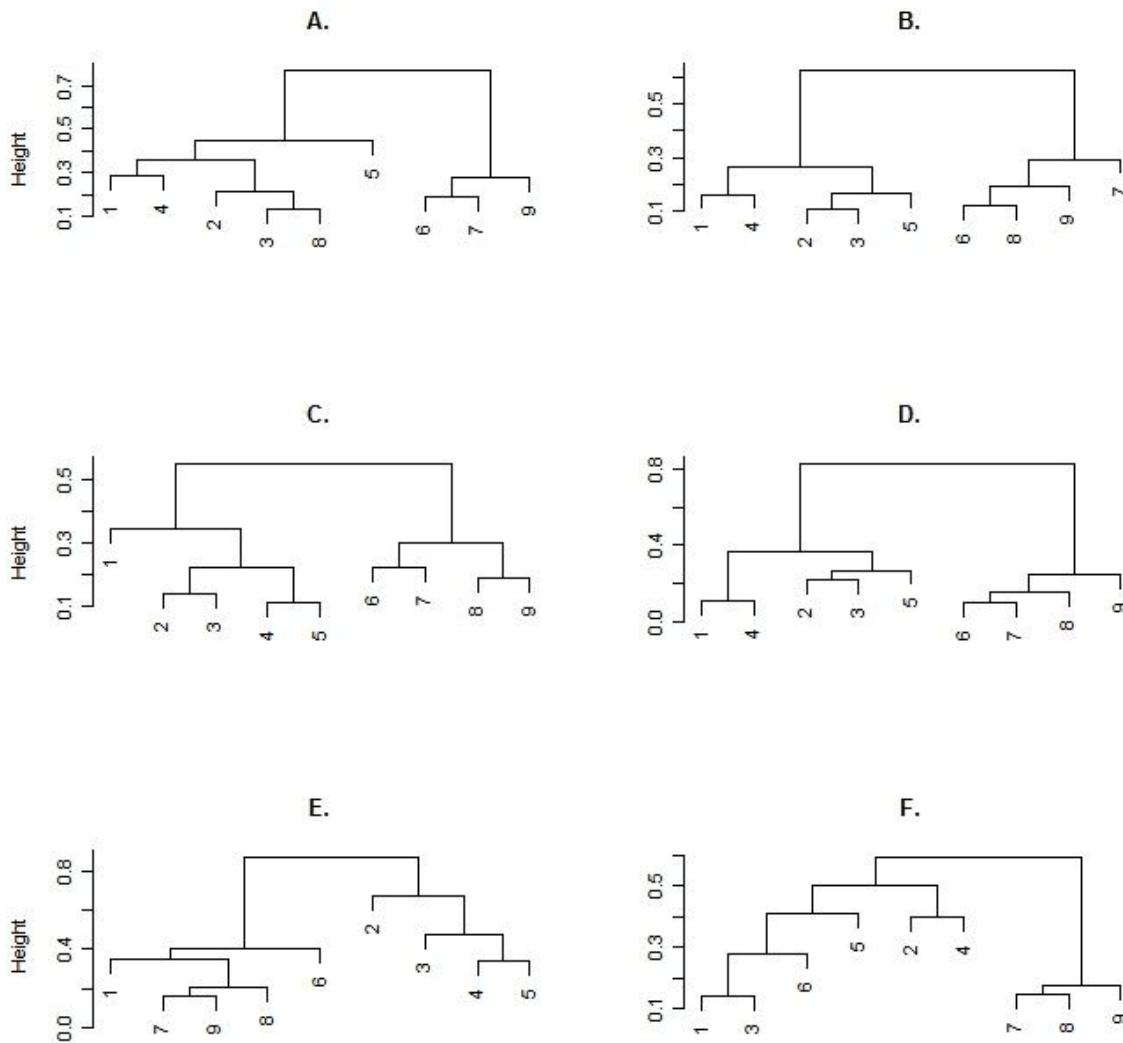


Figure 3.5. Cluster plots of the dissimilarity between assemblages of small mammals across a conservation/agriculture land-use gradient at 3 sites in the Lowveld of Swaziland. Plots are for each trapline by site by season (Hlane-Mbuluzi: A., B. (dry season, wet season); Crookes: C., D. (dry season, wet season); Nisela: E., F. (dry season, wet season)). Traplines correspond to distances across the gradient (1 = 375 m, 2 = 225 m, 3 = 150 m, 4 = 75 m into the conservation area, 5 = interface [0 m], and 6 = 75 m, 7 = 150, 8 = 225 m, 9 = 375 m into the sugarcane). Higher height indicates more dissimilarity. Plots were performed using square root transformed capture data (with Bray-Curtis dissimilarity matrices and flexible beta linkage method with $\beta = -0.25$) gathered between July 2008 and January 2010.

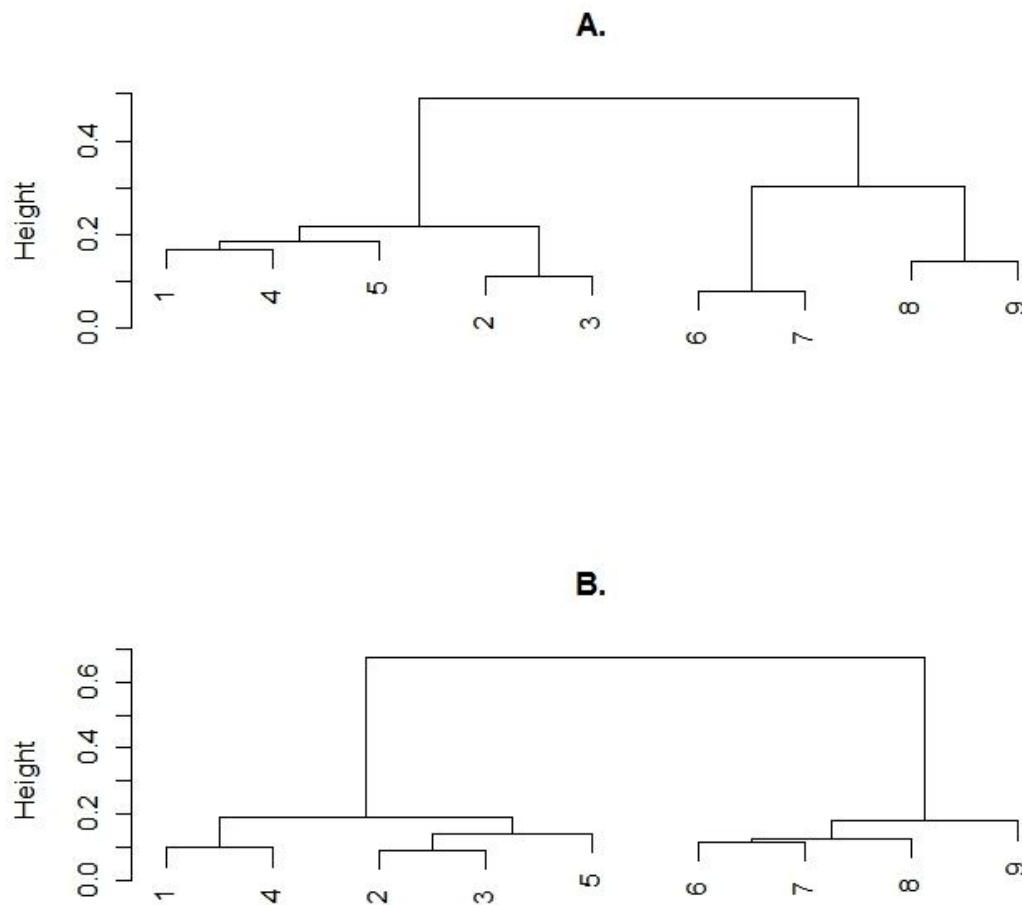


Figure 3.6. Cluster plots of the dissimilarity between assemblages of small mammals across a conservation/agriculture land-use gradient in the Lowveld of Swaziland. Plots are for each trapline by dry (A) and wet (B) using pooled data from 3 sites. Traplines correspond to distances across the gradient (1 = 375 m, 2 = 225 m, 3 = 150 m, 4 = 75 m into the conservation area, 5 = interface [0 m], and 6 = 75 m, 7 = 150, 8 = 225 m, 9 = 375 m into the sugarcane). Height indicates increased dissimilarity. Plots were performed using square root transformed capture data (with Bray-Curtis dissimilarity matrices and flexible beta linkage method with $\beta = -0.25$), gathered between July 2008 and January 2010.

DISCUSSION

My study results suggest that sugarcane surrounding conservation areas has a substantial effect on the diversity and structure of small mammal communities in lowveld savannah: however, intersite variation limited generalizations. I did find a consistent difference between small mammal communities in sugarcane and conservation lands, which indicated a sizable shift in community composition caused by the sugarcane.

In most cases the greatest change in small mammal community composition occurred between 0 m and 75 m into the sugarcane. Other research has suggested similar patterns of change within 75m of the interface. In Hawaiian sugarcane bordering natural vegetation, the diversity of small mammals (none of which are endemic) declined at a distance between 15 m and 76 m into sugarcane (Hood et al. 1971).

At the interface between sugarcane and conservation areas, I found lower species richness at the interface of all sites except Hlane-Mbuluzi. Lower species richness may be a result of certain species avoiding the interface. Small mammal species typically have different affinities for interface environments (Malcolm 1994, Lidicker 1999). Nonetheless, lower species richness at the interface did not necessarily equate to large changes in small mammal community composition. ANOSIM and cluster analysis suggested some differences in community structure; however results were not significant. Minor changes in community structure were likely due to loss of species without replacement of other species unique to the interface and slight changes in relative abundances.

Season also appeared to influence small mammal community response to the interface as measured by diversity. During the dry season, pooled and Crookes diversity estimates were slightly lower at the interface, and higher at Hlane-Mbuluzi and Nisela. Conversely, during the wet season diversity was relatively high at the interface, except at Crookes. Only at Hlane-Mbuluzi did diversity clearly increase at the interface across seasons. I expected an increase of diversity at the interface when animals utilized complementary environments across the interface (Leopold 1933). Increased diversity has been a common community response to interface for a variety of taxa (Ries et al. 2004). In my study, the absence of a clearly positive response in diversity at the interface may indicate the unsuitability of sugarcane for most species. The minor change in patterns of diversity relative to the interface may be due to slight changes in vegetation due to the late onset of wet season rains. Increased diversity during the wet season mirrors patterns found in the Swazi Middleveld by Monajem and Perrin (2003) who associated changes in diversity with a decrease in the most abundant species, *Mastomys natalensis*.

