Multi-scale habitat selection of *Mus minutoides* in the Lowveld of Swaziland

Andrea K. Long[1,3], Karen Bailey[1,4], Daniel U. Greene[1,5], Courtney Tye[1,6], Courtnee Parr[1,7], Heather K. Lepage[1,7], Kurt H. Gielow[1,8], Ara Monadjem[2,3,10], Robert A. McCleery[1,11]

[1]*Department of Wildlife Ecology and Conservation, University of Florida, 110 Newins-Ziegler Hall, PO Box 110430, Gainesville, FL, 32611, USA*
[2] *Department of Biological Sciences, University of Swaziland, P/Bag 4, Kwaluseni, Swaziland*
[3]*Mammal Research Institute, Department of Zoology & Entomology, University of Pretoria, Private Bag 20, Hatfield 0028, Pretoria, South Africa*

aklong@ufl.edu[3], karen.bailey@ufl.edu[4], greenda@ufl.edu[5], jpcah@ufl.edu[1,6], parrcj02@gmail.com[1,7], heatherklepage@gmail.com [1,8], gielowk@gmail.com[1,9], aramonadjem@googlemail.com[2,10], ramccleery@ufl.edu[1,11]

Corresponding author: Andrea K. Long

ABSTRACT

We investigated habitat selection of *Mus minutoides* in northeastern Swaziland. We used powder tracking to determine how *M. minutoides* selected habitat at a fine scale and a broader path scale. At the fine scale, we measured percent cover of grass and shrubs, the number of forbs, and visual obstruction at five evenly-spaced points along a mouse's pathway and at a paired random location. At the path scale, we calculated the relative displacement (RD) of each path as the ratio of the distance from the start to the end point of the path to the total length of the path (values near one indicate less preference). We found that *M. minutoides* were positively associated with increases in visual obstruction, grass cover, and shrub cover at the fine scale, but not at the path scale. Our results indicate that *M. minutoides* selection of vegetative features at the path scale are not as important as their fine scale selection of vegetative structure. Additionally, the shrub encroachment on our study site may be directly beneficial to *M. minutoides* at the fine scale. Our results provide us with an increased understanding of the basic ecology of *M. minutoides* and information on their response to a changing landscape.

Key Words: pygmy mice, *Mus minutoides,* Swaziland, habitat selection, fluorescent tracking, shrub encroachment

INTRODUCTION

Small mammals play an important role in most ecosystems as herbivores, seed predators, and prey species and can be indicators of ecosystem health (Keesing, 2000; Manson, Ostfield, & Canham, 2001; Monadjem and Perrin, 2003; Avenant & Cavallini, 2007). However, we know relatively little about the basic ecology (e.g. habitat selection, diet, competitive interactions) of many of sub-Saharan Africa's murid rodents. As quantifying habitat selection is vital to understanding an organism's basic ecology, one obvious place to start is to understand how murid rodents select habitats (Johnson, 1980).

Throughout southern Africa, land use changes and practices have led to increased shrub encroachment (Roques, O'Conner, & Watkinson, 2001). In northeastern Swaziland, Sirami & Monadjem (2012) documented an increase in shrub cover from 30 % to 40 % from 1998 to 2008. One study on the consequences of shrub encroachment on local rodent abundance showed variable responses (Blaum, Rossmanith, & Jeltsch et al., 2007a). For example some rodent species (e.g. *Gerbillurus paeba, Desmodillus auricularis,* and *Tatera leucogaster*) responded negatively while other species (e.g. *Rhabdomys pumilio* and *Tatera brantsii*) showed a hump-shaped response, increasing in abundance until a certain threshold of shrub cover and then decreasing (Blaum et al., 2007a). Understanding the relationship between habitat selection of ecologically important small mammals and shrub encroachment is important for land managers hoping to maintain and enhance biodiversity and ecosystem health (Blaum et al., 2007a,b).

African pygmy mice (*Mus* spp.) are an assemblage of small (4-12 g) murine rodents (subgenus *Nannomys*) distributed throughout sub-Saharan Africa. Pygmy mice have been the

1

subject of much taxonomic confusion (Veyrunes et al., 2005; Kouassi et al., 2008; Mboumba et al., 2011). They are presently recognized as a complex of 17-19 morphologically similar species, and may contain a number of species and subspecies not yet described (Marshall, 1981; Macholan, 2001; Musser & Carleton, 2005; Britton-Davidson, Robinson, & Veyrunes, 2012). Pygmy mice occupy a wide range of land cover types, including forests, cultivations, recently burned grasslands, and rocky habitats, at elevations up to 2,400 m (Skinner & Chimimba, 2005; Veyrunes et al., 2004; 2005; Kouassi et al., 2008; Fichet-Calvet et al., 2010), but are primarily considered a savanna species (Mboumba et al., 2011). We only know of four studies examining pygmy mouse habitat selection, all of which used trapping location to quantify habitat use. Nel & Rautenbach (1975) found that Mus minutoides preferred low or high dunes on riverbanks to silt riverbeds or raised plateaus and Nel (1978) found that Mus minutoides used all habitats in which they trapped during their study (e.g. low dunes, plateaus, riverbed, and high dunes). Monadjem (1997a) measured vegetative features within 1 m^2 plots around each trap and was unable to correlate pygmy mouse occurrence to vegetative features but noted that they were generally caught in areas with grass cover. In a second study, Monadjem (1999a) was unable to assess the use of burned and unburned areas by pygmy mice due to low trap success following the fire. Although Monadjem (1997a) quantified vegetative features at a fine scale, determining habitat selection relative to traps may lead to inaccurate measures of habitat selection as bait may cause atypical selection of foraging sites. Similarly, a potential reason for the inconclusive results found in Monadjem (1999a) is that small mammals often select foraging areas based on fine scale vegetative features to decrease the risk of predation (Kotler, 1984; Bowers, 1990) and not at the broader scale measured in their study. Thus, it is important to assess pygmy mice habitat

