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Breaking Ground: Quantitative Fossorial Herpetofaunal Ecology in South Africa

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Abstract.—Basic ecological data are lacking for many species of herpetofauna, particularly fossorial species. Quantitative analyses of the factors that may influence the occurrence of fossorial herpetofaunal species are rare, with minimal work conducted in southern Africa. We mapped the absolute and relative fossorial herpetofaunal species richness across South Africa in order to highlight underlying trends in diversity. We also quantitatively surveyed fossorial herpetofauna at a site in Zululand, KwaZulu-Natal, South Africa, using two methods. The first method has previously been used for surveying fossorial herpetofauna and involved two investigators excavating 28 clusters of five 1 m x 1 m x 0.3 m pits (total of 71 tons), placing all excavated soil on a plastic sheet and searching through the excavated soil by hand. The second method involved the use of heavy-duty, earthmoving machinery to systematically excavate 19 3 m x 3 m x 1 m pits (total of 234 tons), passing all soil through a custom-built table-sieve to expose herpetofauna. At each site, soil compaction, particle size distribution, and land use were recorded. A Generalized Linear/Nonlinear Model (GLZ) was used to test for factors that predicted fossorial herpetofaunal density. Only seven specimens were captured from three species, yielding density estimates of between 0 and 0.4 individuals.m^{-2}. None of the measured factors predicted fossorial herpetofaunal density, possibly because of the low capture rates. Our data indicate that fossorial herpetofauna occurrence was patchy and individuals occurred at low densities at the site. We explore several possible explanations for these patterns.

Key words.—Fossorial herpetofauna, diversity, abundance, South Africa, mapping.

Terrestrial ecologists generally rank soil as one of the least-studied micro-habitats on earth (Copley 2000). Some of the most basic questions about the diversity and abundance of this microhabitat's megafauna remain almost entirely unanswered, even for soil mega-fauna such as fossorial herpetofauna. These organisms may have important functions in the environment (Lavelle et al. 1997), may constitute high biomass in some situations, and contribute significantly to biodiversity (Measey 2006), yet they remain poorly studied.

The fossorial herpetofauna comprise a suite of phylogenetically unrelated, and morphologically diverse, reptiles and amphibians. Measey (2006) defined fossorial herpetofauna as rep-tiles and amphibians that either utilize the soil and soil debris for refuge, or those that spend the majority of their lives living, feeding, and breeding in the soil. Because species show differing degrees of fossorial habits, it is useful to define two groups of fossorial species (Measey 2006). While this distinction is particularly useful for separating classically fossorial taxa such as amphisbaenids from taxa that simply take refuge below the surface either for short periods of time or extended periods of inactivity, problems with this classification remain, especially among species that exhibit intermediate degrees of fossoriality, or those species for which little ecological information is available.

Here, we adopt Measey's (2006) sensu lato definition of fossorial herpetofauna as those reptiles and amphibians that use the soil (including leaf litter, wood, etc.) as a refuge. Thus, fossorial species may have a range of lifestyles from strictly fossorial, spending nearly all their active time below ground, to only constructing burrows for the purposes of shelter, sand-swimming, or simply shuffling into friable substrate for ambush or thermoregulatory purposes. We also subjectively defined a subset of these species as being "strictly fossorial" and included in this group only species that have a strictly fossorial lifestyle and display morphological, physiological, or behavioral adaptations to the fossorial micro-environment. Common to the majority of the species in this group is the fact that attributes of substrate type are likely to act as important constraints to their occurrence.

Most available ecological data for fossorial herpetofauna have been inferred from the morphology and the examination and dissection of museum specimens. As a result, a bias exists toward information on feeding preferences and reproductive biology, which has been deduced from analysis of gut contents and gonad condition of voucher specimens (e.g., Shine & Webb 1990; Webb et al. 2000; Webb et al. 2001). Patterns of diversity and abundance remain poorly documented, largely because quantitative data are very difficult to collect due to the exceedingly cryptic nature of fossorial animals. Without even a rudimentary understanding of patterns of abundance and diversity and the factors driving these patterns, the function of such organisms in community ecology remains entirely speculative. As a first step, development and testing of appropriate quantitative survey methods is crucial (Measey et al. 2003). Secondly, these must be applied at multiple scales so that an understanding of the nature of fossorial herpetofauna emerges.

