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ORIGINAL ARTICLE

Integrating small mammal community variables into aircraft–wildlife collision management plans at Namibian airports

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Abstract

Understanding ecosystems within and around airports can help to determine the causes and possible mitigation measures for collisions between aircraft and wildlife. Small mammal communities are an important component of the semi-arid savanna ecosystems of Namibia, its productivity and its ecosystem integrity. They are also a major direct attractant for raptors at airports. The present study compared the abundance and diversity of small mammals between Namibia's 2 main airport properties (Hosea Kutako International Airport and Eros Airport), and among areas of land used for various purposes surrounding the airports. A total of 2150 small mammals (3 orders, 11 species) were captured over 4 trapping seasons. Small mammal abundance was significantly higher at the end of the growing season than during the non-growing season. The grass mowing regimen in current management plans at the airports resulted in a significant reduction of small mammal abundance at Hosea Kutako during the non-growing season only, thus indicating that annual mowing is effective but insufficient to reduce the overall abundance of mammal prey species for raptors. Small mammal numbers were significantly higher at Hosea Kutako Airport compared to the cattle and game farming land surrounding the airport, while no differences in small mammal densities or diversity were found for areas with different land uses at and surrounding Eros. The study suggests that the fence around Hosea Kutako provides a refuge for small mammals, resulting in higher densities. It also indicates that different surrounding land use practices result in altered ecosystem function and productivity, an important consideration when identifying wildlife attractants at airports.

Key words: airport ecosystems, bird strike risk, Namibia, small mammal indicators

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INTRODUCTION

Aircraft wildlife collisions (AWCs), more commonly termed bird strikes, are a global safety and financial concern for the aviation industry (Allan 2000; Robinson 2000; Froneman 2001; Sodhi 2002; Thorpe 2003; Burma & Den Haag 2004; IBSC 2006; Blackwell *et*

al. 2013). The majority of AWCs occur within 13 km of take-off and landing, and below an altitude of 2000 ft (Dolbeer 2006; IBSC 2006). At Namibia's 2 busiest airports, Hosea Kutako (international) and Eros (local), 128 AWC incidents were recorded between 2006 and 2010 (Hauptfleisch *et al.* 2013). Although none led to serious injury or death, 1 major incident led to direct costs in excess of N\$30m and another to costs of more than N\$1m (Namibia Airports Company, unpublished incident reports 2006 and 2010).

To reduce the risk of AWCs, the International Bird-strike Committee (IBSC) produced 9 standards for the control of wildlife hazards at aerodromes (IBSC 2006). Standard 2 refers to the management of features attracting wildlife to an airport and standard 9 to the management of a 13-km radius around an airport to minimize wildlife attractants, as land management at and in the vicinity of airports has been purported to have a distinct influence on the risk of aircraft-wildlife collisions (Blackwell *et al.* 2013; Schmidt *et al.* 2013). The present study is relevant to both these standards as: (i) small mammals are an important attractant for raptors and other predators (Baker & Brooks 1981; Witmer & Fantinato 2003; Witmer 2011), 2 of the groups that have been identified as responsible for AWCs at Hosea Kutako and Eros (Hauptfleisch *et al.* 2013); and (ii) the study compared small mammal abundance and diversity at the airports to surrounding areas of land used for various purposes as a measure of ecosystem productivity and integrity.

Airports are unique and often productive habitats providing niches and ecosystem services such as shelter, nesting sites, water and primary food supply (grass/vegetation, insects, small mammals and carrion) (Soldatini *et al.* 2010). As such, airports can be viewed as islands with unique ecosystems, influenced indirectly by external factors in surrounding areas. (MacArthur & Wilson 1967). The monitoring of small mammals as an ecosystem component may be useful to airport wildlife management as it has been described as a relatively quick and inexpensive tool for determining ecosystem health and functioning (Avenant & Cavallini 2007; Avenant *et al.* 2008; Avenant 2011), and can indicate varying environmental contexts and responses (De Graaff 1974; Ferreira & Avenant 2003; Avenant *et al.* 2008).

Some small mammal species' abundance may be indicative of the primary productivity of ecosystems (Avenant 2011), but small mammals are also valuable prey and predator species. They are known prey for a variety of raptor species (e.g. the black-shouldered kite, *Elanus*

caeruleus [Desfontaines, 1789], the secretarybird, *Sagittarius serpentarius* [Miller, 1779], the greater kestrel, *Falco rupicoloides* [Smith, 1829] and the tawny eagle, *Aquila rapax* [Temminck, 1828; Hockey *et al.* 2005]) that were observed to frequent the 2 study sites (Hauptfleisch 2014). In addition, they are dispersers of seeds, soil nutrients and aeration benefactors, and are habitat modifiers that can determine vegetation composition through selective utilization of seeds and other reproductive plant parts (Malan & Crowe 1996; Avenant 2000; Perrin & Bodbijn 2001; Avenant 2005; Witmer 2011). This makes them a causal and indicative group likely to indirectly affect the risk of AWCs at airports.

Whereas Baker and Brooks (1981) found population fluctuations in predatory raptors in response to the meadow vole *Microtus pennsylvanicus* in Canada, Barros *et al.* (2000) could not find any correlation between small mammal densities and raptor densities at JF Kennedy Airport: an indication that the relationship between raptors and small mammals is not necessarily a simple one. Nevertheless, the management of rodent populations through habitat augmentation or population control has been recommended to reduce raptor numbers at airports (Witmer & Fantinato 2003; Witmer 2011). Avenant *et al.* (2008) and Avenant (2011) describe the use of small mammals as indicators of ecosystem integrity in southern African grasslands. In arid and semi-arid environments (as is the case with the Namibian study sites) Hoffman and Zeller (2005) found an understanding of small mammal community structure to be important in recommending practical ecosystem management guidelines.

The present study compared small mammal abundance and diversity under different land uses and vegetation management regimes within a 13-km radius of Namibia's 2 largest and busiest airports, Hosea Kutako (international) and Eros (national), in order to understand ecosystem productivity and integrity, and indirectly, AWC risk with varying land uses and airport grassland management regimes. No analysis of small mammal density or diversity has, to date, been published for any African airport.

STUDY AREA

Hosea Kutako (22°28'S, 17°28'E; Fig. 1a) is Namibia's primary international airport. Situated approximately 40 km east of Windhoek, the capital city, the airport is the largest of Namibia's 9 parastatal airports. Its main runway length is 4.575 km, making it capable of allowing safe take-off and landing of all sizes and capacity

of aircraft. A relatively low volume of aircraft ($\pm 16\,000$ flights per year) use the airport, but most of these flights carry over 100 passengers each to and from various international destinations.

Eros Aerodrome ($22^{\circ}36'S$, $17^{\circ}04'E$; Fig. 1b) predominantly caters for domestic flights. It is situated in the capital city of Windhoek, surrounded on 3 sides by suburban and business properties, and by the Windhoek Golf Course on the other. This airport carries the highest flight volumes in Namibia ($\pm 32\,000$ flights per year).