on the scales that are relevant to them and, apart from Monadjem's (1997a) study, we know of no studies examining pygmy mouse habitat selection at fine scales.

*Mus minutoides (*A. Smith 1834*),* one species of pygmy mice found in Africa, is rarely caught in large numbers but is common throughout Swaziland and possibly the dominant small mammal species in some nature reserves (Cheeseman & Delany, 1979; Sheppe & Haas, 1981; Monadjem, 1997a; Monadjem, 1999b; Mahlaba & Perrin, 2003). Working in the lowveld of Swaziland provided us with an excellent opportunity to address our goal of understanding the basic ecology of *M. minutoides* by investigating their habitat selection. Moreover, with shrubs as the dominate vegetative feature on the landscape we can assess the influence of shrub encroachment on *M. minutoides*. Shrubs could affect *M. minutoides* fine scale and nightly movement by providing cover from predators or negatively influence them by decreasing the abundance of seeds for forage through the displacement of forbs and grasses across the landscape. To better understand *M. minutoides* ecology and it use of the savannah we investigated their movements on two spatial scales. Specifically, our objectives for this study were to 1) determine *M. minutoides* habitat selection on a fine ($1\ m^2$) scale and 2) determine the influence of shrub cover relative to their nightly movements at a broader path scale. We quantified vegetation within $1\ m^2$ plots along the pygmy mouse's path to quantify fine scale movement as vegetative features at this scale have been show to be important to small mammals. Similarly, quantifying vegetation at the path scale provided information on habitat selection within areas encompassed by an individual's nightly movement.

MATERIALS AND METHODS

Study area

Our study was conducted in the Mlawula Nature Reserve in northeastern Swaziland. We trapped rodents in sour lowland bushveld vegetation (Low & Rebelo, 1996) characterized by grass cover (*Themda* spp., *Panicum maximum*), a substantial shrub layer dominated by *Dichrostachys cinerea* (Sirami & Monadjem, 2012) and intermittent tree cover dominated by *Acacia nigrescens* and *Sclerocarya birrea*. Large mammal species in the area included blue wildebeest (*Connochaetes taurinus*), impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*), and warthog (*Phacochoerus africanus*). Some common predators of *Mus minutoides* found in the reserve include serval (*Felis serval*), large-spotted genets (Genetta tigrina), and the African barred owl (*Glaucidium capense*). The mean annual rainfall of our study site ranges from 550-725 mm (Matondo et al., 2005).

Sampling design

We trapped rodents during May and June 2011 at two sites separated by 1 km. We established 10 trapping transects (10 traps each) spaced 40 m apart on each site. We placed Sherman live-traps (7.6 x 9.5 x 30.5 cm, H. B. Sherman Traps, Inc., Tallahassee, Florida) at 10 m increments along each transect. We baited traps with oats, opened them at sunset and checked them at sunrise. To assess movements within the habitat, we dusted the first *M. minutoides* captured on each transect with fluorescent powder (A-15-N blaze orange pigment, DayGlo Color Corp.) and then each additional mouse that was trapped at least 30 m away to minimize overlapping pathways. To apply fluorescent powder we placed each mouse into a bag containing powder and gently shook them (Duplantier et al., 1984; Lemen & Freeman, 1985; Mullican,

4

1988). We released each individual at their capture location the following evening. Three hours after we released the mice, we followed each travel pathway using a UV light. We flagged each pathway at 1 m increments for its visible length or up to 30 m. The total length of the traveled pathway was measured the following day.

Habitat assessment

To assess *M. minutoides* fine scale habitat selection, we measured vegetation characteristics at five points every 5 m along the travel pathway (Figure 1). On paths shorter than 25 m, we quantified vegetative features for our fifth point at the last point along the pathway. We paired used locations with random points by randomly selecting a direction and distance (2-6 m) from each used point on the pathway (Figure 1). At each used and random point we placed a 1 m^2 circular plot and measured the percent cover of grass (Grass), shrub (Shrub), and the number of forbs (Forbs). We visually classified the percent cover of grass and shrubs into 10 equal classes ranging from 0-100% (Higgins et al., 1996). We used a robel pole centered within the circular plots to measure visual obstruction (a measure of horizontal cover; VO) at a mouse's level in decimeters from a distance of 4 m in each cardinal direction (Robel et al., 1970; Smith, 2008) to determine if the height and density of the vegetation influenced a mouse's ability to traverse the landscape. The robel method has been shown to be an effective measure of available cover in wildlife studies (Robel et al., 1970; Smith, 2008).