Recently, Measey et al. (2003) and Measey (2006) have described two methods of survey-ing fossorial herpetofauna, and have applied them in the measurement of densities for fossorial herpetofauna from a number of regions, albeit at fairly localized spatial scales. This work has targeted particular taxa and has not been aimed at estimating diversity of the fossorial herpetofaunal assemblage. In southern Africa, such surveys are truly scarce. Pooley et al. (1973) excavated pits in northern KwaZulu-Natal, South Africa, and recorded the density and diversity of fossorial herpetofauna. Measey (2006) reported on surveys conducted in the same area, but the investigations suffered from small sample size and poor capture rates. Few other anecdotal observations of fossorial herpetofaunal densities have been published (e.g., Burger 1993), but these were rarely quantitative.

The paucity of previous quantitative fossorial herpetofaunal surveys provides a strong indication of the difficulties involved in performing such surveys. These can be broadly classed into two categories: those problems arising from the ecology and behaviour of fossorial herpetofauna, and those problems arising from the difficulties associated with the physical movement of sufficient soil.

Certain biological traits exhibited by some fossorial species make collecting specimens and ecological data difficult. Escape behaviour and locomotion of fossorial herpetofauna need to be considered when surveying these animals, as they can have major implications for detection probability and accuracy of estimates derived from the data. Most techniques employed to survey organisms assume very high detection probabilities. Yet, in general, escape behaviour for many herpetofaunal species is poorly known, with most studies focusing on abundant terrestrial species (e.g., Losos et al. 2002; Diego-Rasilla 2003; Whiting et al. 2003; Downes & Hoefer 2004). Locomotion in fossorial herpetofauna has not been extensively studied either (but see Gans

1985; Leonard 1989; Navas et al. 2004), and mechanisms of escape are poorly known. In the case of snakes and apodal lizards, escape mechanisms are likely to represent a serpentine undulation through the substrate (Leonard 1989).

Anecdotal evidence suggests that several species of southern African herpetofauna have the potential to move rapidly through the soil (e.g., *Scelotes* spp. pers. obs.). Several fossorial species are known to construct a network of burrows, through which they can move rapidly, resulting in easy escape (*Breviceps* spp. - Minter 2004; *Ptenopus* spp. - Branch 1998). Thus it is particularly difficult to quantify the magnitude to which escaping fossorial herpetofauna influence estimates of density and diversity within a sample plot.

Some fossorial herpetofaunal species may reside deep underground, making accessing such species very difficult. Branch (1998) suggested that the snake *Rhinotyphlops lalandii* burrows to great depths but gives no estimate of the depth. Cowles (1941) reported *Chionactis occipitalis* from depths of up to 600 mm and Barbour et al. (1969) inferred that *Carphophis amoenus* burrows to depths of over 450 mm. These reports indicate that fossorial herpetofauna may be able to attain depths that current survey methods do not, with obvious implications for species detection.

Measey (2006) stated that excavation is the most efficient way of surveying fossorial herpetofauna. However, such techniques often have logistical drawbacks, especially at larger scales and greater depths. The first and most obvious of these is the amount of work required to process adequate samples of soil. Soil from our study site weighed approximately 1650 kg.m^{-3}. Excavation of a small plot of 1 m^2, to a depth of approximately 300 mm, required the movement of more than 0.5 metric tons of soil. The calorimetric implications to the herpetolo-

gist excavating by hand are obvious.

Here, we attempt to advance the study of fossorial herpetofaunal ecology in South Africa. We have several objectives: We map the distributions of fossorial reptile and amphibian species in South Africa, highlighting areas of high absolute fossorial species richness and richness relative to the entire reptile or amphibian community in general. We introduce a new quantitative method for surveying fossorial herpetofauna with heavy-duty earthmoving machinery. We compare our novel method with a previously described method in an attempt to make our data comparable to other published data. We produce density estimates at both the landscape scale (the entire study site) and for the different land uses on the site. We attempt to tease apart some of the factors that may be driving observed patterns and discuss how some of the difficulties involved in surveying fossorial herpetofauna may be overcome so as to advance fossorial herpetofaunal ecology.

MATERIALS AND METHODS

Distribution mapping.—In order to clarify the underlying trends in geographic distribution of South African fossorial herpetofauna, we mapped the distributions of reptiles and amphibians in South Africa. By digitizing and georeferencing distribution data from Branch (1998, reptiles) and Minter et al. (2000, amphibians), and summing the resultant maps, we produced reptile and amphibian species richness maps at Quarter Degree Square (QDS) resolution. Similarly, by summing all the distribution data for all fossorial forms in South Africa (Table 1), we produced fossorial reptile and amphibian species richness maps. Finally, by dividing the number of fossorial species in each QDS by the number of reptile or amphibian species in that QDS, we produced maps showing the proportion of the reptile or amphibian assemblage in each QDS that have

fossorial lifestyles. The resultant maps provide an indication of the proportion of herpetofaunal community at any study site that show fossorial habits and allow us to place the data collected from our study site into a South African context.