Both airports are situated in the Highland Shrubland Tree and Shrub Savanna (Mendelsohn *et al.* 2002), which is characterized by low unpredictable rainfall (350–400 mm; Mendelsohn *et al.* 2002) that falls mostly during the summer months from October to April. This results in a distinct growing season (GS) and non-growing season (NG). Dominant woody species include a number of *Acacia* species (e.g. *Acacia mellifera*, *Acacia hebeclada* and *Acacia hereroensis*), while climax grass species are dominated by *Antheophora pubescens*, *Brachiaria nigropedata* and *Heteropogon contortus* (Joubert *et al.* 2008). The study sites fall on the edge of the Kalahari Desert, characterized by substrates of deep sandy soils (Mendelsohn *et al.* 2002).

MATERIALS AND METHODS

Small mammals were trapped, marked and released to determine the abundance and diversity of rodents, shrews and elephant shrews (Orders Rodentia, Eulipotyphla and Macroscelidea, respectively). Single line transects were laid out in representative areas of similar environmental characteristics (soil type and topography),

but different land use or vegetation management, both within and around the 2 airports. At Hosea Kutako these were: (i) 2 areas within the airport where grass was not disturbed (labelled HL and HL2); (ii) 2 areas where grass was mown annually (HS and HS2); and (iii) 1 area in the neighboring game and cattle ranch (HF) (Fig. 1a). At Eros they were: (i) an area within the airport where grass was not disturbed (EL); (ii) an area within the airport where grass was mown annually (ES); (iii) a neighboring golf course “rough” (EG); and (iv) the neighboring Arebbusch urban Travel Lodge (EA) (Fig. 1b). Linear transects were preferred to grids as space utilization at airports is relative to runways, causing airport properties to be largely linear with long, narrow ecotones. Larger areas are also covered with the same number of traps laid out in a transect (Pearson & Ruggiero 2003), increasing the opportunity to trap more species as these are not homogeneously distributed over an area (Avenant 2011). Transects were more than 250 m apart from each other.

Sampling was conducted at the end of the dry non-growing season (in September 2010 and September 2011) and the end of the wet growing season (in March 2011 and March 2012). One hundred well-ventilated stainless steel box traps ($7.6 \times 7.6 \times 25.4$ cm) were spaced 5 m apart on a single 495-m line transect in each habitat (following Avenant 1996, 2000, 2003, 2011; Avenant & Cavallini 2007; Seamans *et al.* 2007; Avenant *et al.* 2008). The traps were baited with a mixture of peanut butter, rolled oats, sunflower oil and a meat extract, Bovril. Each trap was checked and re-baited at dawn and dusk for 4 consecutive days in order to consistently sample diurnal and nocturnal small mam-

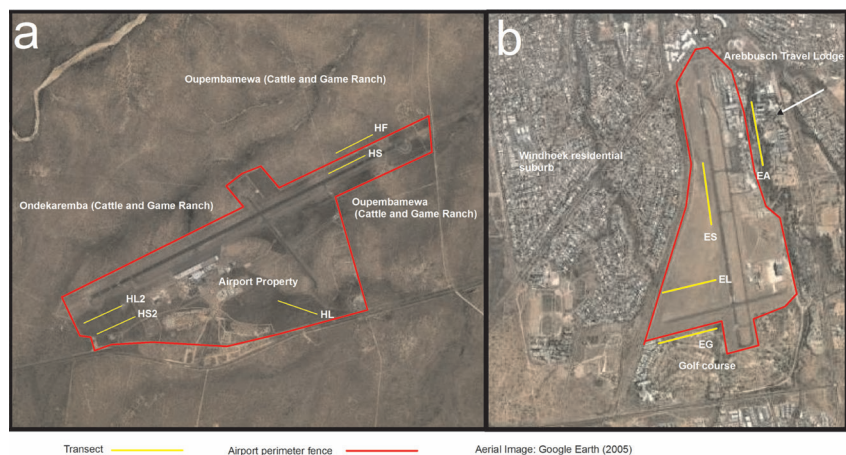


Figure 1 Maps of the study area and small mammal transects at: (a) Hosea Kutako and (b) Eros airports, Namibia.

mal species (following Muck & Zeller [2006] in similar habitat in Namibia and Avenant [2011] in South African grasslands). Captured specimens were identified, sexed and marked with fur pattern clippings to ensure identification of retrapped individuals.

The term “trap night” was used to describe 1 trap which was set for a 24-h period (Rowe-Rowe & Meester 1982). Abundance is the number of small mammals captured/100 trap nights. To act as an indication of density, retrapped individuals were excluded from all analyses, unless stated otherwise; this was to avoid “trap happy” individuals from influencing the density estimates. Diversity was calculated using the Shannon information index (Spellerberg & Fedor 2003; Magurran 2004).

Normality of data was determined using Shapiro–Wilk’s *W* test, and the Wilcoxon matched pairs test for 2-way comparison was used to compare abundance and species richness across land uses in specific seasons. All statistical analyses were performed using the computer program Statistica for Windows version 10 (StatSoft 2011), and the 95% level ($P < 0.05$) was regarded as statistically significant for all tests.

RESULTS

A total of 2150 individual small mammals were captured over the 4 trapping seasons (1570 at Hosea Kutako and 580 at Eros), with considerable differences

between transects and between seasons in the same transects, at both airports (Table 1). When data from transects were pooled, significantly more small mammals were trapped at rural Hosea Kutako than at the suburban Eros airport (Fig. 2). This excluded the retrapped individuals, which contributed a fair percentage to the total number of catches (16.18% at Hosea Kutako and 9.80% at Eros). This contribution by retraps was commonly more pronounced at the end of the non-growing season ($23.11\% \pm 25.77\%$ vs $12.68\% \pm 9.46\%$ at the end of the growing seasons).

Of the total number of individuals, 1317 were trapped in the growing seasons and 833 in the non-growing seasons (Table 1). This phenomenon, where more individuals were trapped at the end of the growing season than at the end of the following non-growing season, repeated itself at 8 and 5 of the 9 transects, respectively. Significantly more small mammals were caught at the end of the first growing season (GS1; $n = 686$) than at the end of the following non-growing season (NG1; $n = 198$); from the end of the second growing season (GS2) to the end of the second non-growing season (NG2) the total number of individuals trapped stayed unchanged (630 and 635, respectively).

At the end of the growing season the mean abundance was, in the first year only, significantly higher at both airports compared to the non-growing season ($P < 0.05$; Fig. 2).