To assess habitat selection at a broader scale that encompassed nightly movement, we calculated the relative displacement of each path as the ratio of the straight line distance from the beginning to the end of the path to the total trail length (Figure 1; Stapp, 1997). This path scale analysis was used to provide information on whether *M. minutoides* were using certain vegetation features for activities such as foraging or simply moving through the area (Stapp,

1997). Specifically, this allowed us to quantify how nightly movements were affected by shrub cover and other vegetative features. We assumed that straight trails, with values close to 1, indicated less preference for an area (Stapp, 1997). To assess path scale vegetative features, we ran a transect through the center of each pathway from the start to end point of the path and used the line-intercept method to assess overstory cover (Overstory) and shrub cover (Shrub Cover) (Figure 1; Higgins et al., 1996). We also quantified the number of trees (Trees) with trunks touching each transect.

Data analysis

We developed and evaluated *a priori* models to determine fine scale and path scale selection by *M. minutoides*. We did not include interaction terms in the models due to our limited vegetative measures. For fine scale selection, we compared used locations to random locations with11 models, consisting of 9 *a priori* models, a global model with all vegetative measures, and a null model with only the y-intercept (Table 1). We considered four vegetative measures in these models including VO, Shrub, Grass, and Forbs. We fit models with a logistic regression based on generalized estimating equations (GEE) using PROC GENMOD (SAS, 2011) and the REPEATED statement to account for the paired used/random locations nested by individual. (Pan, 2001). We evaluated the models using the quasi-likelihood under the independence model criterion (QIC; Pan, 2001). QIC is roughly equivalent to Akaike's Information Criterion (AIC) for models estimated using the GEE approach (Pan, 2001). We determined our best approximating models based on the relative difference to the smallest QIC in each model set (DQIC) and model weights (w_i; Probability of a model being the best given the candidate models and data set) (Burnham and Anderson,2002; Ward, 2008). We considered models with a DQIC $\leq$ 2 competing models and averaged the regression coefficients (on average, indicates what change

in a dependent variable is associated with a unit change in an independent variable; *b*) and 95%

confidence intervals for each model parameter based on w_i (Kass and Raftery, 1995; Burnham &

Anderson, 2002; Zar, 2009). We log-transformed and exponentiated the logistic regression

analysis to form a logistic prediction model (Guthery & Bingham, 2007). We used the resulting

prediction model to determine how the independent variables influenced pygmy mouse fine scale

selection of the measured vegetative features. We held each variable constant at its mean while

allowing one variable to vary and completed this for all four vegetative measures (Guthery &

Bingham, 2007).

To evaluate path scale selection we compared all possible combinations of vegetative

features, a global model with all variables, and a null model with only the y-intercept (Table 3).

We used 6 variables including mean VO, Grass, and Forbs determined by averaging values from

the 5 points where vegetative characteristics were sampled along each path and Overstory, Shrub

Cover, and Trees from the line-intercept data. We used our calculated ratio of displacement as

the dependent variable and ran a generalized linear regression model in Program R (R

Development Core Team, 2005). We evaluated path scale selection models using Bayesian

Information Criteria (BIC) (Posada and Buckley, 2004; Ward, 2008). BIC often selects models

that are more simplistic compared to Akaike's Information Criteria and is better at determining

which model best explains the processes underlying a data set (Akaike, 1973; Link and Barker,

2006; Ward, 2008). Thus, it was most appropriate for our data due to the simplicity of our

models and observations. We determined our best approximating models based on the relative

difference to the smallest BIC in each model set (DBIC) and model weights (Burnham and

Anderson,2002; Ward, 2008). We considered models with a DBIC ≤ 2 competing models and

averaged the regression coefficients (*b*) and 95% confidence intervals for each model parameter based on w_i (Kass and Raftery, 1995; Burnham & Anderson, 2002; Zar, 2009).

RESULTS

We had 142 captures of *M. minutoides* and 2 captures of other species per 800 trap nights. We tracked 20 individual *M. minutoides* (10 females, 10 males). The average trail length was 26.2 m (SD = 3.53 m). For fine scale selection, the DQIC values and w_i indicated that our global model, which included all variables measured, was the best approximating model (Table 1). This model had a w_i of 0.28, indicating a 28% probability that it provided the best explanation of the data. However, two models (Grass + Shrub & VO + Shrub) were competing with our top model (DQIC $\leq$ 2). The sum of w_i for our three top models indicated a 63% probability that one of these models provided the best explanation of our data.

Three of the model averaged variables evaluated, VO, Grass, and Shrub, had 95% confidence intervals that did not overlap 0 (Table 2). Our fourth variable, Forb, had a 95% confidence interval overlapping 0 suggesting it was not a relevant parameter (Table 2). The prediction model and averaged individual parameters indicated a positive relationship between use and all vegetative features (Figure 2).