Responses to the interface extended beyond the interface itself. With few exceptions, (Nisela and 375 m at Crookes), diversity decreased with distance into the sugarcane and clusters were largely arranged along the gradient into the sugarcane. ANOSIM *R*-scores indicated that the farthest interior (reference) sugarcane trapline was the most distinct trapline in the study, and was highly separated from the farthest interior (reference) conservation trapline, as well as, the interface (Clarke and Gorley 2001). Within sugarcane-fragmented lowveld savanna, 375 m may represent a distance near a

threshold across which small mammal community structure disintegrates (Metzger and Décamps 1997, Hanski 1999). At 375 m distance, the small mammal community was reduced from > 5 species to one comprised of ~ 2 generalist species able to persist solely within a sugarcane monoculture, which translates into a loss of specialist species and a community dominated by a few generalists (Andren 1994, Fahrig 2003, Avenant and Cavallini 2007).

Within conservation lands, small mammal communities were highly variable as evidenced by cluster analysis, ANOSIM and diversity estimates. The order of clusters varied across sites, and ANOSIM indicated that traplines did not differ in composition. Furthermore, patterns of diversity differed between sites. Conversely, in the sugarcane, patterns were less variable, highlighting its relative lack of heterogeneity despite disparate agricultural practices.

Lack of uniform responses in small mammal community parameters across sites demonstrates the complex nature of edge responses, and may indicate that responses vary with factors that are not associated with distance to the interface, namely vegetation characteristics or species interactions. In short, environmental variables may elicit different responses to the land-use interface. Conversely, within the sugarcane monoculture, vegetation heterogeneity was greatly reduced, potentially increasing the relative influence of variables associated with the interface.

Several characteristics of site-level community responses further highlight important aspects of the sugarcane-native vegetation system. Crookes had a slight increase in diversity at the farthest interior sugarcane trapline (9, 375 m) when compared

to the previous distance (8, 225 m). Trapline 9 fell within an uncultivated strip for portions of 2 transects, and illustrates the potential utility that patches of natural vegetation embedded within agricultural matrices have for biodiversity conservation (Aschwanden et al. 2007, Heroldova et al. 2007, Silva and Prince 2008). Nisela exhibited less extreme shifts differences between land-uses than at the other sites. At Nisela, traplines near the interface were clustered together, and diversity did not exhibit the sharp decrease found at the other sites. The maintenance of diversity farther into sugarcane may have been attributable to increased importance of the sugarcane resources due to poor conservation area vegetation condition, as well as, increased native vegetation in the interstices of fields irrigated by center pivot (3 transects). Studies in Brazil have found seasonal exploitation of agriculture resources during times of resource scarcity (Freitas et al. 2008). Ironically, higher diversity at the interface or within the sugarcane may be a symptom of less suitable conservation area environments.

From my study, I recommend that sugarcane agricultural practices in the Lowveld and throughout Southern Africa incorporate: interstitial spaces, vegetation patches, or uncultivated strips into their designs to allow for connectivity of conservation lands. Furthermore, these features should be within 375 m of each other to ensure that community structure is maintained. The extent of of sugarcane-conservation land interfaces should also be minimized. In Swaziland, small mammals are not considered a pest of sugarcane, and may provide ecosystem services preying upon invertebrate pests of sugarcane, and foraging on seeds and herbage of unwanted inter-row vegetation. Maintaining landscape connectivity within sugarcane also would have benefits for

management of neighboring conservation areas, including maintenance of gene flow and increased resilience of wildlife populations (Laurance 1991, Hanski 1999, Fahrig 2002).

CHAPTER IV

RESPONSE OF SMALL MAMMAL COMMUNITIES TO ENVIRONMENTAL AND INTERFACE-RELATED VARIABLES

SYNOPSIS

Within Southern Africa, and in tropical climates throughout the world, sugarcane cultivation accounts for a substantial proportion of lands devoted to agriculture. The sugarcane-native vegetation interface has received little research interest, despite its effect on wildlife communities. I trapped small mammals on a gradient extending from sugarcane into native vegetation at 3 sites. I evaluated whether small mammal communities had interactive or non-interactive responses to the interface. I conducted canonical correspondence analysis both overall and at the site level. From this analysis I determined that, overall, small mammal communities had non-interactive responses attributable to environmental variables. The effects of sugarcane did not extend into adjoining natural vegetation. Grass biomass, litter depth and shrub density played important roles in structuring the communities. Between sites, variation in community structure attributable to the sugarcane interface varied. The site with poorest vegetation condition quality had the highest relative importance of distance to the interface. I identified 1 species (*Steatomys pratensis*) that was negatively affected by distance to the interface.

INTRODUCTION

Agriculture currently is the dominant land-use on the planet (Foley et al. 2005, Ramankutty et al. 2008). As the human population grows, it is expected that agricultural land conversion will continue for at least the next 50 years (Tilman et al. 2001). Within Southern Africa, and in tropical climates throughout the world, sugarcane cultivation accounts for a substantial proportion of lands devoted to agriculture, in some areas nearing 20% of land-use (Leff et al. 2004). The current focus on biofuel production, as well as human consumption, ensures that in the future sugarcane cultivation will be maintained or increase (Lourenco Nass et al. 2007, Yamba et al. 2008).

In arid environments, sugarcane cultivation requires irrigation and fertilization. When bordering intact native vegetation, the resource-intensive nature of sugarcane cultivation creates a juxtaposition of disparate vegetation types. Contrasting vegetation types result in interfaces that are homogeneous, abrupt, and widespread (Strayer et al. 2003).

There are 2 models that explain changes in wildlife communities from adjoining land-uses, non-interactive and interactive effects (Lidicker 1999, Strayer et al. 2003). Non-interactive effects are responses expected from an average of environmental conditions on both sides of an interface (Lidicker 1999, Strayer et al. 2003). Interactive effects are caused by the interaction between environmental variables and variables associated with the interface, producing responses of greater magnitude than those expected from each variable in isolation (Lidicker 1999, Strayer et al. 2003). As with

most ecological processes, each classification may be present to differing degrees (Begon et al. 2006).

Leopold (1933) proposed that diversity along interfaces increased because of complementary resources provided by the adjoining vegetation types. Non-interactive effects expand Leopold's hypothesis by incorporating the location and availability of biotic and abiotic resources across the interface (Cadenasso et al. 2003, Ries et al. 2004, Ries and Sisk 2004). Non-interactive effects are the most prevalent community-level responses and have been documented for small mammals along agricultural interfaces (Morris 1997, Hodara and Busch 2010). Small mammals also have shown interactive effects, by responding to distance from the interface more strongly than suitability of the habitat (Kristan et al. 2003).

Proper identification of the mechanisms responsible for interface effects is essential for adequate management and conservation of wildlife species (Lidicker 1999, Laurance 2008). Attributing interface-related community variation to interactive or non-interactive effects may identify key variables and the scale at which processes are operating (Morris 1987, Kingston and Morris 2000, Strayer et al. 2003, Abu Baker and Brown in press). If non-interactive effects are driving mechanisms of community structure, vegetation variables can be managed to mitigate the influence of adjoining lands (Lidicker 1999, Kingston and Morris 2000, Strayer et al. 2003). If community responses are predominantly interactive, the effects of environmental variables on small mammal community parameters are greater than those expected in isolation. Interactive effects of sugarcane may extend into adjacent lands, highlighting the need for mitigation

of deleterious edge effects, such as loss of diversity due to increased predation or edge aversion (Sisk et al. 1997, Lidicker 1999, Strayer et al. 2003).

Limited research suggests sugarcane reduces avian and small mammal species richness in adjoining vegetation (Hood et al. 1971, Candido Jr. 2000, Chapter 2). However, there has been no research investigating the degree to which sugarcane cultivation may be influencing community composition of wildlife in adjacent areas of native vegetation.

In this study, I evaluated factors influencing community composition of small mammals along the sugarcane-natural vegetation interface. Specifically, I assessed the amount of variation in small mammal community structure explained by environmental variables and distance to the interface to determine if sugarcane plantations influenced small mammal communities in adjoining vegetation. Furthermore, I identified environmental variables that correlated most strongly with community structure, and the occurrence of individual species.

STUDY AREA

My study was conducted in the Lowveld of Swaziland, the low-lying region between the northern Drakensburg Escarpment to the west and the Lubombo Mountains to the east (Fig. 2.1). My study area was in the eastern half of the country and is its lowest, warmest, and driest region. The Lowveld's elevation was 150–400 m above sea level, with annual precipitation averaging 550–725 mm (Matondo et al. 2005). Its mean average temperature was 22°C with mean monthly temperatures of 26°C in January and 18°C in July (Monadjem 1999). Swaziland has a subtropical climate, and exhibits

distinct wet (October–March) and dry (April–September) seasons, 75% and 25% of rains fall during these respective seasons (Matondo et al. 2004). The Lowveld is prone to droughts due to the combination of erratic rain events and high summer temperatures (Matondo et al. 2004). Vegetation in the region is characterized as lowveld savannah, with 3 distinct broad-scale vegetation types: acacia savannah, broadleaved woodland, and riverine forest (Mucina and Rutherford 2006).

I conducted sampling at 3 sites that had conservation lands directly adjoining large-scale sugarcane plantations (Figs. 2.1, 2.2). The Hlane-Mbuluzi site included lands administered by Hlane Royal National Park, Mbuluzi Private Game Reserve, Tongaat Hulett Sugar (Tabankulu Estate), and Royal Swazi Sugar Corporation (Simunye and Mhlume Estates). Conservation areas were managed with the explicit goal of wildlife conservation and had excluded cattle grazing and conducted prescribed burning. Dirt and graveled access roads and 2-m high fence separated the conservation areas and sugarcane, restricting the movements of medium- to large sized mammals.

The Crookes site included lands managed by Crookes Brothers Plantation and Bar J Cattle Ranch (Figs 2.1, 2.2). Conservation lands fell within the Big Bend Conservancy and were managed for wildlife conservation; sustainable stocking rates, rotational grazing, and prescribed burning was practiced on these lands. There were abrupt differences in substrate at the land-use interface; dirt access roads and low, barbed wire fences separated the two land-uses. Irrigation canals were present at the interface.

The Nisela site was overseen by Nisela Farms; conservation lands were managed for wildlife viewing, conservation, and grazing (Figs 2.1, 2.2). Prescribed burning and free-range grazing were practiced on conservation lands. There were no edaphic discontinuities between land-uses. Access roads, railroad tracks, and an electrified 2-m fence separated the two land-uses.

METHODS

Sampling Design

Using ground-truthed aerial photographs, Landsat images and a GIS (ArcGIS 9.3, ESRI, Redlands, CA), I randomly placed 4 transects at each site along the identified conservation/agriculture interface. I placed transects perpendicular to the interface using handheld GPS and compass bearings; transects extended 375 m into the conservation land-use with the fence line between land-uses identified as 0-m distance (Fig. 4.1). Along each transect, I placed trap-lines at 0, 75, 150, 225, and 375 m into the conservation land-use, paralleling the interface (Fig. 4.1). Traplines consisted of a pitfall array and 20 Sherman live traps spaced 10 m apart. A total of 100 traps was placed along the entire transect. I spaced the traplines 75 m apart and transects at least 400 m apart to ensure independence of sampling units based upon expected small mammal home ranges (Monadjem and Perrin 1998). At Nisela, a limited amount of conservation-agriculture interface required transects to be placed 300 m apart.