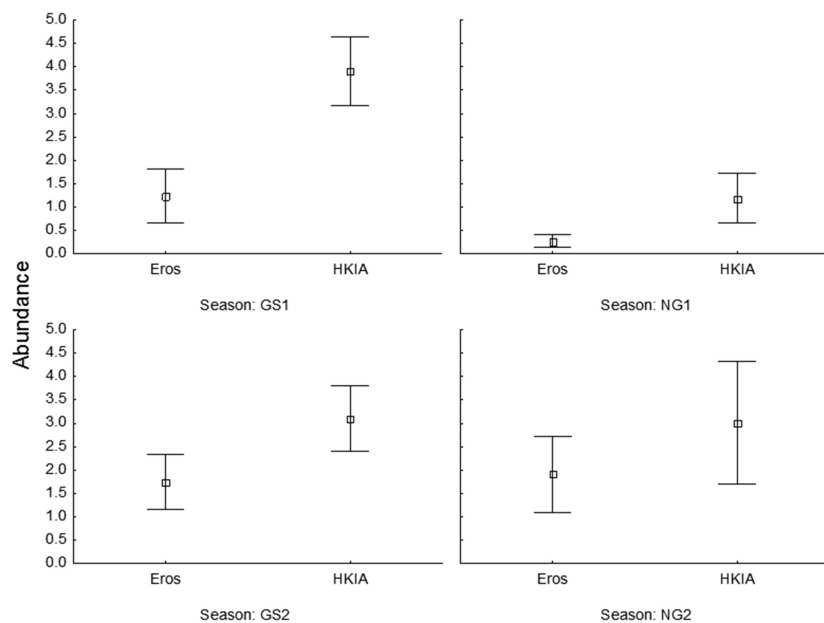


Figure 2 The mean (indicated with 95% confidence intervals) small mammal abundance at the end of each growing (GS and GS2) and non-growing (NG1 and NG2) season, respectively.

Table 1 Percentage contribution of small mammal species trapped on areas with different land uses in and surrounding Hosea Kutako and Eros Airports

Season	Species	Hosea Kutako				Eros				
		Farm (HF)	Un-mown (HL)	Un-mown2 (HL2)	Mown (HS)	Mown 2 (HS2)	Travel Lodge (EA)	Golf course (EG)	Un-mown (EL)	Mown (ES)
Order: Rodentia										
GS 1	<i>Desmodillus</i>	—	—	1.26 (2)	—	—	—	—	—	8.33 (1)
NGS 1	<i>auricularis</i>	—	—	—	—	—	—	—	—	—
GS 2	(Smith, 1834)	2.86 (1)	1.05 (1)	—	—	—	—	—	—	—
NGS 2		—	—	—	—	—	—	—	—	—
GS 1	<i>Gerbilliscus</i>	5.08 (3)	8.14 (14)	6.92 (11)	—	16.67 (12)	—	8.43 (7)	—	—
NGS 1	<i>leucogaster</i>	12.5 (2)	9.52 (10)	40.48 (17)	—	66.67 (2)	—	—	—	—
GS 2	(Peters, 1852)	17.14 (6)	1.05 (1)	5.56 (6)	5.0 (6)	12.82 (10)	—	4.55 (3)	8.51 (8)	20 (4)
NGS 2		7.14 (1)	2.94 (7)	16.25 (26)	—	33.33 (1)	—	—	4.13 (5)	—
GS 1	<i>Mastomys</i>	30.51 (18)	13.95 (24)	20.75 (33)	18.82 (16)	31.94 (23)	60 (3)	60.24 (50)	40 (16)	66.67 (8)
NGS 1	<i>coucha</i>	—	3.81 (4)	21.43 (9)	—	—	—	30 (3)	25 (1)	100 (3)
GS 2	(Smith, 1836)	25.71 (9)	4.21 (4)	16.67 (18)	17.8 (21)	7.69 (6)	25 (4)	39.39 (26)	29.79 (28)	75 (15)
NGS 2		35.71 (5)	8.82 (21)	9.38 (15)	57.14 (4)	—	—	24.44 (22)	26.45 (32)	—
GS 1	<i>Mus musculus</i>	—	—	—	—	—	—	—	—	—
NGS 1	(Linnaeus, 1758)	—	—	—	—	—	—	—	—	—
GS 2		—	—	5.56 (6)	—	—	—	—	—	—
NGS 2		—	—	—	—	—	—	—	—	—
GS 1	<i>Mus indutus</i>	—	—	—	—	—	—	—	5 (2)	8.33 (1)
NGS 1	(Thomas, 1910)	—	1.9 (2)	4.76 (2)	100 (1)	—	—	—	50 (2)	—
GS 2		—	—	—	—	—	—	—	—	—
NGS 2		—	—	0.63 (1)	—	—	—	—	—	—
GS 1	<i>Rhabdomys</i>	45.76 (27)	68.6 (118)	69.81 (111)	70.59 (60)	51.39 (37)	20 (1)	27.71 (23)	55 (22)	16.67 (2)
NGS 1	<i>pumilio</i>	12.5 (2)	75.24 (79)	33.33 (14)	—	33.33 (1)	92.86 (13)	60 (6)	—	—
GS 2	(Sparrmann, 1784)	54.29 (19)	93.68 (89)	72.22 (78)	73.73 (87)	78.21 (61)	75 (12)	54.55 (36)	61.7 (58)	5 (2)
NGS 2		57.14 (8)	88.24 (210)	73.75 (118)	42.86 (3)	66.67 (2)	100 (2)	74.44(67)	53.72 (65)	—
GS 1	<i>Saccostomus</i>	3.39 (2)	6.4 (11)	0.63 (1)	7.06 (6)	—	—	—	—	—
NGS 1	<i>campestris</i>	25 (4)	2.86 (3)	—	—	—	—	—	25 (1)	—
GS 2	(Peters, 1846)	—	—	—	2.54 (3)	1.28 (1)	—	—	—	-
NGS 2		—	—	—	—	—	—	—	0.83 (1)	-
GS 1	<i>Thallomys</i>	—	—	—	—	—	—	—	—	-
NGS 1	<i>paedulus</i>	—	—	—	—	—	7.14 (1)	—	—	-
GS 2	(Sundevall, 1846)	—	—	—	—	—	—	—	—	-
NGS 2		—	—	—	—	—	—	—	—	-