For path scale selection, the best models (Forb only and the null model) were separated by DBIC < 0.01 (Table 3). The model with Forb as the only variable was the better of the two models, but the 95 % CI of Forb overlapped 0 (β = 0.0325, 95 % CI = - 0.0046 – 0.0697) indicating it was not a relevant parameter. Four additional models (VO + Grass, Grass, Overstory, VO + Forb) competed with our two top models (Table 3) but they were all ranked below the null model and had no variables with 95% CIs that did not intercept 0 (Table 3).

DISCUSSION

At a fine scale, *M. minutoides* were positively associated with visual obstruction, shrub cover, grass cover and the number of forbs, although Forb was not an important parameter in the model. This relationship was not unexpected as cover is necessary for small mammals to evade predators (Ylönen & Brown, 2007). Moreover, as seeds from grasses and forbs are a large component of the diet of *M. minutoides* (Skinner & Chimimba, 2005), increased seed abundance from grasses likely influences their movement and selection of cover through the environment. Our results concurred with Monadjem's (1997a) assertion that grass cover was important for *M. minutoides*. Moreover, our research elucidated that shrub cover and visual obstruction were also important for *M. minutoides* at the fine scale, adding to our basic ecological understanding of this species.

The path scale allowed us to assess if *M. minutoides* altered their nightly movements in response to vegetative features. Interestingly, it did not appear that *M. minutoides* were influenced by vegetative structure. This suggests that the areas encompassed by their nightly movement were not nearly as important as their fine scale selection of vegetative structure. The influence of vegetative structure at the fine scale may be a function of the diminutive size of *Mus minutoides*. Body size is a useful indicator of the scales at which animals respond to the environment (Hostetler 2001). With small animals responding at a fine scale it seems fitting that the mice in this study (weighing approximately 4.5 grams) responded strongly to vegetative structure at a 1 m^2 scale.

At the path scale, even though shrub cover ranged from 0-78% ($\bar{x} = 46\%$), we did not find that *M. minutoides* changed their movement patterns in response to this variation. This suggests that the shrub encroachment found at our study site and commonly throughout the

region (Roques et al., 2001, Sirami and Monadjem, 2012) does not directly influence the nightly movements of *M. minutoides*. Nonetheless, our high capture rates of *M. minutoides* compared to other species captures revealed that *M. minutoides* was the dominant species in an area with increased shrub cover. One possible explanation for this pattern is that shrub encroachment may reduce the prevalence of other rodents which compete with *M. minutoides,* thus indirectly enhancing the viability of *M. minutoides*. Although *M. minutoides* are omnivorous and grass seeds comprise a part of their diet, they are seed generalists (Oguge, 1995; Monadjem, 1997b). Thus, they may be less impacted by a loss of grass cover from encroachment than species with specialized diets. Furthermore, at the scales that are important to *M. minutoides*, there may still be ample area that has not been altered by excessive encroachment. Alternatively, our study sites may not have had the range of shrub cover necessary to detect the hump shaped relationships at the path scale that has been found in other species. Similarly, the scale of our study may not have allowed us to measure the landscape level changes in vegetative structure that drive habitat selection by *M. minutoides* and other rodents.

From our study, it is clear that *M. minutoides* need grass and cover at the fine scale. However, continued shrub encroachment often leads to decreases in ground cover, even at fine scales (Blaum et al., 2007a). Thus, at a certain threshold of shrub cover it will be impossible for *M. minutoides* to find environments of increased grass cover and visual obstruction that they selected for in our study. Although under current conditions in the lowveld of Swaziland *M. minutoides* appears to thriving and benefiting directly at a fine scale, and were not impacted by the increased shrub cover found in the region at the path scale, this suggests that if ground cover was eventually lost at the expense of shrub cover it would be detrimental to *M. minutoides*. Our study provides the first step in understanding habitat selection of *M. minutoides* in a changing

landscape and has added to our understanding of their basic ecology. In the future, we suggest that this study be repeated in a variety of habitats with varying levels of shrub encroachment to better understand the influence of shrub encroachment on *M. minutoides*.

REFERENCES

AKAIKE, H. (1973) Information theory as an extension of the maximum likelihood principle. In: *2nd International Symposium on Information Theory* (eds. B. N. PETROV & F. CSAKSI). Akademiai Kiado, Budapest, Hungary.

AVENANT, N. L. & CAVALLINI, P. (2007) Correlating rodent community structure with ecological integrity, Tussen-die-Riviere Nature Reserve, Free State province, South Africa. *Integr. Zool.* 2, 212-219.

BLAUM, N., ROSSMANITH, E. & JELTSCH, F. (2007a) Land use affects rodent communities in Kalahari savannah rangelands. *Afr. J. Ecol.* 45, 189-195.

BLAUM, N., ROSSMANITH, E., POPP, A. & JELTSCH, F. (2007b) Shrub encroachment affects mammalian carnivore abundance and species richness in semiarid rangelands. *Acta Oecol*. 31, 86-92.