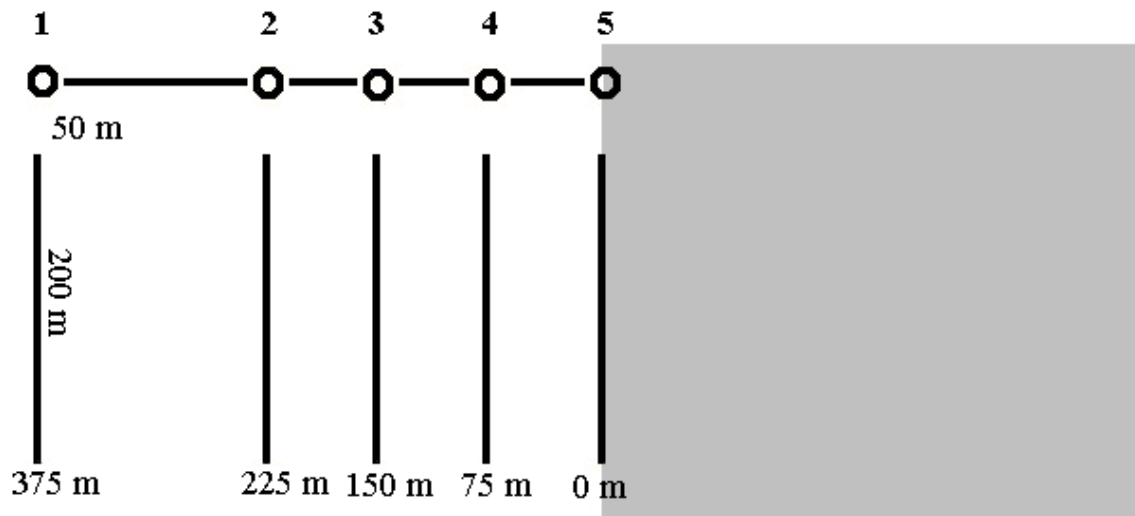


Figure 4.1. Schematic representation of the sampling protocol for small mammals in conservation lands. Transects extended from conservation/sugarcane agriculture (gray shading) land-use interface into the conservation land-use. Sherman traps were placed along traplines (20 traps, 10 m apart) (vertical lines), traplines were offset 50 m from the main transect. Pitfalls were placed along the transect (circles). Traplines were placed at 0, 75, 150, 225, and 375 m into the conservation land-use and were numbered from 1 to 5, with 1 being the farthest interior conservation trapline and 5 the interface.

Along each transect, I placed pitfall arrays at each trap-line origin in order to sample for insectivores (Jones et al. 1996; Fig. 4.1). Pitfall arrays consisted of 7 total buckets. They had a central bucket with 3 (10-m long), radiating drift fences set 120 degrees apart; additional buckets were placed at 5 m and at each fence terminus. Drift fences were comprised of 30-cm tall plastic sheeting, staked vertically with the bottom buried; buckets were at least 40-cm deep to eliminate the chance of escape and were flush with the ground (Jones et al. 1996). There were a total of 35 buckets placed along each transect.

Sherman traps were offset from each pitfall by 50 m. Deploying traps in a transect design yields high levels of area surveyed per trap, and the relatively close spacing of traps ensured adequate sampling for species richness (Jones et al. 1996, Pearson and Ruggiero 2003). I placed each trap within 2 m of the assigned point in an area that would provide increased potential for capture and reduced weather exposure.

During each survey, I trapped the entire transect for 4 consecutive nights to allow for adequate sampling of species richness (Jones et al. 1996). Traps were baited with a combination of oats and peanut butter, and were checked every morning. For each capture, I recorded species, age, sex, and reproductive condition (Kunz et al. 1996, Skinner and Chimimba 2005). I gave each individual weighing over 15 g a unique ear tag identifier (1005-1, National band Co., Newport, KY, USA), smaller individuals and *Mus minutoides* were given ear punches (INS500075-5, Kent Scientific, Torrington, CT, USA). Individuals that received ear punches were identified using a combination of

measurements, including: mass, tail length, body length, and hind foot length, as well as, initial capture location.

I performed captures and data collection following guidelines outlined by the American Society of Mammalogists (Gannon and Sikes 2009) and the study was conducted under Texas A&M University's Animal Use Protocol (permit number 2008-98).

Vegetation Sampling

I sampled vegetation parameters on each transect during the wet season (Table 4.1), focusing on biologically relevant variables shown to affect the distribution of small mammal species (Anderson et al. 2001a). At each transect, I sampled the vegetation at randomly selected trap locations along each trapline within the conservation land-use. On average I sampled 9 (range 5–18) trap locations on each trapline. The vegetation at each site was measured to a maximum radius of 50 m, I truncated at this distance because it exceeded the expected range size of small mammals in the region (Monadjem and Perrin 1998).

I measured both distance to the interface and environmental variables (Table 4.1). Distance to the interface (INTdist) was measured to encompass potential interactive mechanisms that were a function of the sugarcane or the interface. I categorized the remainder as non-interactive environmental variables. I recorded the presence of a rocky component (RockySoil; gravel, cobble, or rock) in the substrate at each location. I used a range pole to estimate height (PlntHt) and biomass (Biom) of grass

Table 4.1. Description of variables collected from October 2008–January 2009 in the Lowveld of Swaziland. Variables were measured at an average of 9 locations per trapline, the variables represent the average or proportion for the entire trapline.

Variable	Description
INTdist	average distance to the land-use interface (m)
Rockysoil	proportion of locations with a gravel, cobble, or rock component
Biom	average obstruction height to the nearest 0.1 m, an index of biomass
PlntHt	average grass height to the nearest 0.1 m
SHR	average number of shrub stems at 1.5 m height along 2-, 15-m ² transects
LITT	average litter depth (cm) along 2-, 15- m ² transects
CAN	average canopy obstruction (%) along 2-, 15- m ² transects
Over	average distance to the nearest overstory tree (m) within 50 m
Under	average distance to the nearest understory tree (m) within 50 m
Snag	average distance to the nearest snag (m)
Log	average distance to the nearest log (m)
CumLen	average cumulative length (m) of logs within 20 m of the location
ACover	proportion of overstory trees that are <i>Acacia</i> spp.
ACunder	proportion of understory trees that are <i>Acacia</i> spp.

in the 4 cardinal directions at each sampled trap location (Robel et al. 1970). Visual obstruction provides an index of the amount of grass biomass within the sampled area (Robel et al. 1970). I conducted point-centered quarter sampling to estimate the dominance of *Acacia* and density of overstory trees (ACover; Over; respectively), understory trees (ACunder; Under; respectively), snags (Snag) and logs (Log), as well as, the cumulative length of logs (CumLen). I adapted methods from Deuser and Shugart (1978), to estimate canopy closure (CAN; classes=1: ≤ 5 , 2: 6–25, 3: 26–50, 4: 51–75, 5: 76–95, 6: ≥ 95), litter depth (LITT; cm), and shrub density (SHR; number of stem hits at transect 1.5 m high and 1.5 m wide) along 2 10-m long transects that ran parallel and perpendicular to the trapline and were centered on the trap location. Each of these 3 variables was measured at each meter along the 10-m transect.

Minimum Number Alive

To compare the small mammal community responses to the land-use interface I used minimum number known alive (MNA) estimates from each trapline per transect to calculate community matrices (Krebs 1999). Despite its shortcomings, MNA provides an index of species abundances (Slade and Blair 2000). I used MNA because the high variability of individual species captured limited estimation that could be made between species and across traplines.

Canonical Correspondence Analysis

I performed canonical correspondence analysis (CCA), for the combined data, as well as, for each site, using parameters identified from analysis of the combined data (ter

Braak 1986, De'ath 2002, Peres-Neto et al. 2006). CCA is an ordination technique that seeks to fit one set of multivariate data into a space dictated by another, by constraining an ordination to a multiple linear regression of another matrix (McCune et al. 2002). I used CCA analyses to evaluate variation between sites and the influence of distance to the interface and environmental variables on small mammal community composition. CCA assumes there is a unimodal model of responses to the variables and only examines the variation in community structure that is attributable to the variables measured (McCune et al. 2002).

I square root transformed the capture data to decrease the importance of numerically dominant species prior to CCA and evaluated the CCA using weighted average scores (WA). WA scores are the inter-set correlation, and are less susceptible to variation in environmental variables than linear contrast scores (McCune et al. 2002). I presented the plots with WA scores because of the variability that was present in environmental variables.

I constructed a global CCA model, containing all of the measured variables and tested the significance of individual variables using permutation *F*-tests, with a maximum of 999 permutations. Next, I compared the inertia (variance among the multiple regressions) of CCAs that consisted of the entire set of environmental variables, to one that included only distance to the interface, as well as, site-level comparisons that included relevant environmental variables from the permutation tests (McCune et al. 2002). Unadjusted inertia estimates often overestimate the amount of variance attributable to each matrix, so I only used inertias as a means of relative comparison

among models (Peres-Neto et al. 2006). I then tested the variance inflation factor (VIF) to ensure that collinearity within the data was not present in the data.

I used permutation tests and biplot distances to identify environmental characteristics with the greatest correlation to small mammal community structure. Biplot distances are eigen values standardized to one axis, and are an accurate way to interpret the strength of responses. Longer biplot scores indicate a stronger correlative relationship and represent better predictors of community composition (McCune et al. 2002).

I also used biplots to evaluate the relationship between species and environmental variables. Perpendicular distances to biplot arrows can be interpreted as the strength of species relationships to environmental data, species falling on the same side of the centroid as the tip of the biplot arrow have a stronger than average, positive relationship to that variable (McCune et al. 2002). I identified species with strong relationships with certain variables, as well as species that were associated with similar groupings of variables.

RESULTS

Combined CCA

Between 15 October 2008, and 7 January 2009, I captured a total of 377 unique individuals of 12 species (*Aethomys ineptus*, *Crocidura fuscomurina*, *Crocidura hirta*, *Dendromus mystacalis*, *Elephantulus brachyrhynchus*, *Gerbilliscus leucogaster*, *Lemniscomys rosalia*, *Mastomys natalensis*, *Mus minutoides*, *Saccostomys campestris*, *Suncus lixus*) during 11,664 (8640 Sherman, 3024 pitfall) trap nights. CCA of a global

model containing all environmental variables and distance to the interface, produced inertias of 0.73 and 1.37 for the constrained and unconstrained ordinations, respectively (Fig. 4.2). The global model explained 35% of the variation in small mammal communities. Permutation tests of the main effects indicated the factors most important in determining the variability in the small mammal community were Rockysoil ($F = 2.33$, $P = 0.04$), Biom ($F = 2.43$, $P = 0.01$), SHR ($F = 3.21$, $P = 0.01$), and LITT ($F = 2.41$, $P = 0.01$, Table 4.2). Distance to the interface was not significant ($F = 0.81$, $P = 0.77$; Table 4.2). The biplot distances, of SHR, CAN, LITT, Biom, Over, Under, PlntHt, Snag, and ACunder were greater than INTdist (Fig. 4.2). The data were widely dispersed indicating high variability among the sampling locations. An analysis of the VIF, showed little collinearity ($VIF < 10$) among the variables included in the CCA.