Season	Species	Hosea Kutako					Eros			
		Farm (HF)	Un-mown (HL)	Un-mown2 (HL2)	Mown (HS)	Mown 2 (HS2)	Travel Lodge (EA)	Golf course (EG)	Un-mown (EL)	Mown (ES)
Order: Eulipotyphla										
GS 1	<i>Crocidura sp1</i>	1.69 (1)	0.58 (1)	0.63 (1)	—	—	—	—	—	-
NGS 1		—	—	—	—	—	—	—	—	-
GS 2		—	—	—	0.85 (1)	—	—	—	—	-
NGS 2		—	—	—	—	—	—	—	—	-
GS 1	<i>Crocidura sp2</i>	—	—	—	1.18 (1)	—	—	—	—	-
NGS 1		—	—	—	—	—	—	—	—	-
GS 2		—	—	—	—	—	—	—	—	-
NGS 2		—	—	—	—	—	—	—	—	-
Order: Macroscelidea										
GS 1	<i>Elephantulus intufi</i> (Smith, 1836)	13.56 (8)	2.33 (4)	—	2.35 (2)	—	—	3.61 (3)	—	-
NGS 1		50 (8)	6.67 (7)	—	—	—	—	10 (1)	—	-
GS 2		—	—	—	—	—	—	1.52 (1)	14.88 (18)	-
NGS 2		—	—	—	—	—	—	1.11 (1)	—	-
Totals										
GS 1	Numbers trapped	59	172	159	85	72	4	83	40	12
NGS 1		16	105	42	1	3	14	10	4	3
GS 2		35	95	108	118	78	16	66	94	20
NGS 2		14	238	160	7	3	2	90	121	0
GS 1	Species richness	6	6	6	5	3	2	4	4	4
NGS 1		4	6	4	1	2	2	3	3	1
GS 2		4	4	4	5	4	2	4	3	3
NGS 2		3	2	4	2	2	1	3	4	0
Total		7	8	8	8	4	3	4	6	5
GS 1	Shannon diversity	1.91	1.49	1.27	1.28	1.45	1.37	1.43	1.22	1.42
NGS 1		1.75	1.33	1.74	0	0.92	0.37	1.30	1.52	0
GS 2		1.57	0.42	0.98	1.18	1.02	0.81	1.30	1.25	0.99
NGS 2		1.26	0.62	1.11	0.99	0.92	0	0.89	1.65	0

The numbers of individuals trapped are in parentheses. GS, growing season; NGS, non-growing season. Dashes (-) represent none trapped.

Per individual transect, mean daily abundance at Hosea Kutako in the first growing season (GS1) was highest in the 2 unmown transects (HL = 24.57 ± 9.22 ; HL2 = 22.71 ± 3.50), followed by the 2 mown transects (HS = 12.14 ± 4.22 ; HS2 = 10.29 ± 5.02). The game and cattle farm (HF) showed the lowest abundance at the Hosea Kutako study site (HF = 8.43 ± 4.24) (Fig. 3a). This was

significantly lower than HL ($Z = 2.37, P < 0.05$), HL2 ($Z = 2.37, P < 0.05$) and HS ($Z = 2.20, P < 0.05$). Further significant differences were observed between HL and HS ($Z = 2.20, P < 0.05$), HL and HS2 ($Z = 2.37, P < 0.05$), HL2 and HS ($Z = 2.37, P < 0.05$) and HL2 and HS2 ($Z = 2.37, P < 0.05$). The pattern was similar in the first non-growing season, with mean abundance highest

in the 2 unmown transects (HL = 15.00 ± 2.38 , HL2 = 6.00 ± 5.42). During this season, however, no significant difference in small mammal abundance could be found between the game and cattle farm and the 2 on-airport mown transects (HF = 2.29 ± 2.36 ; HS = 0.14 ± 0.38 ; HS2 = 0.43 ± 0.79 ; Fig. 3b). The difference was significant between HL and HS ($Z = 2.37$, $P < 0.05$), HL and HS2 ($Z = 2.37$, $P < 0.05$), HL2 and HS ($Z = 2.37$, $P < 0.05$), HL2 and HS2 ($Z = 2.37$, $P < 0.05$), HF and HL ($Z = 2.37$, $P < 0.05$) and HF and HL2 ($Z = 2.37$, $P < 0.05$).

At the end of the second growing season at Hosea Kutako (Fig. 3c), 1 mown transect (HS) had the highest daily abundance (16.86 ± 7.47) followed by the 2 unmown transects (HL 13.57 ± 10.53 ; HL2 = 15.43 ± 4.08).

As in the first growing season, the farm (HF) had the lowest abundance (5.00 ± 2.71). Differences were significant between HL2 and HS2 ($Z = 2.37$, $P < 0.05$) and HS and HS2 ($Z = 2.21$, $P < 0.05$). HF again had a significantly lower abundance than HL ($Z = 2.03$, $P < 0.05$) and HL2 ($Z = 1.99$, $P < 0.05$). At the end of the second non-growing season (Fig. 3d), the 2 unmown transects again had the highest mean abundance (HL = 34.00 ± 13.79 ; HL2 = 22.86 ± 3.29), followed by the cattle and game farm (HF = 2.00 ± 2.77). The 2 mown transects had the lowest abundance (HS = 1.00 ± 1.73 ; HS2 = 0.43 ± 0.79). HL had significantly higher abundance than HS ($Z = 2.37$, $P < 0.05$) and HF ($Z = 2.37$, $P < 0.05$). HL2 had a significantly higher abundance than HS ($Z = 2.37$, $P < 0.05$). No other differences were significant.