BOWERS, M.A. (1990) Exploitation of seed aggregates by Merriam's kangaroo rat: harvesting rates and predatory risk. *Ecology,* 71:2334-2344

BRITTON-DAVIDIAN, J., ROBINSON, T.J. & VEYRUNES, F. (2012) Systematics and evolution of the African pygmy mice, subgenus *Nannomys*: A review. *Acta Oecol. 42, 41-49.*

BURNHAM, K. P. & ANDERSON, D.R. (2002) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York.

CHEESEMAN, C.L. & DELANY, M.J. (1979) The population dynamics of small rodents in a tropical grassland. *J. Zool*. 188, 451-475.

DUCHESNE, T., FORTIN, D., & COURBIN, N. (2010) Mixed conditional logistic regression for habitat selection studies. *J. Anim. Ecol.* 79, 548-555.

DUPLANTIER, J.M., CASSAING, J., ORSINI, P., & CROSET, H. (1984) Utilisation de poudres fluorescentes pour l'analyse des déplacements des petits rongeurs dams la nature. *Mammalia*, 48, 293-298.

FICHET-CALVET, E., AUDENAERT, L., BARRIERE, P. & VERHEYEN, E. (2010) Diversity, dynamics and reproduction in a community of small mammals in Upper Guinea, with emphasis on pygmy mice ecology. *Afr. J. Ecol*. 48, 600-614.

GUTHERY, F.S. & BINGHAM, R.L. (2007) A primer on interpreting regression models. *J. Wildlife Manage*. 71, 684-692.

HIGGINS, K.F., OLDEMEYER, J.L., JENKINS, K.J., CLAMBEY, G.K., & HARLOW, R.F. (1996) Vegetation sampling and measurement. In: *Research and Management Techniques for Wildlife and Habitats* (Ed. T.A. BOOKHOUT). The Wildlife Society, Allen Press, Inc., Lawrence, KS.

HOSTETLER, M. (2001) The importance of multi-scale analyses in avian habitat selection studies in urban environments. In: *Avian ecology and conservation in an urbanizing world* (Ed. J.M. MARZLUFF, R. BOWMAN, & R. DONELLY). Kluwer Academic Publishers, Boston, MA.

JOHNSON, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61, 65-71.

KASS, R.E. & RAFTERY, A.E. (1995) Bayes factors. *J. Am. Stat. Assoc.* 90, 773-795.

KEESING, F. (2000) Cyptic consumers and the ecology of an African savannah. *Bioscience*, 50, 205-215.

KOTLER, B.P. (1984) Risk of predation and the structure of desert rodent communities. *Ecology,* 65:689-701.

KOUASSI, S.K., NICOLAS, V., ANISKINE, V., LALIS, A., CRUAUD, C., COULOUX, A., COLYN, M., DOSSO, M., KOIVOGUI, L.,VERHEYEN, E., AKOUA-KOFFI, C., & DENYS, C. (2008) Taxonomy and biogeography of the African Pygmy mice, Subgenus

Nannomys (Rodentia, Murinae, *Mus*) in Ivory Coast and Guinea (West Africa). *Mammalia* 72, 237-252.

LEMEN, C. A. & FREEMAN, P. W. (1985) Tracking mammals with fluorescent pigments – a new technique. *J. Mammal.* 66, 134-136.

LINK, W. & BARKER, R. (2006) Model weights and the foundations of multimodel inference. *Ecology,* 87**,** 2626-2635.

LOW, A.B. & REBELO, A.G. (eds). (1996) Vegetation of South Africa, Lesotho, and Swaziland. Department of Environmental Affairs and Tourism, Pretoria.

MACHOLÁN, M. (2001) Multivariate Analysis of Morphometric Variation in Asian *Mus* and Sub-Saharan *Nannomys* (Rodentia: Muridae). *Zool. Anz.* 240, 7-14.

MAHLABA, T. A. M. & PERRIN, M.R. (2003) Population Dynamics of Small Mammals at Mlawula, Swaziland. *Afr. J. Ecol.* 41, 317-323.

MANSON, R., OSTFELD, R. & CANHAM, C. (2001) Long-term effects of rodent herbivores on tree invasion dynamics along forest-field edges. *Ecology* 82, 3320-3329.

MARSHALL, J.T. (1981) Taxonomy. In: *The Mouse in Biomedical Research* (Ed. H.L. FOSTER, J.D. SMALL & J.G. FOX). Academic Press, New York.

MBOUMBA, J. F., DELEPORTE, P., COLYN, M. & NICOLAS, V. (2011) Phylogeography of *Mus* (*Nannomys*) *minutoides* (Rodentia, Muridae) in West Central African savannahs: singular vicariance in neighbouring populations. *J. Zool. Syst. Evol. Res.* 49, 77-85.

MONADJEM, A. (1997a) Habitat preferences and biomasses of small mammals in

Swaziland. *Afr. J. Ecol.* 35, 64-72.

MONADJEM, A. (1997b) Stomach contents of 19 species of small mammals from Swaziland. *S.*

Afr. J. Zool. 32, 23-26.