A CCA model of only environmental variables explained 33% of the variation in community structure and had constrained and unconstrained inertias of 0.69 and 1.41, respectively. A CCA model of INTdist had constrained and unconstrained inertias of 0.03 and 2.07, 1% of the variation in community structure was explained by the model. Permutation tests indicated that the INTdist CCA was not significant ($F = 0.70$, $P = 0.82$).

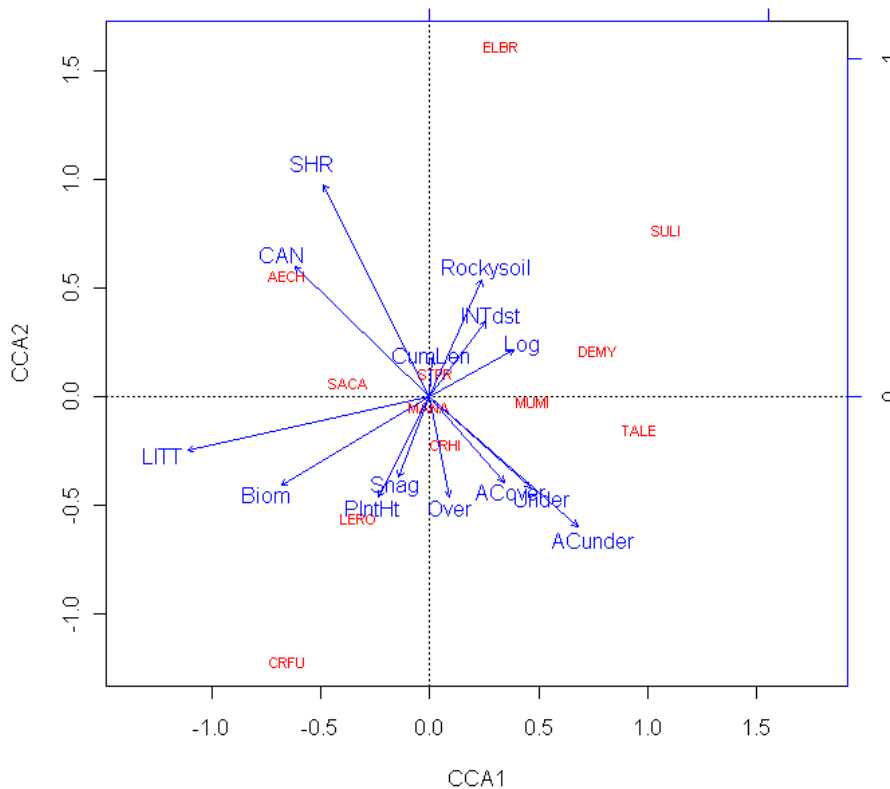


Figure 4.2. Canonical Correspondence Analysis of environmental variables and distance to the interface constrained to the assemblages of small mammal species captured in the Lowveld of Swaziland between 15-October, 2008 and 07-January, 2009. The plots are of the WA scores and the arrows indicate the scaled biplot distance, longer arrows indicate a stronger relationship. Axes are 2 dimensional representations of the ordination space. Species are in red (AEIN, *Aethomys ineptus*; CRFU, *Crocidura fuscomurina*; CRHI, *Crocidurahirta*; DEMY, *Dendromus mystacalis*; ELBR, *Elephantulus brachyrhynchus*; GELE, *Gerbilliscus leucogaster*; LERO, *Lemniscomys rosalia*; MANA, *Mastomys natalensis*; MUMI, *Mus minutoides*; SACA, *Saccostomys pratensis*; STPR, *Steatomys pratensis*; SULI, *Suncuslixus*). The axis are standardized, numbers reflect standard deviations. Variables are: Rockysoil, % of sites with rocky substrate component; Biom, average Robel obstruction height; PlntHt, average plant height; SHR, average number of shrub hits; LITT, average litter depth; CAN, average % canopy; INTdst, distance to the land-use interface.

Site-level CCAs

Site-level CCAs, restricted analysis to environmental variables identified as relevant from the pooled analysis: Rockysoil, Biom, PlntHt, SHR, LITT, CAN, INTdst. CCAs of the focal environmental variables for Hlane-Mbuluzi, Crookes and Nisela accounted for 43%, 46%, and 41% of the inertia, respectively (Table 4.3). Conversely, the interaction model that consisted of distance to the interface explained, 0.04, 0.03, and 0.06 of the inertia for Hlane-Mbuluzi, Crookes, and Nisela, respectively (Table 4.3). At Hlane-Mbuluzi and Crookes, INTdst had the shortest biplot distance (Figs. 4.3, 4.4). At Nisela, only Biom and LITT had longer biplot distances than INTdst (Fig. 4.5).

Species Responses

Species were widely dispersed within the ordination space. Apart from species found in the center of the ordination space (*Mastomys natalensis*, *Steatomys pratensis*), there were few species consistently associated together (Figs. 4.2–4.5). *Mus minutoides* and *Gerbilliscus leucogaster* were more closely associated with each other than with any other species, both were negatively associated with LITT and BIOM. *Aethomys ineptus* was positively associated with SHR and CAN. *Lemniscomys rosalia* was positively correlated to BIOM. *Steatomys pratensis* had a positive response to INTdst.

Table 4.2. Summary of Chi-square (χ^2) permutation F -tests (F) for different environmental variables analyzed by Canonical Correspondence Analysis, with degrees of freedom (DF). Significance is denoted by asterisks (0.05 = *; 0.01 = **).

	Df	χ^2	F
INTdst	1	0.027	0.81
Rockysoil	1	0.078	2.33*
Biom	1	0.0813	2.43**
PlntHt	1	0.0486	1.45
SHR	1	0.1072	3.21**
LITT	1	0.0806	2.41**
CAN	1	0.0451	1.35
Over	1	0.0338	1.00
Under	1	0.0368	1.10
Snag	1	0.0358	1.07
Log	1	0.0258	0.77
ACover	1	0.0483	1.44
ACunder	1	0.0452	1.35
CumLen	1	0.0315	0.94
Residual	41	1.3713	

Table 4.3. Constrained and unconstrained inertias for 3 models containing: focal environmental variables (environmental) and distance to interface (Distance) overall and at 3 sites (Hlane-Mbuluzi, Crookes, Nisela) in the Lowveld of Swaziland. Proportion of inertia for each model are in parenthesis.

Site	Inertia	Model ^a	
		Environmental	Distance
Overall	Constrained	0.44 (0.21)	0.03 (0.01)
	Unconstrained	1.65 (0.79)	2.07 (0.99)
Hlane-Mbuluzi	Constrained	0.48 (0.43)	0.04 (0.04)
	Unconstrained	0.65 (0.57)	1.09 (0.96)
Crookes	Constrained	0.85 (0.46)	0.05 (0.03)
	Unconstrained	0.99 (0.54)	1.78 (0.97)
Nisela	Constrained	1.13 (0.41)	0.17 (0.06)
	Unconstrained	1.66 (0.59)	2.62 (0.94)

^amodel variables^b: Environmental = Rockysoil+Biom+PlntHt+SHR+LITT+CAN; Distance = INTdist;

^bvariables: Rockysoil = % of sites with rocky substrate component; Biom = average Robel obstruction height; PlntHt = average plant height; SHR = average number of shrub hits; LITT=average litter depth; CAN = average % canopy; INTdist = distance to the land-use interface

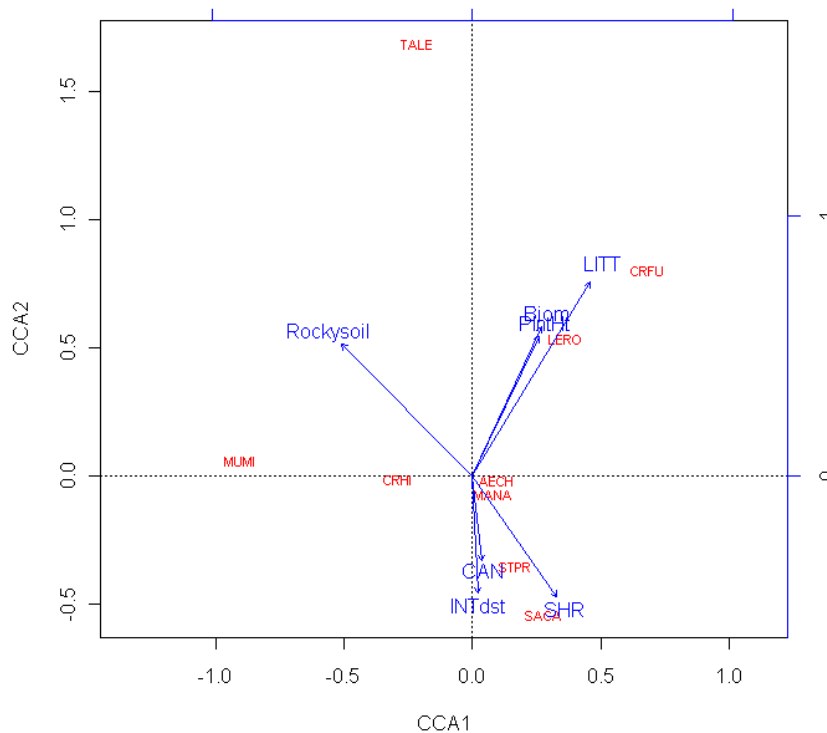


Figure 4.3. Canonical Correspondence Analysis of environmental variables and distance to the interface constrained to the assemblages of small mammal species captured at Hlane-Mbuluzi in the Lowveld of Swaziland between 15-October, 2008 and 07-January, 2009. The plots are of the WA scores and the arrows indicate the scaled biplot distance, longer arrows indicate a stronger relationship. Axes are 2 dimensional representations of the ordination space. Species are in red (AEIN, *Aethomys ineptus*; CRFU, *Crocidura fuscomurina*; CRHI, *Crocidurahirta*; DEMY, *Dendromus mystacalis*; ELBR, *Elephantulus brachyrhynchus*; GELE, *Gerbilliscus leucogaster*; LERO, *Lemniscomys rosalia*; MANA, *Mastomys natalensis*; MUMI, *Mus minutoides*; SACA, *Saccostomys pratensis*; STPR, *Steatomys pratensis*; SULI, *Suncuslixus*). The axis are standardized, numbers reflect standard deviations. Variables are: Rockysoil, % of sites with rocky substrate component; Biom, average Robel obstruction height; PlntHt, average plant height; SHR, average number of shrub hits; LITT, average litter depth; CAN, average % canopy; INTdst, distance to the land-use interface.