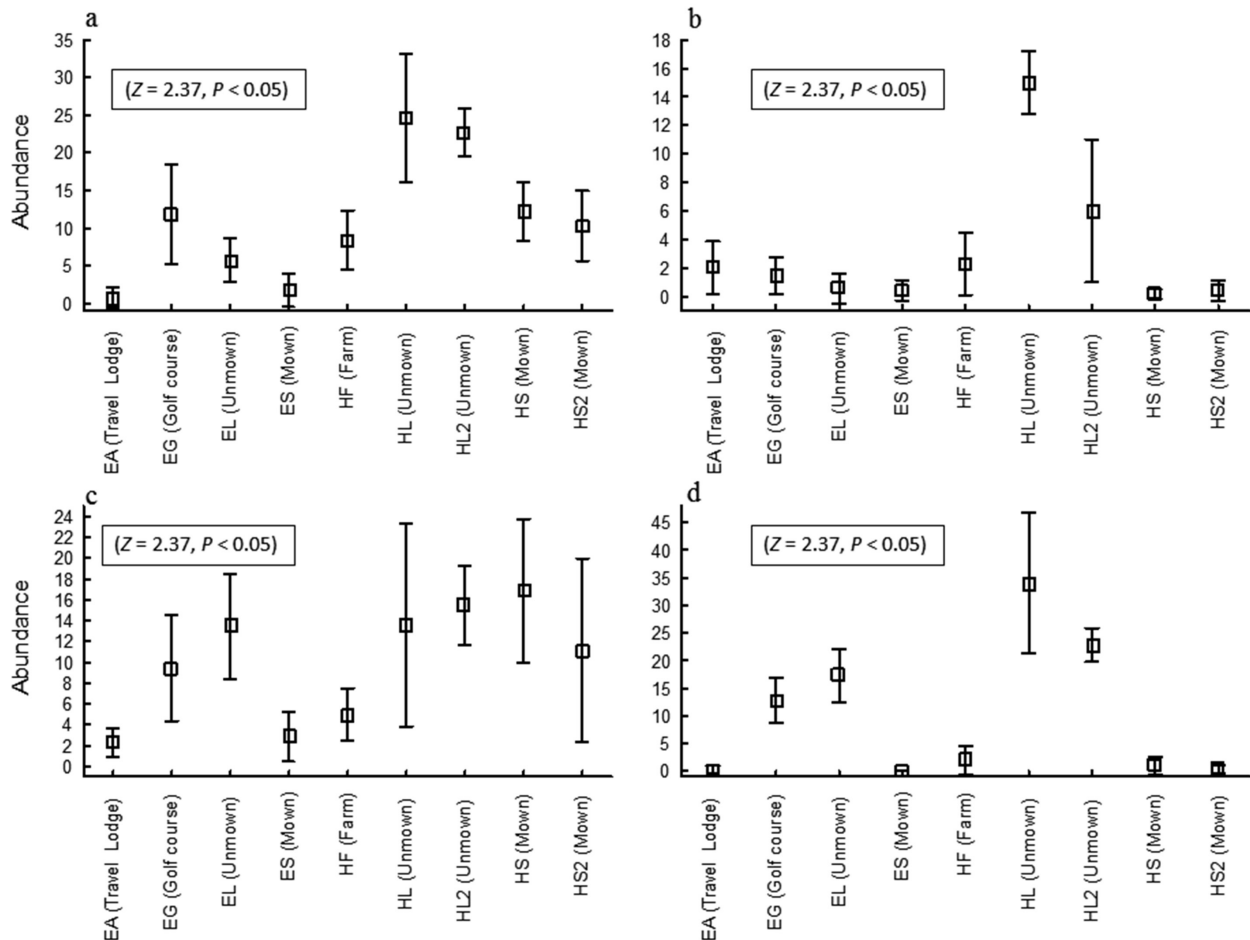


Figure 3 Mean (indicated with 95% confidence intervals) daily small mammal abundance per transect at the end of 4 consecutive seasons: (a) growing season 1, GS1; (b) non-growing season 1, NG1; (c) growing season 2, GS2; and (d) non-growing season 2, NG2.

At Eros, abundance was highest at the end of the first growing season (GS1) at the golf course (EG = 11.86 ± 7.17) and lowest at the Travel Lodge (EA = 0.71 ± 1.50) (Fig. 3a). There were significant differences between EA and EG ($Z = 2.37, P < 0.05$) as well as EA and EL ($Z = 2.37, P < 0.05$). A further significant difference was found between EG and ES ($Z = 2.37, P < 0.05$). At the end of the first non-growing season (NG1) abundance was highest at the Travel Lodge (EA = 2 ± 2) and lowest at the on-airport mown transect ES (0.43 ± 0.79) (Fig. 3b). There were significant differences between EA and EG ($Z = 2.20, P < 0.05$), EA and EL ($Z = 2.37, P < 0.05$), EA and ES ($Z = 2.03, P < 0.05$), EG and ES ($Z = 2.37, P < 0.05$) and EL and ES ($Z = 2.37, P < 0.05$). After the second growing season (GS 2) abundance was highest in the on-airport mown transect EL (13.43 ± 5.41) and lowest in the on airport unmown transect ES (2.86 ± 2.61). The off airport transects resulted in mean abundance of 9.43 ± 5.47 at the golf course (EG) and 2.29 ± 1.50 at the Travel Lodge EA (Fig. 3c). There were significant differences only between EG and ES ($Z = 2.03, P < 0.05$). After the second non-growing season (NG2) abundance was again highest in the on-airport mown transect EL (17.29 ± 5.25) and lowest in the on airport unmown transect where no small mammals were trapped (Fig. 3d). There were significant differences between EA and EG ($Z = 2.20, P < 0.05$), EA and EL ($Z = 2.20, P < 0.05$), EA and ES ($Z = 2.02, P < 0.05$), EG and ES ($Z = 2.02, P < 0.05$) and EL and ES ($Z = 2.02, P < 0.05$).

In total, 11 species of small mammal were recorded (Table 1). This includes 8 rodents (*Desmodillus auricularis* Smith, 1834, *Mastomys coucha* Smith, 1836, *Mus musculus* Linnaeus, 1758, *Mus indutus* Thomas, 1910, *Rhabdomys pumilio* Sparrmann, 1784, *Saccostomus campestris* Peters, 1846, *Gerbilliscus leucogaster* Peters, 1852, *Thallomys paedulus* Sundevall, 1846 and 1 elephant shrew *Elephantulus intufi* Smith, 1836) and 2 unidentified shrews of the genus *Crocidura*. All of the above species besides *T. paedulus* were trapped at Hosea Kutako; at Eros, *M. musculus* and the 2 species of *Crocidura* were not detected.

Except for the most common species *R. pumilio*, *M. coucha* and *G. leucogaster*, notable differences were observed where and when specific species were found (Table 1). For example, at Hosea Kutako: *D. auricularis* was only found at unmown sites, and also only at the end of the growing season; 80% of the *Mus indutus* individuals were found at unmown sites, at the end of the non-growing season; and the commensal *M. musculus*

was only found at unmown site HL2, relatively close to the airport freight store. *Crocidura* sp.1 was found in unmown habitats, except at HS where a drainage line cuts through the habitat. Relatively large numbers of *E. intufi* and *S. campestris* were collected, in a range of habitats, at both airports; in contrast, only 1 individual of *T. paedulus* was trapped (on the banks of a dry riverbed at the Arebbusch Travel Lodge next to Eros Airport).

Both the dominant diurnal and nocturnal species, *R. pumilio* and *M. coucha*, respectively (Table 1), were commonly trapped at all transects, at both airports. With both these species similar fluctuation curves were observed almost throughout and at all transects (Table 1; Figs 4,5), with numbers higher at the end of the growing season than at the end of the non-growing season.

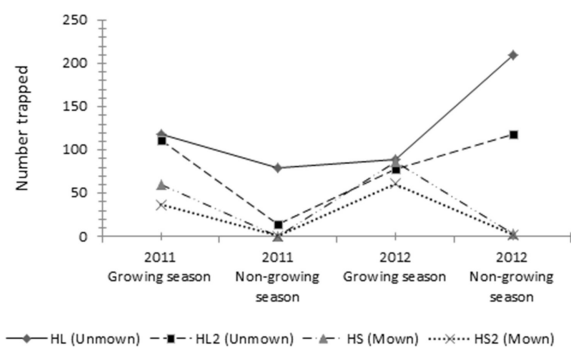


Figure 4 The number of *Rhabdomys pumilio* individuals trapped on standard transects at 2 mown and 2 unmown habitats at Hosea Kutako International Airport.