MONADJEM, A. (1999a) Population dynamics of *Mus minutoides* and *Steatomys pratensis*

(Muridae: Rodentia) in a subtropical grassland in Swaziland. *Afr. J. Ecol.* 37, 202-210.

MONADJEM, A. (1999b) Geographic distribution patterns of small mammals in Swaziland in

relation to abiotic factors and human land-use activity. *Biodivers Conserv.* 8, 223-237.

MONADJEM, A. & PERRIN, M. (2003) Population fluctuations and community structure of

small mammals in a Swaziland grassland over a three-year period. *Afr. Zoo.* 38, 127-137.

MATONDO, J.I., PETER G., & MSIBI, K.M. (2005) Managing water under climate change for

peace and prosperity in Swaziland. Phys Chem Earth Pt. A/B/C 30: 943–949.

MULLICAN, T.R. (1988) Radio telemetry and fluorescent pigments: a comparison of

techniques. *J. Wildlife Manage.* 52, 627-631.

MUSSER, G.G. & CARLETON, M.D. (2005) Superfamily Muroidea. In: *Mammal Species of*

the World: A Taxonomica and Geographic Reference, 3rd ed (Eds. D.E. WILSON &

D.M. REEDER). The Johns Hopkins University Press, Cambridge.

NEL, J.A.J. (1978) Habitat heterogeneity and changes in small mammal community structure and resource utilization in the southern Kalahari. Bulletin of the Carnegie Museum of Natural History 6, 118-131.

NEL,J.A.J. & RAUTENBACH I.L. (1975) Habitat use and community structure of rodents in the southern Kalahari. Mammalia 39, 9-29

OGUGE, N. (1995) Diet, seasonal abundance and microhabitats of *Praomys (Mastomys) natalensis* (Rodentia, muridae) and other small rodents in a Kenyan subhumid grassland community. *Afr. J. Ecol.* 33, 211-223.

PAN, W. (2001) Akaike's information criterion in generalized estimating equations. *Biometrics* 57, 120-125.

POSADA, D. & BUCKLEY, T. (2004) Model selection and model averaging in phylogenetics: Advantages of akaike information criterion and Bayesian approaches over likelihood ratio tests. *Syst. Biol.* 53, 793-808.

R DEVELOPMENT CORE TEAM (2005) R: A language and environment for statistical computing, reference index version 2.14.1. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

ROBEL, R.J., J.N. BRIGGS, A.D., DAYTON, & L.C., HULBERT (1970) Relationships between visual obstruction measurements and weight of grassland vegetation. *J. Range. Manage.* 23, 295-297.

ROQUES, K. G., O'CONNOR, T. G. & WATKINSON, A. R. (2001) Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *J. Appl. Ecol.* 38, 268-280.

SAS INSTITUTE INC. (2011) SAS/STAT® 9.3 User's Guide. Cary, NC.

SHEPPE, W. & HAAS, P. (1981) The annual cycle of small mammal populations along the Chobe River, Botswana. *Mammalia* 45, 157-176.

SIRAMI, C. & MONADJEM, A. (2012) Changes in bird communities in Swaziland savannas between 1998 and 2008 owing to shrub encroachment. *Divers. Distrib*. 18, 390-400.

SKINNER, J.D. & CHIMIMBA, C.T. (2005) *The Mammals of the Southern African Subregion*. Cambridge University Press, Cambridge.

SMITH, M.A. (2008). *Robel pole technique and data interpretation* (MP-111.10) Laramie: University of Wyoming Extension, Retrieved April 10, 2012, from http://www.wyomingextension.org/publications/.

STAPP, P. (1997) Habitat selection by an insectivorous rodent: Patterns and mechanisms across multiple scales. *J. Mammal.* 78, 1128-1143.

VEYRUNES, F., CATALAN, J., SICARD, B., ROBINSON, T. J., DUPLANTIER, J. M., GRANJON, L., DOBIGNY, G. & BRITTON-DAVIDIAN, J. (2004) Autosome and sex chromosome diversity among the African pygmy mice, subgenus *Nannomys* (Murinae; *Mus*). *Chromosome Res.* 12, 369-382.

VEYRUNES, F., BRITTON-DAVIDIAN, J., ROBINSON, T. J., CALVET, E., DENYS, C. & CHEVRET, P. (2005) Molecular phylogeny of the African pygmy mice, subgenus *Nannomys* (Rodentia, Murinae, *Mus*): Implications for chromosomal evolution. *Mol. Phylogenet. Evol.* 36, 358-369.

WARD, E. (2008) A review and comparison of four commonly used Bayesian and maximum likelihood model selection tools. *Ecol. Model.,* 211**,** 1-10.

YLÖNEN, H. & BROWN, J.S. (2007) Fear and the foraging, breeding and sociality in rodents. In: *Rodent societies* (Ed. J.O. WOLFF & P.W. SHERMAN). University of Chicago Press, Chicago, IL.

ZAR, J.H. 2009. *Biostatistical Analysis*, *5th ed*. Prentice Hall, Upper Saddle River, NJ.