Study Site.—To test our new survey method, we selected an area with high herpetofaunal richness and a relatively high proportion of fossorial species. The site, Fairbreeze C Extension mine, immediately south of the town of Mtunzini, KwaZulu-Natal, South Africa (28.961° S; 31.749° E), has already been earmarked for strip mining of heavy minerals. These include titanium-rich minerals such as ilmenite ($FeTiO_2$), rutile (TiO_2), zircon ($ZrSiO_4$), and leucoxene, which occur in aeolian sand deposits (Norman & Whitfield, 2006). It had been suggested by Alexander (2004) that these aeolian sand deposits may sustain high densities of fossorial herpetofauna, and so the study was also aimed at assessing the impact that mining may have on the fossorial herpetofaunal community.

The area forms part of the Maputaland-Pondoland-Albany Biodiversity Hotspot (Mittermeier et al. 2005). Historically coastal forest and grassland, the area was transformed by agriculture, initially to sugarcane, and subsequently to Eucalyptus plantations in the 1930s (Van der Elst et al. 1999). These crops predominate today but are interspersed with "semi-natural" forested areas. The area is underlain by aeolian sands, which were deposited between 350,000 and 400,000 years ago (Maud & Botha 2000). Climate in the area is sub-tropical, receiving more than 1200 mm rain per annum (Shulze 1997).

Currently, habitats in the area show varying levels of disturbance. While large tracts of land have been converted to sugarcane and timber production, areas of "semi-natural" woodland habitat remain (Maritz & Alexander 2007).

Less obviously, agricultural activities in recent years have reduced mean annual runoff in the two major catchments in the area, the Amanzinyama and Siyayi River Catchments (Van der Elst et al. 1999; Sheperd et al. 2004), modifying habitats.

Fossorial herpetofaunal surveys.—We quantitatively surveyed fossorial herpetofauna by excavating 218.6 m³ of soil, covering an area of 311 m² and weighing approximately 360.7 metric tons from 47 sites. The soil was thoroughly sieved and searched, and all herpetofauna were captured and identified.

Method 1 was based on the method developed by Measey et al. (2003). Each survey comprised five pits randomly distributed within a 100 m² site. Holes measuring 1 m x 1 m and 0.3 m deep were excavated rapidly by two people using shovels. All excavated soil was placed onto a plastic sheet. Both people then sieved through the excavated soil by hand and removed any reptiles or amphibians. Collected animals were identified, counted, and released at point of capture. Method 1 surveys were performed at 28 sites.

Method 2 entailed digging large-scale excavations with earthmoving machinery and passing the excavated soil through a custom built sieve to expose any reptiles or amphibians that were buried in the soil. Excavations involved the digging of four trenches approximately 1.5 m deep and 0.75 m wide to form a "soil island" measuring 3 m x 3 m in area. The top meter of the soil island was then systematically scooped and placed onto a custom built sieve. The sieve (Fig. 1), a table-like structure, measured 1 m x 0.75 m and stood approximately 1.2 m high, was constructed from two sheets of expanded metal, each with diamond shape apertures measuring approximately 25 mm x 15 mm, overlaid on each other. Two or more people carefully sifted the soil through the sieve so that all soil was thoroughly examined for the presence

of reptiles and amphibians. The efficacy of sieving was proven by the fact that even small invertebrates such as isopterans, coleopterans (adults and larvae), blattodeans, isopods, arachnids, and annelids, many no bigger than 15 mm in length, were easily recovered. Collected reptiles and amphibians were identified, counted, and released at point of capture. Method 2 surveys were performed at 19 sites.

The habitat at each site was classified according to its land use (categories: *Eucalyptus* plantation, Sugarcane, Forest, or Grassland). Longitude and latitude were recorded using a GPS (datum: WGS84). A soil sample (approximately 1 litre), comprising three sub-samples from the immediate area (within 2 m of the point of excavation), was taken from each site for analysis of particle size distribution. Particle size distribution within a soil sample can be used to assess soil texture (Oberthür et al. 1999), a physical characteristic that may influence the occurrence of organisms (Rietkerk et al. 2002). Particle size distribution was assessed by passing each soil sample through sieves with screen sizes ranging from 800 μm to 45 μm.