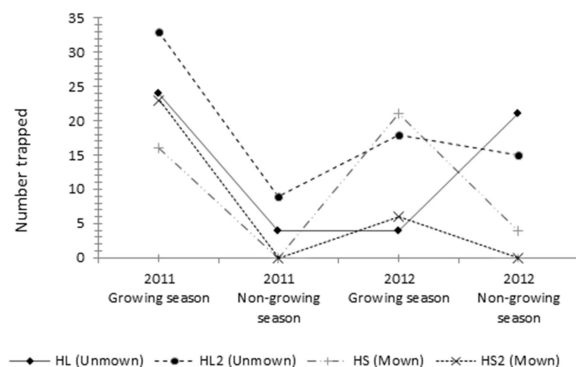


Figure 5 The number of *Mastomys coucha* individuals trapped on standard transects at 2 mown and 2 unmown habitats at Hosea Kutako International Airport.

When considering species richness (Table 1), the pattern where richness decreases from the end of the growing season to the end of the following non-growing season could be found at HF, HS1, HS2, EA, EG and ES. At HL and HL2 this trend was not evident. Conversely, species richness increased at EL from the second growing season to non-growing season. Species richness

(mean per trap night) was significantly higher at Hosea Kutako than at Eros in the first growing season ($Z = 3.67, P < 0.01$) and the first non-growing season ($Z = 3.06, P < 0.01$). In both seasons of the second year the difference was not significant (Fig. 6).

When broken down per transect for growing and non-growing seasons (Fig. 7), the only significant dif-

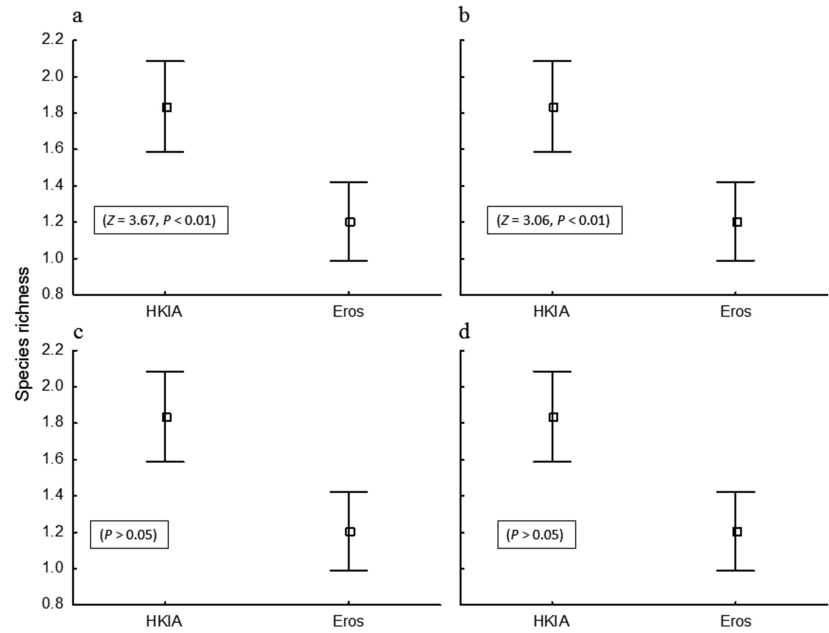


Figure 6 Mean small mammal species richness in: (a) first growing season, GS1; (b) first non-growing season, NG1; (c) second growing season, GS2; and (d) second non-growing season, NG2. Whiskers indicate 95% confidence limits.

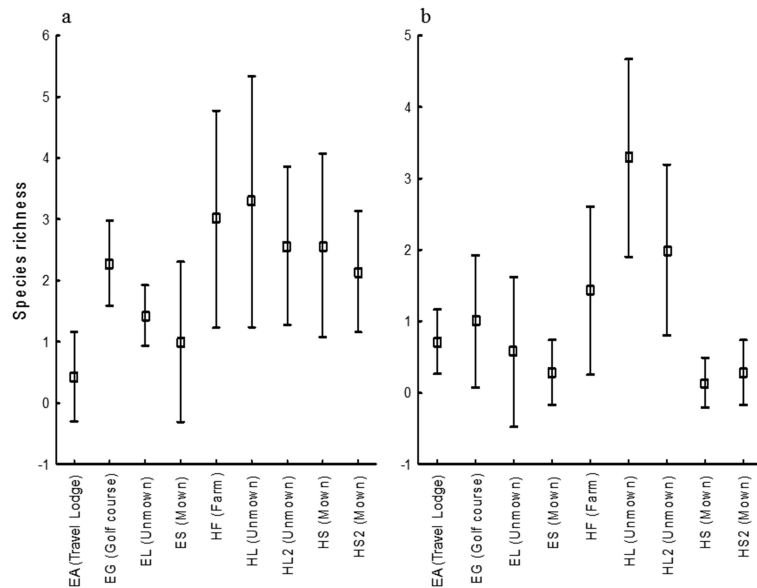


Figure 7 Mean (with 95% confidence) small mammal species richness on 9 transects at Eros and Hosea Kutako airports at the ends of both (a) growing and (b) non-growing seasons.

ference in species richness was at Eros where the travel lodge EA showed significantly lower species richness than the golf course EG ($Z = 2.18$, $P < 0.05$). At the end of the non-growing season species richness was significantly higher in the unmown transects than in the mown transects at Hosea Kutako (HL vs HS: $Z = 3.06$, $P < 0.01$; HL vs HS2: $Z = 2.82$, $P < 0.01$; HL2 vs HS: $Z = 3.18$, $P < 0.05$; HL2 vs HS2: $Z = 2.71$, $P < 0.01$) and at Eros between EL and ES ($Z = 2.93$, $P < 0.01$).

Shannon diversity was the highest during the first growing season per transect (1.22–1.91, mean: 1.43), and dropped during the first non-growing season (0–1.75, mean: 0.99) (Table 1). It was marginally higher in the second growing season (0.42–1.57 mean: 1.06) and then dropped again, to its lowest value, in the second non-growing season (0–1.65, mean: 0.83). At Hosea Kutako, diversity was highest at the farm transect HF (1.26–1.91, mean: 1.62) and lowest in the mown transect HS (0–1.28, mean: 0.86); at Eros, diversity was highest in the unmown transect EL (1.22–1.65, mean: 1.41) and lowest at the mown transect ES (0–1.42, mean: 0.60). When compared within seasons, however, the following fairly common pattern appeared: at 7 of the 9 transects diversity dropped from the end of 1 growing season to the end of the next non-growing season. The decline was significant between GS1 and GS2 ($Z = 2.55$, $P < 0.05$), and between GS1 and NG2 ($Z = 2.31$, $P < 0.05$).