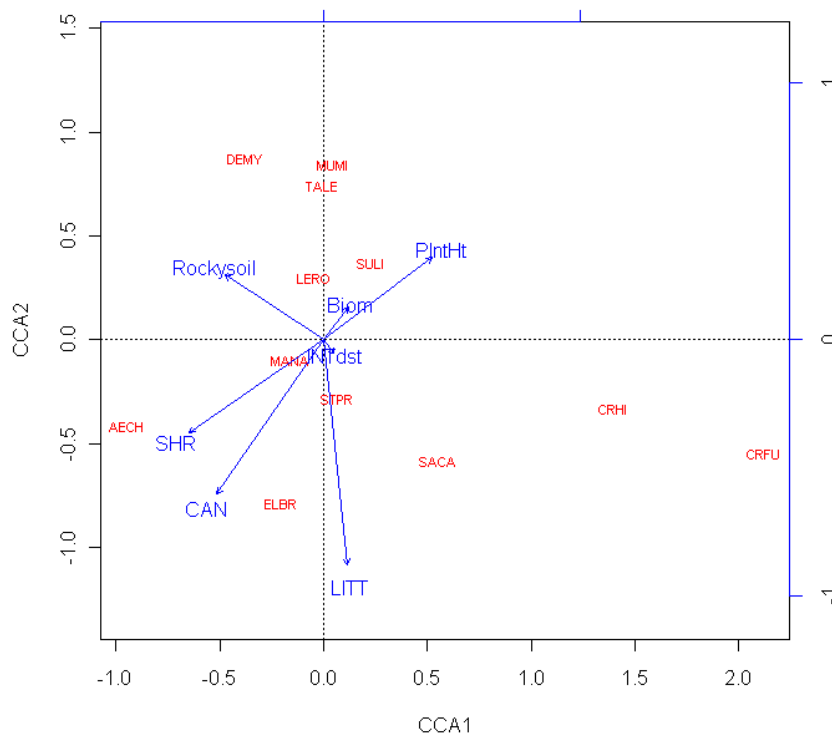


Figure 4.4. Canonical Correspondence Analysis of environmental variables and distance to the interface constrained to the assemblages of small mammal species captured at Crookes in the Lowveld of Swaziland between 15-October, 2008 and 07-January, 2009. The plots are of the WA scores and the arrows indicate the scaled biplot distance, longer arrows indicate a stronger relationship. Axes are 2 dimensional representations of the ordination space. Species are in red (AEIN, *Aethomys ineptus*; CRFU, *Crocidura fuscomurina*; CRHI, *Crocidurahirta*; DEMY, *Dendromus mystacalis*; ELBR, *Elephantulus brachyrhynchus*; GELE, *Gerbilliscus leucogaster*; LERO, *Lemniscomys rosalia*; MANA, *Mastomys natalensis*; MUMI, *Mus minutoides*; SACA, *Saccostomys pratensis*; STPR, *Steatomys pratensis*; SULI, *Suncuslixus*). The axis are standardized, numbers reflect standard deviations. Variables are: Rockysoil, % of sites with rocky substrate component; Biom, average Robel obstruction height; PlntHt, average plant height; SHR, average number of shrub hits; LITT, average litter depth; CAN, average % canopy; INTdst, distance to the land-use interface.

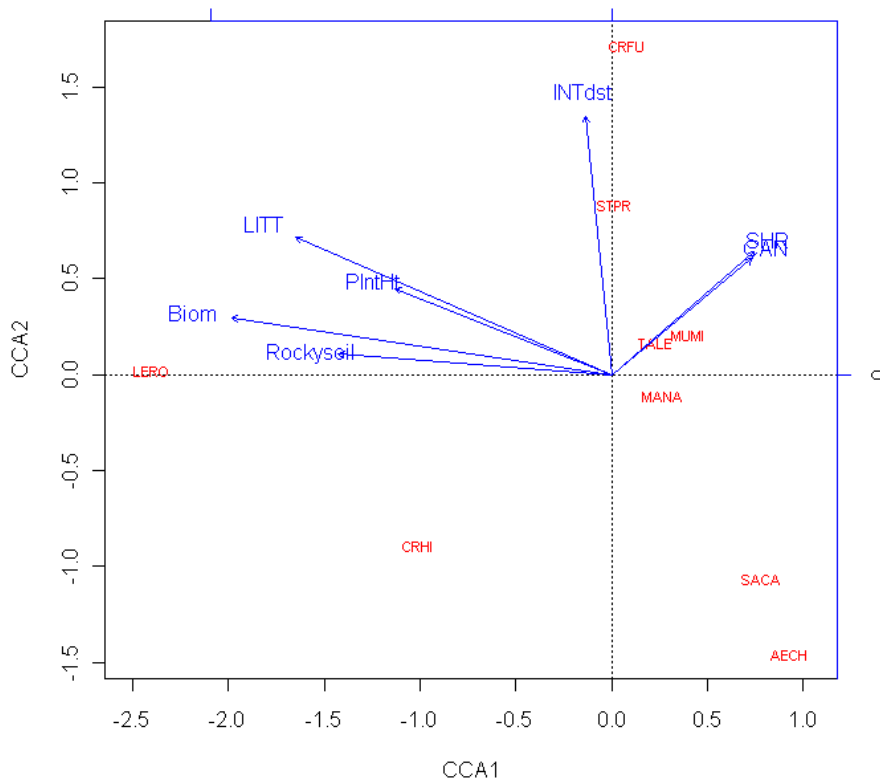


Figure 4.5. Canonical Correspondence Analysis of environmental variables and distance to the interface constrained to the assemblages of small mammal species captured at Nisela in the Lowveld of Swaziland between 15-October, 2008 and 07-January, 2009. The plots are of the WA scores and the arrows indicate the scaled biplot distance, longer arrows indicate a stronger relationship. Axes are 2 dimensional representations of the ordination space. Species are in red (AEIN, *Aethomys ineptus*; CRFU, *Crocidura fuscomurina*; CRHI, *Crocidurahirta*; DEMY, *Dendromus mystacalis*; ELBR, *Elephantulus brachyrhynchus*; GELE, *Gerbilliscus leucogaster*; LERO, *Lemniscomys rosalia*; MANA, *Mastomys natalensis*; MUMI, *Mus minutoides*; SACA, *Saccostomys pratensis*; STPR, *Steatomys pratensis*; SULI, *Suncus lixus*). The axis are standardized, numbers reflect standard deviations. Variables are: Rockysoil, % of sites with rocky substrate component; Biom, average Robel obstruction height; PlntHt, average plant height; SHR, average number of shrub hits; LITT, average litter depth; CAN, average % canopy; INTdst, distance to the land-use interface.

DISCUSSION

The results of my study indicated the conservation–sugarcane interface played a limited role in the variation of small mammal community composition in the Lowveld of Swaziland. The low amount of community variation explained by interactive edge effects indicated that sugarcane did not elicit substantial effects on community structure that extended into conservation areas. There was stronger support for a non-interactive effect attributable to environmental variables.

Within the small mammal community, only *Steatomys pratensis* had a response to distance to the interface, further indicating the limited role that the land use interface plays. However, the positive relationship of abundance with distance to the interface indicated that *Steatomys pratensis* was susceptible to deleterious effects of sugarcane-induced habitat fragmentation.

Despite the agriculture-conservation interface exhibiting predominantly non-interactive edge effects, there was some evidence of interactive effects to influencing communities at the site level. Inertias of CCAs indicated that variance in community composition attributable to interface distance varied among sites. At Nisela the biplot distances and inertias indicated that distance to the interface was more important than 4 of 6 environmental variables. Nisela had the lowest small mammal abundances. Thus, it is plausible that poor vegetation condition may increase the relative importance of sugarcane interfaces on small mammal community structure.

Only *Lemniscomys rosalia* and *Gerbilliscus leucogaster* exhibited strong responses to only 1 environmental variable, and could be thought of as specialists. The

combination of permutation tests and length of biplot distances overall and at each site, suggest that, grass biomass, litter depth, and shrub density could be indicators of habitat quality because of their correlation with variation in small mammal community structure.

Previously within the region, grass cover had been identified as the most important predictor of small mammal diversity (Monadjem 1997, Yarnell et al. 2007). In my study, the grass biomass biplot distance was consistently among the longest and the permutation test *P*-value indicated that it was highly significant. Despite the community-level importance of grass biomass in my study, only 1 species (*Lemniscomys rosalia*) had a strong, positive association with grass biomass. The disparity in the importance of grass at the community and species level, may be attributable to most species' need for a certain amount of biomass to occur in an area, with increases above this baseline amount having little effect on abundance. *Lemniscomys rosalia* may not respond in this way; its increasing abundance with grass cover which may be attributable to its diurnal habits (Monadjem 1997, Monadjem and Perrin 1997, Skinner and Chimimba 2005, Yarnell et al. 2007).

In this study, litter generally had a positive relationship with species diversity. In the Lowveld, litter depth is likely a function of vegetative cover and fire frequency. Thus, although previous small mammal studies in Swaziland and nearby Kruger National Park did not evaluate litter depth directly, their findings may be applicable. These 2 studies found low ground cover and fire events reduced diversity, mirroring my results (Kern 1981, Monadjem 1997, Monadjem and Perrin 2003).

Despite shrub density's importance to community structure in this study, the relationship varied among sites. Shrub density has an inverse relationship to grass biomass, but provides cover, nesting habitat, and large seeds (Miller 1994, Richter et al. 2001, Yarnell et al. 2008). Lowveld species have been shown to respond differently to shrub density, some species (i.e., *Elephantulus brachyrhynchus*, *Aethomys ineptus*) are found in areas with high shrub density, while others are not (i.e., *Gerbilliscus leucogaster*, *Mus minutoides*) (Monadjem 1997, Taylor 1998, Yarnell et al. 2007). Thus the influence of shrub density on community structure in this study is understandable. I found only the semi-arboreal *Aethomys ineptus* had a strong positive relationship to shrub density, which appears to be an important vegetative feature for this species (Linzey and Kesner 1997, Monadjem 1997, Ferreira and Van Aarde 1999).

Apart from *Mus minutoides* and *Gerbilliscus leucogaster*, no 2 species had similar responses to environmental conditions. Substantial co-occurrence in barn owl diets (*Tyto alba*) at other sites within southern Africa, indicates *Mus minutoides* and *Gerbilliscus leucogaster* may select similar environmental variables throughout their overlapping range (Dean 1975, Stenkewitz et al. 2001). In this study, the negative response of *Mus minutoides* and *Gerbilliscus leucogaster* to litter depth and biomass and *Gerbilliscus leucogaster*'s negative response to canopy cover indicates that they are able to persist in areas with low ground cover and high fire frequency and may be prone to high owl predation rates (Kern 1981, Monadjem 1997, Stenkewitz et al. 2001, Monadjem and Perrin 2003, Yarnell et al. 2007).