TABLES

Table 1. *A priori* models of *Mus minutoides* fine scale (1 m^2) selection relative to grass cover (Grass), visual obstruction (VO), shrub cover (Shrub), and the number of forbs (Forb) based on fluorescent powder tracking conducted in northeastern Swaziland, Africa.

Model	QIC	K	DQIC	w_i
Global	267.6	5	0	0.28
Grass + Shrub	268.5	3	0.87	0.18
VO + Shrub	268.6	3	0.97	0.17
VO + Grass	269.7	3	2.06	0.10
Forb	270.0	2	2.34	0.09
Vo + Grass + Forb	270.0	4	2.34	0.09
VO	270.9	2	3.24	0.05
Shrub	272.6	2	4.90	0.02
Grass + Forb	274.0	3	6.35	0.01
Grass	274.1	2	6.45	0.01
Null	279.3	1	11.61	0.00

Table 2. Averaged model parameters, regression coefficients (*b*), and 95% confidence intervals for determining *Mus minutoides* fine scale (1 m^2) selection relative to grass cover (Grass), visual obstruction (VO), shrub cover (Shrub), and the number of forbs (Forb) based on fluorescent powder tracking conducted in northeastern Swaziland, Africa.

Vegetative feature	*b*	95% CI
VO	0.1593	0.0015 to 0.3171
Shrub	0.1556	0.0393 to 0.2718
Grass	0.1511	0.0290 to 0.2731
Forb	0.1168	-0.0290 to 0.2626

Table 3. Models of *Mus minutoides* path scale selection relative to average visual obstruction (VO), grass cover (Grass), and the number of forbs (Forb) quantified within 1 m^2 circular plots and the number of trees (Trees), shrub cover (Shrub Cover), and overstory cover (Overstory) quantified along transects based on fluorescent powder tracking conducted in northeastern Swaziland, Africa.

Model	BIC	K	DBIC	w_i
Forb	-32.9	3	0.0	0.13
Null	-32.9	2	0.0	0.12
VO + Grass	-32.0	4	0.9	0.08
Grass	-31.6	3	1.3	0.07
Overstory	-31.3	3	1.6	0.06
VO + Forb	-31.1	4	1.8	0.05
VO	-30.9	3	2.0	0.05
VO + Grass + Overstory	-30.7	5	2.2	0.04
Grass + Forb	-30.5	4	2.4	0.04
Forb + Trees	-30.3	4	2.6	0.04
Shrub Cover	-30.1	3	2.8	0.03
Trees	-30.1	3	2.8	0.03
Trees + Overstory	-30.0	4	2.9	0.03
Shrub Cover + Forb	-29.9	4	3.0	0.03
VO + Overstory	-29.9	4	3.0	0.03
Grass + Overstory	-29.7	4	3.2	0.03
Shrub Cover + Grass	-29.2	4	3.7	0.02
VO + Shrub Cover+ Grass	-29.1	5	3.8	0.02
Shrub Cover + Overstory	-28.5	4	4.4	0.01
Grass + Forb + Overstory	-28.3	5	4.6	0.01
VO + Shrub Cover + Forb	-28.2	5	4.7	0.01
Grass + Trees + Overstory	-28.0	5	4.9	0.01
VO + Shrub Cover	-27.9	4	5.0	0.01
VO + Trees	-27.9	4	5.0	0.01
Shrub Cover + Forb + Trees	-27.3	5	5.6	0.01
Shrub Cover + Trees	-27.3	4	5.6	0.01
Shrub Cover + Grass + Overstory	-27.1	5	5.8	0.01
VO + Shrub Cover + Overstory	-26.9	5	6.0	0.01
VO + Grass + Forb + Tree + Overstory	-26.4	7	6.5	0.00
VO + Shrub Cover + Grass + Forb + Overstory	-25.8	7	7.1	0.00
VO + Shrub Cover + Grass + Trees + Overstory	-25.1	7	7.8	0.00
VO + Shrub Cover + Forb + Trees + Overstory	-25.1	7	7.8	0.00
VO + Shrub Cover + Trees	-24.9	5	8.0	0.00
VO + Shrub Cover + Grass + Forb + Trees	-24.4	7	8.5	0.00
Global	-23.5	8	9.4	0.00

FIGURE LEGENDS

Figure 1. A schematic of the used and paired random locations sampled every 5 m along a mouse's pathway used to assess *Mus minutoides* fine scale habitat selection (1 m^2) and the equation used to calculate the ratio of displacement (RD) for each pathway including examples of pathways with low RD and high RD showing the transects used to measure vegetative features to assess selection at the path scale.

Figure 2. The predicted probability of selection and +/- 1 standard error (S.E.) of the prediction based on the logistic regression predictive model of *Mus minutoides'* fine scale selection as a function of visual obstruction (VO; top left), grass cover class[1] (Grass; top right), shrub cover class[1] (Shrub; bottom left), and number of forbs (Forb; bottom right) based on fluorescent powder tracking conducted in northeastern Swaziland, Africa.

Figure 1.