DISCUSSION

Since little information has been published on small mammal trapping events at airports, it was difficult to contextualize the abundances found during this study. Results of only one other published small mammal survey at airports was found (Baker & Brooks 1981), while Seamans *et al.* (2007) studied small mammals in simulated airport vegetation regimes. Of these studies, only Seamans *et al.* (2007) expressed small mammal density in abundance per 100 trap nights and, in that case, it was considerably lower than what was found during the present study. This elevates the importance of small mammals at the Namibian airports studied, and confirms a conclusion of Mendelsohn *et al.* (2002) that Namibia's abundant wildlife is a unique aspect of the country.

The dominant species at both study sites (*R. pumilio*) was also found to be the only diurnal species present. With the majority of flights at both airports being during daylight hours (Hauptfleisch *et al.* 2013) it is considered an important attractant to bird species encountered at

the airport. Black-shouldered kite *E. caeruleus* prey predominantly on this species of small mammal (Tarboton 1978; Mendelsohn & Jaksic 1989). In addition, it has been found to make up a major proportion of prey for other common raptors, such as the African marsh harrier *Circus ranivorus* Daudin, 1800 (Simmons *et al.* 1991) and the barn owl *Tyto alba* Scopoli, 1769 (Torok 1999; Avenant 2005). Of the other 8 raptor species recorded at Hosea Kutako and Eros on numerous occasions (Hauptfleisch 2014), the yellow-billed kite *Milvus aegyptius* Boddaert, 1783 (Dean 2005), the rock kestrel *Falco tinnuculus* Daudin, 1800 (Jenkins 2005a), the greater kestrel *Falco rupicoloides* Jenkins 2005b, the southern pale-chanting goshawk *Melierax canorus* Rislachi, 1799 (Allan 2005) and the secretarybird *S. serpentarius* (Dean & Simmons 2005) are diurnal small mammal predators.

This study, at least for small mammals, confirmed what Price *et al.* (2010) described: that subtropical savannas are highly seasonal systems in flux, where water availability, soil nutrients, vegetation composition, fire, grazing regimes and topography play varying roles. The higher numbers, diversity and species richness of small mammals caught at the end of the growing season corresponds with the findings of Coetzee (1965), Swanepoel (1980), Bronner *et al.* (1988) and Avenant (2011), who, in the central South African grasslands, found the highest abundance and species richness in late autumn (the end of the growing season), followed by a population reduction throughout winter and recovery thereafter (the reproductive peak is during the latter part of the rainy season and stops at the beginning of the dry season). This conforms to the findings of Coetzee (1965), Swanepoel (1980), Bronner *et al.* (1988) and others (e.g. Delany 1975; Taylor & Green 1976; Neal 1977) throughout Africa. These cycles could be coupled to the reproductive cycles of the dominant species trapped during this study, where scrotal males and reproductive active females are commonly observed between August and May, and young are only present in traps from September to late-May/early June (personal observation, Avenant 2011). During winter the old and young individuals presumably die first, and drastic declines in populations have been reported (see Coetzee 1965; Neal 1977; Bronner *et al.* 1988; Avenant 2011). During July, the coldest month of the year (Mendelsohn *et al.* 2002), minimum temperatures are on average between 2 and 4°C, confirming Andrews and O'Brien's (2000) and Muck and Zeller's (2006) comments that thermal seasonality may have an important influence on small mammal numbers. However, the current results show that this seasonal pattern is not nec-

essarily as simple and constant in central Namibia: in the final (2012) non-growing season an unexpected increase in small mammal numbers (particularly *R. pumilio* and *M. coucha*) was found at the unmown transects at both airports. A possible reason for this could be the above average rainfall event of 2011, when the annual rainfall of 1221.8 mm was noted (weather.namsearch.com), 3.4 times the mean annual of 362.8 mm (Windhoek City – MOWT, 2012). Andrews and O'Brien (2000) and Yarnell *et al.* (2007) found that rainfall had a positive influence on small mammal population numbers, with species-specific lag periods. More and late rain may extend the growing period, and having more food available may lengthen the small mammal reproductive season and decrease mortality during the dry winter months. Similarly, good early rains may lead to an early start of the reproductive season (Linn 1991). Wirminghaus and Perrin (1993) found that body fat and water levels, as affected by food quality, controlled breeding of small mammals, particularly r-selected species (such as *R. pumilio* and *M. coucha*). This may indirectly imply that predator species (e.g. raptor) occurrences at the airports, and, hence, bird collisions with aircraft, would be highest at the end of high rainfall seasons, and may also extend later into the dry season. It remains, however, important to note that healthy small mammal populations can exist at airports throughout the year (as also confirmed by Witmer 2011).

Another likely reason for the high numbers of small mammals in the second non-growing season during the present study may be the airport mowing regimen. Areas in the vicinity of runways and aircraft maneuvering sites are mown annually, at the end of the growing season (personal observation 2010–2013). Not all grassland at either airport was mown, leaving patches of unmown grassland often adjacent to mown areas. Upon mowing at the end of the 2012 growing season, approximately 8 weeks before the current small mammal survey, small mammals may have merely moved into adjacent unmown areas, resulting in increased densities in these areas. Studies on small mammals elsewhere (e.g. on *Microtus spp.* in North America [Edge *et al.* 1995]) found that, although mowing reduces their abundance, populations recover quickly thereafter. The dominant species at the 2 Windhoek airports, *R. pumilio*, for example, has been found to move its home range readily in relation to its requirements (Schradin & Pillay 2004; Schradin & Pillay 2006). Recently mown grass can provide nesting material and, as such, also act as corridors for travel between unmown areas (Witmer 2011; Gar-

rett *et al.* 2012). In the present study area the movement of small mammals to undisturbed “hotspots” of increased small mammal densities, when compared to neighboring areas, can, therefore, not be excluded. Such “raptor restaurants” may increase the AWC risk. Baker and Brooks (1981) and Schmidt *et al.* (2013) warn that prey abundance should be considered in parallel to prey availability, as a high abundance of small mammals in dense grassland will be less vulnerable to predators than in sparse vegetation. This is considered less of a factor in the semi-arid conditions of Hosea Kutako and Eros, where grass density even in above average rainfall years is low when compared to the mesic and temperate environments where the studies by Baker and Brooks (1981) and Schmidt *et al.* (2013) were done. Unpublished data on grass standing biomass at Hosea Kutako and Eros found grass standing biomass to vary between 56.2 and 458 kg/ha.