The differential responses to environmental variables among species, few clear generalist species (*Mastomys natalensis* and *Steatomys pratensis*), and lack of discrete community-level environmental responses, suggests that management of areas adjacent to sugarcane should focus on maintaining heterogeneous environmental conditions. Rocky soils, although not a manageable parameter, had a negative effect on the small mammal community as indicated by biplot scores and permutation tests. Rocky substrates can have wide-ranging effects, affecting both the composition of vegetative and small mammal communities and may affect small mammal burrowing, nesting and distribution (Reichman and Smith 1990, Monadjem 1997). In Swaziland, the extent of sugarcane plantations is often limited by the presence of rocky substrates and the resultant decrease in sugar yields. Thus along interfaces, proportion of rocky substrate may be elevated, a pattern likely found throughout southern Africa. In Hawaii, small mammals used burrows located outside of sugarcane fields but spent the majority of their time foraging within them (Nass 1977). Rocky soils may present an indirect effect of sugarcane cultivation on small mammals, by affecting accessibility to the resources provided by the sugarcane.

It is also important to consider that the weak influence of distance to the interface seen in this study may have been a function of spurious or unmeasured effects. Other studies suggest that unmeasured environmental variables, edge permeability, or species interactions (competition, predation, and mutualisms) may have influenced community structure (Ries et al. 2004, Kristan et al. 2003). Additionally there could have been

processes affecting small mammal communities at scales not addressed in this study (Morris 1987, Cadenasso et al. 2003).

Another possible explanation for a weak response to distance may have been sampling design. Small mammal sampling at each transect may have not have adequately identified the small mammal community at each trapline. Additionally the response of small mammals to the interface may have been resolved between 0 and 75 m, thus traplines may not have been close enough to observe the influence of the interface. The timing of this study during the wet season, a time of resource abundance, may have also affected the relative importance of different variables. As resources become less abundant within conservation lands, the complementary resources provided by the sugarcane matrix may become more important and the potential for interactive edge effects may increase.

CHAPTER V

CONCLUSION

My study indicates the profound effect that sugarcane has on small mammal communities that inhabit the Lowveld of Swaziland. The effect of sugarcane was demonstrated both at the species and community level. However, responses were highly variable across sites highlighting the complex nature of responses, and limiting the generalizations that could be drawn. Within the sugarcane responses were less variable illustrating its relative lack of heterogeneity despite disparate agricultural practices among sites.

I found that species had different responses to sugarcane and the land-use interface. Species (*Aethomys ineptus*, *Elephantulus brachyrhynchus*, *Steatomys pratensis*, *Saccostomys campestris*, *Gerbilliscus leucogaster*) with restricted environmental tolerances or diets were excluded from the sugarcane. Sugarcane may not provide environmental features that approximate shrubs, trees, or rocky substrates for some species, as evidenced by the exclusion of *Aethomys ineptus*. Species with well-developed burrow systems (*Steatomys pratensis*), that eat a high proportion of seeds (*Steatomys pratensis*, *Saccostomys campestris*), or select for low ground cover (*Gerbilliscus leucogaster*) may be detrimentally affected by sugarcane.

Generalist species (*Mastomys natalensis* and *Lemniscomys rosalia*) were able to persist within sugarcane, as did some insectivores. *Mastomys natalensis* and *Lemniscomys rosalia* increased in abundance with distance into the sugarcane, and at

Nisela sugarcane may have had utility in maintaining their populations. Sugarcane may also provide favorable habitat for *Crocidura silacea* and *Crocidura fuscomurina*, both insectivores that were restricted to sugarcane in my study. Species (*Mus minutoides* and *Crocidura hirta*) with large geographic ranges and environmental tolerances may have selected for the interface, and the complementary resources found there.

I found that negatively affected species (*Aethomys ineptus*, *Elephantulus brachyrhynchus*, *Steatomys pratensis*, *Saccostomys campestris*, *Gerbilliscus leucogaster*) were all absent at 375 m into the sugarcane. These negatively affected species may be more prone to expatriation. Furthermore, absence at 375 m suggests that sugarcane may be impermeable to a large number of small mammal species.

The effects of sugarcane were also seen within the small mammal communities. There was a consistent difference between small mammal communities in sugarcane and conservation lands, which indicated a sizable shift in community composition caused by the sugarcane. In most cases the greatest change in small mammal community composition occurred between 0 m and 75 m into the sugarcane. At the interface between sugarcane and conservation areas, I found lower species richness at the interface of all sites except Hlane-Mbuluzi.

Season also appeared to influence small mammal community response to the interface as measured by diversity. During the dry season, diversity estimates overall and at Crookes were slightly lower at the interface, and higher at Hlane-Mbuluzi and Nisela. Conversely, during the wet season diversity was relatively high at the interface, except at Crookes. Only at Hlane-Mbuluzi did diversity clearly increase at the interface

across seasons. In my study, the absence of a clearly positive response in diversity at the interface may indicate the unsuitability of sugarcane for most species.

Small mammal community responses extended beyond the interface itself. With few exceptions, (Nisela and 375 m at Crookes), diversity decreased with distance into the sugarcane and clusters were largely arranged along the gradient into the sugarcane. The farthest interior sugarcane trapline was the most distinct trapline in the study, and was highly separated from the farthest interior conservation trapline, as well as, the interface. Within sugarcane-fragmented lowveld savanna, 375 m may represent a distance near a threshold across which small mammal community structure disintegrates.

Despite the variation in species abundance and small mammal community structure across the land-use gradient, my study indicated the conservation-sugarcane interface played a limited role in explaining variation of small mammal community composition. The low amount of community variation explained by interactive edge effects indicated that sugarcane did not elicit substantial effects on community structure that extended into conservation areas. There was stronger support for a non-interactive effect attributable to environmental variables.

Although *Aethomys ineptus* and *Steatomys pratensis* had lower abundances at the interface, only *Steatomys pratensis* had a response attributable to the interface.

Steatomys pratensis may be susceptible to deleterious effects of sugarcane-induced habitat fragmentation. *Lemniscomys rosalia* and *Gerbilliscus leucogaster* exhibited strong responses to only 1 environmental variable (biomass), and could be thought of as specialists. Apart from *Mus minutoides* and *Gerbilliscus leucogaster*, no 2 species had

similar responses to environmental conditions. My results suggest that, grass biomass, litter depth, and shrub density could be indicators of habitat quality because of their correlation with variation in small mammal community structure.

The combined results of my analysis indicate that sugarcane has a substantial effect on small mammal species that translates to the community level. However, the effect of sugarcane did not appear to extend into the conservation areas. This does not eliminate the potential for indirect effects of sugarcane on conservation areas. The correlation between small mammal community structure and rocky soils may indicate an indirect effect.

From my study, I recommend that sugarcane agricultural practices in the Lowveld and throughout Southern Africa incorporate interstitial spaces, vegetation patches, or uncultivated strips into their designs to allow for connectivity of conservation lands. Furthermore, these features should be within 375 m of each other to ensure that community structure is maintained. The extent of sugarcane-conservation land interfaces should also be minimized, to limit potential decreases in abundance to *Steatomys pratensis*. The differential responses to environmental variables among species, few clear generalist species and lack of discrete community-level environmental responses, suggest that management of areas adjacent to sugarcane should focus on maintaining heterogeneous vegetation.

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APPENDIX I
COMPLETE MODEL OUTPUTS

Table A-1. The number of parameters (k), AIC_c, and ΔAIC_c values for *a priori* site heterogeneity models of *Mastomys natalensis* (MANA), *Mus minutoides* (MUMI), *Lemniscomys rosalia* (LERO), *Aethomys ineptus* (AEIN), and *Steatomys pratensis* (STPR) in the Lowveld of Swaziland. Best fitting models are in bold.

Site heterogeneity model ^{a,b}	Species														
	MANA			AEIN			LERO			MUMI			STPR		
	k	AIC _c	ΔAIC _c	k	AIC _c	ΔAIC _c	k	AIC _c	ΔAIC _c	k	AIC _c	ΔAIC _c	k	AIC _c	ΔAIC _c
(.)	2	4780.18	9.74	4	662.48	4.72	6	802.76	0	1	757.20	3.83	4	199.90	0
(site)	6	4785.63	15.19	12	657.76	0	18	820.45	17.69	3	753.37	0			
(HI/Cr)	4	4781.92	11.49	8	661.35	3.60	12	811.47	8.71	2	754.17	0.80			
(cane)	4	4775.77	5.33	8	669.48	11.73	12	813.29	10.53	2	758.70	5.33	8	200.18	0.28
(dist)	18	4790.83	20.39												
(3cane,3mid)	6	4775.40	4.96	12	674.08	16.32	18	816.53	13.77	3	758.45	5.09			
(int,mid,edge)	10	4782.90	12.46							5	762.52	9.15			
(4res)	4	4774.68	4.25	8	669.72	11.96	12	811.72	8.96	2	758.88	5.52			
(4res,edge)	6	4778.37	7.94	12	674.73	16.97	16	811.03	8.27	3	760.71	7.34			
(dist,cane)	12	4787.65	17.21							6	763.35	9.98			
(season)	4	4784.12	13.69	8	667.445	9.69	12	809.20	6.44	2	758.47	5.10	8	200.18	0.28
(site;season)	12	4791.41	20.98				18	820.45	17.69	6	755.24	1.87			
(HI/Cr;season)	8	4784.81	14.37							4	755.20	1.83			
(cane;season)	8	4783.42	12.98							4	757.08	3.71			
(dist;season)	36	4810.16	39.72												
(3cane,3mid; season)	12	4787.07	16.63							6	759.18	5.81			
(int,mid,edge; season)	20	4781.98	11.54												

Table A-1. continued

	Species														
	MANA			AEIN			LERO			MUMI			STPR		
Site heterogeneity model ^{a,b}	k	AIC _C	ΔAIC _C	k	AIC _C	ΔAIC _C	k	AIC _C	ΔAIC _C	k	AIC _C	ΔAIC _C	k	AIC _C	ΔAIC _C
(4res;season)	8	4782.27	11.83				24	824.29	21.53	4	758.74	5.37			
(4res,edge;season)	12	4785.87	15.44							6	760.96	7.59			
(dist,cane;season)	24	4794.92	24.48				24	829.93	27.17						
(site;cane)	12	4779.39	8.95							6	753.96	0.59			
(site;dist)	27	4785.20	14.76												
(site;3cane,3mid)	18	4770.44	0												
(site;int,mid,edge)	30	4785.34	14.90												
(site;4res)	12	4782.67	12.24							6	756.21	2.84			
(site;4res,edge)	18	4774.72	4.28												
(site;dist,cane)	35	4782.16	11.72												
(HI/Cr;cane)	8	4773.07	2.63	12	665.48	7.72				4	755.86	2.50			
(HI/Cr;dist)	18	4802.69	32.25												
(HI/Cr;3cane,3mid)	12	4774.84	4.4							6	755.18	1.82			
(HI/Cr;int,mid,edge)	20	4786.22	15.78												
(HI/Cr;4res)	8	4774.93	4.50							4	755.77	2.40			
(HI/Cr;4res,edge)	12	4776.27	5.83							5	756.99	3.62			
(HI/Cr;dist,cane)	24	4793.65	23.21												
(site;season;cane)	24	4790.90	20.46												
(site;season;3cane,3mid)	36	4781.13	10.69												
(site;season;4res)	24	4794.69	24.25												
(site;season;4res,edge)	34	4787.57	17.14												