Fine Scale Selection

☆ - Release point
● - Used point
○ - Paired unused point

2 – 6 m

Path Level Selection

$$\text{Ratio of Displacement (RD)} = \frac{Length\ from\ start\ to\ end\ point}{Total\ trail\ length}$$

☆ - Release point
● - End point
- - - - Transect
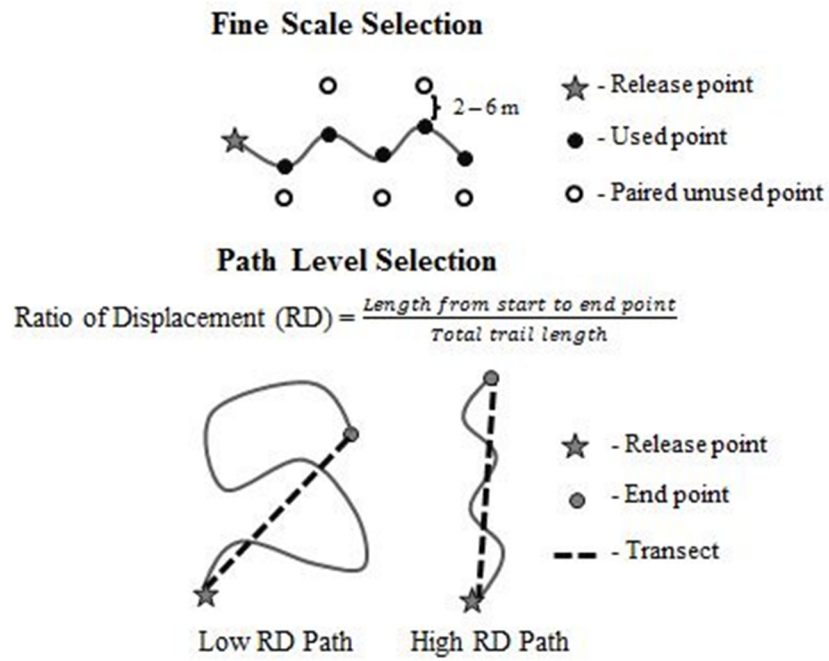
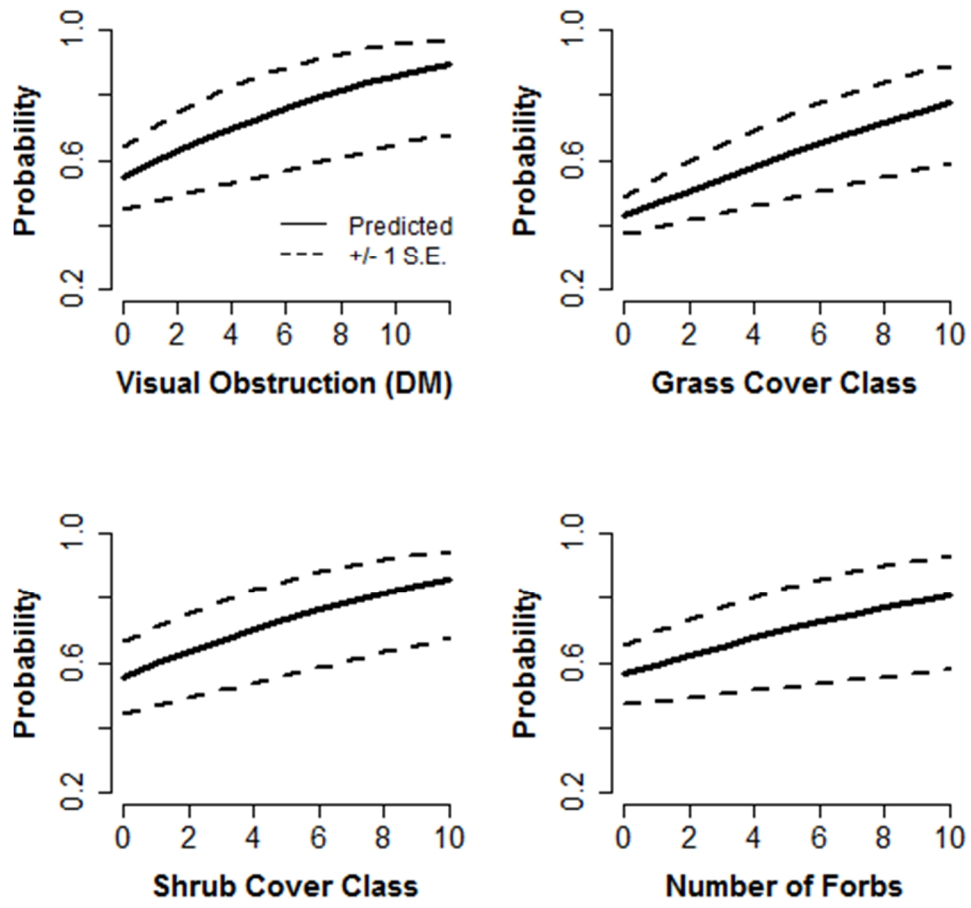Low RD Path   High RD Path

Figure 2.

[1] We visually classified grass and shrub cover into 10 equal cover classes ranging from 0-100%.