In light of the above, the effectiveness of grass mowing as a control measure for the risk of AWCs at airports (ICAO 2006) has, understandably, been found to have varied success and does not guarantee reduced risk (Blackwell *et al.* 2013; DeVault *et al.* 2013). Barras *et al.* (2000) and Dekker and Van der Zee (1996) report that no difference in the densities of birds in mown versus unmown areas has been proven. Where tall grass was found to interfere with feeding and ground movement of birds, it also provides nesting sites and food diversity for other species (Barras & Seamans 2002). Mowing, or other means of reducing grass cover, has been found to reduce small mammal cover and food at airports (Blackwell *et al.* 2013) and to decrease populations in general (Birney *et al.* 1976; Edge *et al.* 1995; Peles & Barrett 1996; Washburn & Seamans 2007; Garrett *et al.* 2012; Moorman *et al.* 2013). In the present study the significantly lower abundance of small mammals in mown compared to unmown transects at both airports, particularly in the non-growing seasons, indicates the effectiveness of mowing to reduce small mammal presence. The consequence of this is a likelihood for reduced raptor presence, with the dominant *R. pumilio* being an important prey component of black-shouldered kite (*E. caeruleus*) (Tarboton 1978; Pickford *et al.* 1989; Hockey *et al.* 2005) and southern pale chanting goshawk (*M. canorus*) (Malan 1998; Hockey *et al.* 2005), which are regularly seen at Hosea Kutako and Eros airports (personal observation). Seamans *et al.* (2007) found a similar reduction in both small mammal and raptor species following mowing in late summer/early winter.

In the present study, however, the effectiveness of annual mowing was greatly reduced through the growing season. Small mammal abundance and, consequently, their predatory raptor species could be reduced at the airports by more frequent mowing (once in early summer and once in late summer, at least) as well as complete (not patchy) mowing of all grassland areas on the airport properties. This is worth investigating, as current patchy mowing (where some areas of grassland around runways are mown and others not) was found to increase small mammal densities in the unmown areas (moving from mown areas), resulting in localized hotspots of exceptionally high small mammal abundance to which raptors are drawn to hunt.

The mean total species richness across the 5 transects at Hosea Kutako (7 ± 1.7) and the 4 at Eros (4.5 ± 1.29) is high when compared to southern African studies in similarly semi-arid areas by Avenant (2011) in the Free State grasslands (mean = 3.1), Nel (1978) in the Fynbos biome (mean = 3.6) and by Kerley (1992) in the Karoo (mean = 3.8); it is also high in comparison to a similar study at Toronto International Airport, where a total of only 4 species were found (Baker & Brooks 1981). The results support the finding of Kelt *et al.* (1996) that arid areas produce high alpha small mammal diversity, coupled to a diverse vegetation community structure and broad resource spectrum (Abramsky 1978; Els & Kerley 1996). Avenant (2011) found species richness between 1 and 7 in a variety of grassland sites. He also observed that species richness in small mammal communities increased with succession until a state of climax, and then decreased to an expected point of equilibrium. Avenant (2005, 2011) then hypothesized that species richness will fluctuate around this point until disturbance such as that caused by fire, drought or overgrazing, after which it may drop further before increasing again with succession. As such, the well-known natural fire regime, that has shaped plant communities in the South African Grassland Biome, correlates also with small mammal community structure where specific species enter and may leave a habitat during different stages of succession, causing species richness and diversity to increase with ecological integrity. Generalist species, such as *Mastomys coucha*, dominate at more disturbed areas, and specialist species, such as *Dendromus melanotis* (expected in central Namibia; Monadjem 2013), increase in composition closer to climax conditions. Indicator species may also enter and exit the small mammal community at specific stages coupled to ecological value or integrity.

This dictates that species richness is highest in an ecosystem with regular light to moderate disturbance. The highest species richness in the unmown transects at Hosea Kutako supports this observation, as some disturbance through occasional fires and human disturbance does take place in these areas. If Tilman's curve (Tilman 1982; Tilman *et al.* 1996) is applied where species richness increases with ecosystem productivity, transects at Hosea Kutako would indicate that unmown areas within the airport have highest ecosystem productivity, with lowest productivity in the neighboring game ranch. This corresponds with Muck and Zeller (2006), in north central Namibia, who found that species richness of small mammals correlates positively with vegetation cover.

Although species richness and mean diversity in the current study were high in comparison to the South African grasslands (Avenant 2011), it was comparable to that of transects in cattle and wildlife farming areas of north-central Namibia (Muck & Zeller 2006). A number of indicators, however, point towards all transects being in disturbed conditions. Avenant (1996, 2000, 2011), Avenant and Cavallini (2007) and Avenant *et al.* (2008) propose the use of *M. coucha* as an indicator of disturbed habitat. Similar to *M. natalensis*, this species was found to dominate in areas of low ecosystem integrity following natural habitat destruction caused by fire and human destruction (Meester *et al.* 1979; Bronner *et al.* 1988), and after long, extended dry periods (Monath *et al.* 1974; Taylor & Green 1976; Linn 1991), with their numbers later decreasing as other more specialized rodents (e.g. *R. pumilio*) increase. In the current study this species was 1 of the 3 most numerous on all transects.

Land use around airports has been found to conflict with airport operations and safety (Blackwell *et al.* 2013). In the current study significant differences in small mammal community structure were found between different land use types in and outside the Hosea Kutako airport property. Inside the airport property densities, species richness and diversity were lower on mown (HS and HS2) than unmown transects (HL and HL2), indicating a higher level of disturbance. Outside, in the neighboring game and cattle ranch, the significantly lower small mammal abundance was most probably caused by overgrazing (evident from a low ecological index value and high percentage [75.6%] of pioneer Increaser IIc grass species found in this transect; see Hauptfleisch 2014). This corresponds with observations by Saetnan and Skarpe (2006), Hoffman and Zeller (2005) and Muck and Zeller (2006) in similar habitat types within Namibia, with, *inter alia*, Monadjem (1999)

and Caro (2001) elsewhere in Africa, and with Moser and Witmer (2000) in North America.

At Eros the urban environment showed lower small mammal numbers in general and confirmed the finding of Lizee *et al.* (2011) that mostly generalist species of wildlife inhabit urban areas. The artificially enhanced productivity of the ecosystem at the golf course (through fertilizer application and irrigation) houses higher small mammal numbers than the neighboring airport, and possibly acts as a source population for the airport small mammals. It is also important to note that significantly more small mammal individuals and species were caught at the airport with rural surrounds (Hosea Kutako) than the airport in the urban setting (Eros).

Higher abundance of small mammals inside Hosea Kutako Airport perimeter could further be caused by the lack of mammalian predators such as the black-backed jackal *Canis mesomelas* (Von Schreber, 1775) and African wildcat *Felis silvestris* (Von Schreber, 1777), which cannot breach the wildlife control perimeter fence. This effectively makes the airport a refuge from nonvolant predators. This sanctuary effect has been mitigated at golf courses and crop fields through installation of owl nest boxes and raptor perches. In this particular case, however, such a measure is likely to be counter-productive.

This study takes cognizance of the snapshot level of the small mammal survey (= during only 2 autumns and 2 springs). Naturally, more accurate conclusions can be drawn from longer-term data (as recommended by Baker & Brooks 1981). Through the Wildlife and Aircraft Research Namibia (WARN) project (initiated as a mitigation measure in this study), longer-term small mammal surveys are to be conducted to strengthen the conclusions drawn at this stage.

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