Table A-1. continued

Site heterogeneity model ^{a,b}	Species														
	MANA			AEIN			LERO			MUMI			STPR		
	k	AIC _c	ΔAIC _c	k	AIC _c	ΔAIC _c	k	AIC _c	ΔAIC _c	k	AIC _c	ΔAIC _c	k	AIC _c	ΔAIC _c
(site;season;4res, edge)	34	4787.57	17.14												
(HI/Cr;season; cane)	16	4781.76	11.33												
(HI/Cr;season; 3cane,3mid)	24	4779.51	9.08												
(HI/Cr;season;int,mid,edge)	38	4794.62	24.18												
(HI/Cr;season; 4res)	16	4781.70	11.26												
(HI/Cr;season; 4res,edge)	22	4782.88	12.44												

^aParameter abbreviations: (.) constant site response, (site) site location, (season) wet or dry season, (HI/Cr) site grouping by habitat condition, (cane) landuse type, (dist) each individual trapline, (3cane, 3 mid) grouping of traplines: 3 sugarcane, 3 middle, and 3 conservation landuse, (int,mid,edge) groupings of traplines: interior, middle and edge for each landuse, (4res) grouping of traplines: 4 interior conservation area, edge/sugarcane, (4res,edge) grouping of traplines: 4 interior conservation area, edge, and sugarcane, and (dist, cane) grouping of traplines: each conservation area, edge, and sugarcane.

^bBlank indicates model with overdispersed data

Table A-2. Maximum likelihood estimates (MLE) and upper ($\uparrow 95\%$) and lower ($\downarrow 95\%$) 95% confidence intervals for the untransformed beta estimates of the capture (p) and recapture (c) for the top ranked closed capture model for each of *Mastomys natalensis* (MANA), *Mus minutoides* (MUMI), and *Aethomys ineptus* (AEIN) in the Lowveld of Swaziland. Traplines span the land-use gradient (1 = 375 m, 2 = 225 m, 3 = 150 m, 4 = 75 m into the conservation area, 5 = interface (0 m), and 6 = 75 m, 7 = 150, 8 = 225 m, 9 = 375 m into the sugarcane).

a	Trapline	Species							
		MANA		AEIN				MUMI	
		$\uparrow 95\%$	$\uparrow 95\%$	$\uparrow 95\%$	$\uparrow 95\%$	$\uparrow 95\%$	$\uparrow 95\%$	$\uparrow 95\%$	$\uparrow 95\%$
		p	c	p_1	p_2	p_3	p_4	p	p
		$\downarrow 95\%$	$\downarrow 95\%$	$\downarrow 95\%$	$\downarrow 95\%$	$\downarrow 95\%$	$\downarrow 95\%$	$\downarrow 95\%$	$\downarrow 95\%$
				-0.29	0.04	0.28	0.70	-1.84	
Hlane/ Mbuluzi				-0.76	-0.41	-0.17	0.24	-2.59	
				-1.22	-0.86	-0.62	-0.23	-3.34	
		-0.04	0.12						
	1-3	-0.44	-0.32						
		-0.83	-0.77						
		-0.41	-0.06						
	4-6	-0.74	-0.42						
		-1.08	-0.78						
		-0.54	0.03						
	7-9	-1.30	-0.69						
		-2.07	-1.42						
				-0.72	-0.12	-0.20	-0.37	-1.45	
Crookes				-1.45	-0.80	-0.88	-1.05	-1.88	
				-2.18	-1.47	-1.56	-1.74	-2.32	

Table A-2. continued

a		Species										
		MANA					AEIN				MUMI	
		↑95%		↑95%		↑95%	↑95%	↑95%	↑95%	↑95%	↑95%	
		<i>p</i>	<i>c</i>	<i>p</i> ₁	<i>p</i> ₂	<i>p</i> ₃	<i>p</i> ₄	<i>p</i>				
Trapline		↓95%		↓95%		↓95%		↓95%		↓95%		
Crookes	1-3		-0.46		0.17							
		-0.85		-0.22								
			-1.24		-0.61							
	4-6		0.05		0.50							
		-0.22		0.19								
			-0.49		-0.12							
Nisela	7-9		-0.44		0.14							
		-1.00		-0.39								
			-1.56		-0.92							
					-0.73	1.13	-2.42	-0.13	-1.13	0.69	-0.13	-2.08
						-2.58		-4.72		-2.94	-3.47	
												-4.86
	1-3		-0.05		0.35							
		-0.29		0.07								
			-0.52		-0.21							
	4-6		-0.24		-0.02							
		-0.54		-0.35								
			-0.84		-0.69							
7-9		-0.11		0.57								
	-0.40		0.25									
			-0.68		-0.08							

Table A-3. Maximum likelihood estimates (MLE) and upper ($\uparrow 95\%$) and lower ($\downarrow 95\%$) 95% confidence intervals for the real estimates of the capture (p) and recapture (c) for the top ranked closed capture model for each of *Mastomys natalensis* (MANA), *Mus minutoides* (MUMI), and *Aethomys chrysophila* (AEIN) in the Lowveld of Swaziland. Traplines span the land-use gradient (1 = 375 m, 2 = 225 m, 3 = 150 m, 4 = 75 m into the conservation area, 5 = interface (0 m), and 6 = 75 m, 7 = 150, 8 = 225 m, 9 = 375 m into the sugarcane).

Trapline	Species							
	MANA		AEIN				MUMI	
	$\uparrow 95\%$	$\uparrow 95\%$	$\uparrow 95\%$	$\uparrow 95\%$	$\uparrow 95\%$	$\uparrow 95\%$	$\uparrow 95\%$	$\uparrow 95\%$
	p	c	p	p	p	p	p	p
	$\downarrow 95\%$	$\downarrow 95\%$	$\downarrow 95\%$	$\downarrow 95\%$	$\downarrow 95\%$	$\downarrow 95\%$	$\downarrow 95\%$	$\downarrow 95\%$
Hlane/ Mbuluzi			0.4285	0.51	0.57	0.67	0.14	
			0.32	0.40	0.46	0.56	0.07	
			0.23	0.30	0.35	0.44	0.03	
		0.49	0.53					
	1-3	0.39	0.42					
		0.30	0.32					
		0.40	0.49					
	4-6	0.32	0.40					
		0.25	0.31					
		0.37	0.50					
Crookes	7-9	0.21	0.33					
		0.11	0.20					
			0.33	0.47	0.45	0.41	0.19	
			0.19	0.31	0.29	0.26	0.13	
			0.10	0.19	0.17	0.15	0.09	

Table A-3. continued

	Trapline	Species									
		MANA		AEIN				MUMI			
		↑95%	↑95%	↑95%	↑95%	↑95%	↑95%	↑95%	↑95%	↑95%	↑95%
		<i>p</i>	<i>c</i>	<i>p</i>	<i>p</i>	<i>p</i>	<i>p</i>	<i>p</i>	<i>p</i>	<i>p</i>	<i>p</i>
		↓95%	↓95%	↓95%	↓95%	↓95%	↓95%	↓95%	↓95%	↓95%	↓95%
Crookes			0.39	0.54							
	1-3	0.30	0.45								
			0.23	0.35							
			0.51	0.62							
	4-6	0.45	0.55								
			0.38	0.47							
			0.39	0.54							
	7-9	0.27	0.40								
			0.17	0.29							
					0.76	0.47	0.67	0.47		0.11	
Nisela				0.33	0.08	0.24	0.08	0.03			
				0.07	0.01	0.05	0.01	0.01		0.01	
			0.49	0.59							
	1-3	0.43	0.52								
			0.37	0.45							
			0.44	0.50							
	4-6	0.37	0.41								
			0.30	0.34							
			0.47	0.64							
	7-9	0.40	0.56								
			0.34	0.48							

Table A-4. Maximum likelihood estimates (MLE) and upper ($\uparrow 95\%$) and lower ($\downarrow 95\%$) 95% confidence intervals for the untransformed beta estimates of the capture (p) and recapture (c) for the top ranked closed capture model for each of *Steatomys pratensis* (STPR) and *Lemniscomys rosalia* (LERO) in the Lowveld of Swaziland.

Parameter		STPR		LERO	
p_1	$\uparrow 95\%$		-1.68		-1.73
		-2.52		-2.17	
	$\downarrow 95\%$		-3.36		-2.61
p_2	$\uparrow 95\%$		-2.17		-0.70
		-3.16		-1.06	
	$\downarrow 95\%$		-4.15		-1.42
p_3	$\uparrow 95\%$		-1.02		-0.26
		-1.80		-0.69	
	$\downarrow 95\%$		-2.57		-1.13
p_4	$\uparrow 95\%$		-0.77		0.19
		-1.54		-0.15	
	$\downarrow 95\%$		-2.32		-0.50
c_1	$\uparrow 95\%$			0.17	0.97
					-0.64
	$\downarrow 95\%$				-0.22
c_2	$\uparrow 95\%$			-0.69	
	$\downarrow 95\%$				-1.16

Table A-5. Maximum likelihood estimates (MLE) and upper ($\uparrow 95\%$) and lower ($\downarrow 95\%$) 95% confidence intervals for the real estimates of the capture (p) and recapture (c) for the top ranked closed capture model for each of *Steatomys pratensis* (STPR) and *Lemniscomys rosalia* (LERO) in the Lowveld of Swaziland.

Parameter		STPR	LERO
p_1	$\uparrow 95\%$	0.16	0.15
		0.08	0.10
	$\downarrow 95\%$	0.03	0.07
p_2	$\uparrow 95\%$	0.10	0.33
		0.04	0.26
	$\downarrow 95\%$	0.02	0.19
p_3	$\uparrow 95\%$	0.27	0.44
		0.14	0.33
	$\downarrow 95\%$	0.07	0.25
p_4	$\uparrow 95\%$	0.32	0.55
		0.18	0.46
	$\downarrow 95\%$	0.09	0.38
c_1	$\uparrow 95\%$		0.73
			0.54
	$\downarrow 95\%$		0.35
c_2	$\uparrow 95\%$		0.45
			0.33
	$\downarrow 95\%$		0.24

Table A-6. The number of parameters (k), AIC_c, and Δ AIC_c values for *a priori* occupancy models of *Saccostomys campestris* (SACA) and *Elephantulus brachyrhynchus* (ELBR) in the Lowveld of Swaziland during the 2008 dry (April–September) season. Top models are in bold.

Occupancy model ^{a,b}	Species					
	SACA			ELBR		
	k	AIC _c	Δ AIC _c	k	AIC _c	Δ AIC _c
$\psi(.)$	3	111.46	5.73	2	71.76	10.56
$\psi(\text{site})$	4	109.87	4.14	3	69.56	8.36
$\psi(\text{Hl/Cr})$	3	110.05	4.32	3	67.62	6.42
$\psi(\text{cane})$	3	110.54	4.81	4	65.72	4.52
$\psi(\text{dist})$						
$\psi(3\text{cane},3\text{mid})$	4	106.59	0.86	4	69.56	8.36
$\psi(\text{int},\text{mid},\text{edge})$	6	108.66	2.93			
$\psi(4\text{res})$	3	112.14	6.41	3	63.38	2.18
$\psi(4\text{res},\text{edge})$	4	107.19	1.46	4	65.54	4.34
$\psi(\text{dist},\text{cane})$						
$\psi(\text{site};\text{cane})$	5	109.9	4.17	5	65.57	4.37
$\psi(\text{site};\text{dist})$						
$\psi(\text{site};3\text{cane},3\text{mid})$	6	105.75	0.02			
$\psi(\text{site};\text{int},\text{mid},\text{edge})$						
$\psi(\text{site};4\text{res})$	5	111.49	5.76	5	63.16	0
$\psi(\text{site};4\text{res},\text{edge})$	6	105.73	0			
$\psi(\text{site};\text{dist},\text{cane})$						
$\psi(\text{Hl/Cr};\text{cane})$	4	110.06	4.33	4	63.6	2.4
$\psi(\text{Hl/Cr};\text{dist})$						
$\psi(\text{Hl/Cr};3\text{cane},3\text{mid})$	5	105.97	0.24			
$\psi(\text{Hl/Cr};\text{int},\text{mid},\text{edge})$						
$\psi(\text{Hl/Cr};4\text{res})$	4	111.69	5.96	4	61.2	1.96
$\psi(\text{Hl/Cr};4\text{res},\text{edge})$	5	106.32	0.59	5	63.4	2.2
$\psi(\text{Hl/Cr};\text{dist},\text{cane})$						

^aParameter abbreviations: (.) constant occupancy, (site) site location, (Hl/Cr) site grouping by vegetation condition, (cane) landuse type, (dist) each individual trapline, (3cane, 3 mid) grouping of traplines: 3 sugarcane, 3 middle, and 3 conservation landuse, (int,mid,edge) groupings of traplines: interior, middle and edge for each landuse, (4res) grouping of traplines: 4 interior conservation area, edge/sugarcane, (4res,edge) grouping of traplines: 4 interior conservation area, edge, and sugarcane, and (dist, cane) grouping of traplines: each conservation area, edge, and sugarcane.

^bblank indicates model with overdispersed data

Table A-7. The number of parameters (k), AIC_c, and Δ AIC_c values for *a priori* occupancy models of *Crocidura hirta* (CRHI), *Suncus lixus* (SULI), *Saccostomys campestris* (SACA), and *Gerbilliscus leucogaster* (GELE) in the Lowveld of Swaziland during the 2008 wet (October–March) season. Best fitting models are in bold.

Occupancy model ^{ab}	Species											
	CRHI			SULI			SACA			GELE		
	k	AIC _c	Δ AIC _c	k	AIC _c	Δ AIC _c	k	AIC _c	Δ AIC _c	k	AIC _c	Δ AIC _c
$\psi(.)$	3	171.86	1.58	2	81.14	0.08	3	172.38	16.08	3	134.46	3.61
$\psi(\text{site})$	4	174.25	3.97				4	163.04	6.74	4	134.2	3.35
$\psi(\text{HI/Cr})$	3	172.34	2.06				3	169.27	12.97	3	134.38	3.53
$\psi(\text{cane})$	3	171.35	1.07	3	81.06	0	3	165.17	8.87	3	130.85	0
$\psi(\text{dist})$												
$\psi(3\text{cane},3\text{mid})$	4	170.28	0				4	170.42	14.12	4	132.35	1.5
$\psi(\text{int},\text{mid},\text{edge})$	6	175.41	5.13				6	169.72	13.42	6	136.18	5.33
$\psi(4\text{res})$	3	171.58	1.3	3	81.99	0.93	3	169.37	13.07	3	132.77	1.92
$\psi(4\text{res},\text{edge})$	4	173.25	2.97	4	83.21	2.15	4	167.07	10.77	4	132.98	2.13
$\psi(\text{dist},\text{cane})$	7	177.49	7.21				7	171.66	15.36			
$\psi(\text{site};\text{cane})$	5	174.43	4.15				5	156.3	0	5	132.58	1.73
$\psi(\text{site};\text{dist})$												
$\psi(\text{site};3\text{cane},3\text{mid})$	6	173.41	3.13				6	162.03	5.73	6	134.15	3.3
$\psi(\text{site};\text{int},\text{mid},\text{edge})$	8	178.62	8.34				8	160.71	4.41			
$\psi(\text{site};4\text{res})$	5	174.7	4.42				5	161.05	4.75	5	134.54	3.69
$\psi(\text{site};4\text{res},\text{edge})$	6	176.35	6.07				6	158.18	1.88	6	134.78	3.93
$\psi(\text{site};\text{dist},\text{cane})$	9	180.67	10.39									
$\psi(\text{HI/Cr};\text{cane})$	4	172.55	2.27				4	163.36	7.06	4	132.8	1.95
$\psi(\text{HI/Cr};\text{dist})$												
$\psi(\text{HI/Cr};3\text{cane},3\text{mid})$	5	171.44	1.16				5	168.71	12.41	5	134.34	3.49
$\psi(\text{HI/Cr};\text{int},\text{mid},\text{edge})$	7	176.71	6.43				7	167.87	11.57			
$\psi(\text{HI/Cr};4\text{res})$	4	172.84	2.56				4	167.7	11.4	4	134.72	3.87
$\psi(\text{HI/Cr};4\text{res},\text{edge})$	5	174.48	4.2				5	165.24	8.94	5	134.96	4.11
$\psi(\text{HI/Cr};\text{dist},\text{cane})$	8	178.76	8.48				8	169.81	13.51			

^a Parameter abbreviations: (.) constant occupancy, (site) site location, (HI/Cr) site grouping by vegetation condition, (cane) landuse type, (dist) each individual trapline, (3cane, 3 mid) grouping of traplines: 3 sugarcane, 3 middle, and 3 conservation landuse, (int,mid,edge) groupings of traplines: interior, middle and edge for each landuse, (4res) grouping of traplines: 4 interior conservation area, edge/sugarcane, (4res,edge) grouping of traplines: 4 interior conservation area, edge, and sugarcane, and (dist, cane) grouping of traplines: each conservation area, edge, and sugarcane.

^bblank indicates model with overdispersed data

Table A-8. Maximum likelihood estimates (MLE) of occupancy (ψ) and detection (p) probability with upper ($\uparrow 95\%$) and lower ($\downarrow 95\%$) 95% confidence intervals for untransformed betas of the top ranked model for each of *Saccostomys campestris* (SACA) and *Elephantulus brachyrhynchus* (ELBR) in the Lowveld of Swaziland during the 2008 dry (April–September) season.

		parameter ^a											
		p(.)		ψ(.)		ψ(site (1))		ψ (site(2))		ψ(4res)		ψ(edge)	
		MLE	↑95%	MLE	↑95%	MLE	↑95%	MLE	↑95%	MLE	↑95%	MLE	↑95%
Species	Model ^a		↓95%		↓95%		↓95%		↓95%		↓95%		↓95%
SACA	ψ(site+4res,edge) p(.)		0.02		-1.63		5.45		3.72		2.40		5.99
		-0.95		-4.48		2.61		0.92		0.44		3.21	
			-1.91		-7.33		-0.23		-1.87		-1.51		0.43
ELBR	ψ(site+4res) p(.)		0.41		-43.00		39.46		39.07		30.33		
		-0.81		-49.70		29.29		28.78		19.28			
			-2.02		-56.41		19.12		18.49		8.23		

^aParameter definitions: (.) constant, (T) temp at dawn, (Site (1)) Hlane/Mbuluzi, (Site(2)) Crookes, (Cane) traplines 6-9, (3cane) traplines 7-9, and (3mid) traplines 4-6.

Table A-9. Maximum likelihood estimates (MLE) of occupancy (ψ) and detection (p) probability with upper ($\uparrow 95\%$) and lower ($\downarrow 95\%$) 95% confidence intervals for untransformed betas of the top ranked model for each of *Crocidura hirta* (CRHI), *Suncus lixus* (SULI), *Saccostomys campestris* (SACA), and *Gerbilliscus leucogaster* (GELE) in the Lowveld of Swaziland during the 2008 wet (October–March) season.

		parameter ^a													
		p(.)		ψ(.)		ψ(site (1))		ψ(site(2))		ψ(cane)		ψ(3cane)		ψ(3mid)	
		↑95%		↑95%		↑95%		↑95%		↑95%		↑95%		↑95%	
		MLE		MLE		MLE		MLE		MLE		MLE		MLE	
Species	Model ^a	↓95%		↓95%		↓95%		↓95%		↓95%		↓95%		↓95%	
		-0.69		0.84								0.25		1.72	
CRHI	ψ(3cane,3mid) p(.)	-1.59		-0.53											
		-2.49		-1.90								-1.60		0.22	
		3.30		-1.15							0.73		-3.46		-1.28
SULI	ψ(cane)p(.)	-0.68		-2.16						-1.47					
		-4.67		-3.17							-3.67				
		0.25		-0.67		4.04		2.07		-0.49					
SACA	ψ(site,cane) p(.)	-0.37		-2.16		2.31		0.0000		-2.18					
		-0.99		-3.64		0.58		-2.07		-3.86					
		1.15		-1.00						0.18					
GELE	ψ(cane)p(.)	0.51		-1.71						-1.40					
		-0.15		-2.42						-2.99					

^b Parameter definitions: (.) constant, (T) temp at dawn, (Site (1)) Hlane/Mbuluzi, (Site(2)) Crookes, (Cane) traplines 6-9, (3cane) traplines 7-9, and (3mid) traplines 4-6.

Table A-10. Maximum likelihood real estimates (MLE) of detection (p) probability with upper ($\uparrow 95\%$) and lower ($\downarrow 95\%$) 95% confidence intervals for the derived parameters of the top ranked model for each of *Saccostomys campestris* (SACA), *Elephantulus brachyrhynchus* (ELBR) *Crocidura hirta* (CRHI), *Suncus lixus* (SULI), and *Gerbilliscus leucogaster* (GELE) in the Lowveld of Swaziland during the 2008 dry (April–September) and wet (October–March) season.

Site	Season			
	Dry		Wet	
	MLE	p	MLE	p
		$\uparrow 95\%$		$\uparrow 95\%$
		$\downarrow 95\%$		$\downarrow 95\%$
SACA	0.28	0.51	0.41	0.56
		0.13		0.27
ELBR	0.31	0.6		
		0.12		
CRHI			0.17	0.34
				0.08
SULI			0.34	0.59
				0.15
GELE			0.62	0.76
				0.46

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