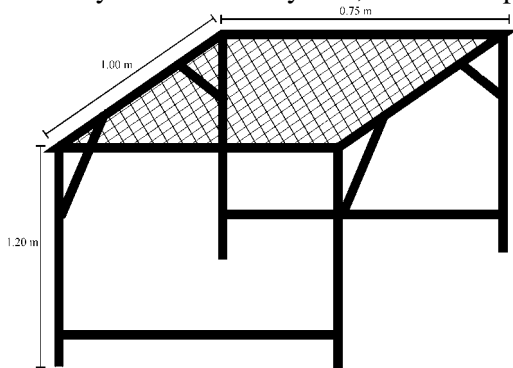Because particle size distribution did not vary extensively over the study site, we developed

Figure 1. Table-like, custom-built sieve used to detect fossorial herpetofauna in sampled sand. Grid consists of a double layer of expanded metal screen with diamond shape apertures (approx. 15 mm x 25 mm). Frame constructed from 55 mm angle-bar.

an index of soil texture by subtracting the proportion of the sample falling above the mean of particle size for all samples, from the proportion falling below this size. This normally-distributed index provided a measure of whether soil at a particular site was more or less coarse than the average. We also measured soil compaction at each site by measuring the depth to which a Dynamic Cone Penetrometer penetrated from three standardized impacts. Measures were repeated at three random positions around the site after excavating the soil.

Data analysis.—All statistical analyses were performed using STATISTICA ver. 6 (StatSoft, Inc. 2002). We used the Generalized Linear/Nonlinear Model (GLZ) function to test for factors that predicted fossorial herpetofaunal density. This non-parametric analysis was performed because the distribution of the response variable (fossorial herpetofaunal density) matched a Poisson distribution rather than a normal distribution, as is assumed by a parametric General Linear Model (GLM). Continuous predictive variables included soil texture (from particle size distribution) and mean soil compaction, whereas land use was included as a categorical predictive variable. We used a Mann-Whitney U-Test to test for differences in mean estimated fossorial herpetofaunal density between survey methods and a Kruskal-Wallis ANOVA to test for differences in estimated fossorial herpetofaunal density between sites under different land uses. Non-parametric analyses were preferred over parametric equivalents because of the skewed data distribution and poor capture rates.

RESULTS

Distribution mapping.—A large proportion of South African herpetofauna show characteristics of a fossorial lifestyle. One hundred seventeen species (± 23 %) of South African reptile species live fossorial lifestyles to some degree,

Table 1: Fossorial herpetofauna of South Africa. Strictly fossorial species are indicated by an asterisk.

Reptiles

Rhinotyphlops lalandei*	Homoroselaps lacteus*	Scelotes inornatus*
Rhinotyphlops schinzi*	Bitis schneideri	Scelotes kasneri*
Rhinotyphlops schlegelii*	Chirindia langi*	Scelotes limpopoensis*
Typhlops fornasinii*	Dalophia pistillum*	Scelotes mirus*
Typhlops bibronii*	Monopeltis capensis*	Scelotes montespectus*
Leptotyphlops longicaudus*	Monopeltis decosteri*	Scelotes mossambicus*
Leptotyphlops nigricans*	Monopeltis infuscata*	Scelotes sexlineatus*
Leptotyphlops incognitus*	Monopeltis leonhardi*	Scelotes vestigifer*
Leptotyphlops scutifrons*	Monopeltis rhodesiana*	Trachylepis capensis
Leptotyphlops telloi*	Monopeltis sphenorhynchus*	Trachylepis depressa
Leptotyphlops distanti*	Zygaspis quadrifrons*	Trachylepis homalocephala
Leptotyphlops sylvicolus*	Zygaspis vandami*	Trachylepis occidentalis
Atractaspis bibronii*	Acontias breviceps*	Trachylepis variegata
Atractaspis duerdeni*	Acontias gracilicauda*	Panaspis walbergii
Aparallactus lunulatus*	Acontias meleagris*	Ichnotropis squamulosa
Aparallactus capensis*	Acontias percivali *	Meroles ctenodactylus
Macrelaps microlepidotus*	Acontias plumbeus*	Meroles cuneirostris
Amblyodipsas concolor*	Acontias poecilus*	Meroles knoxii
Amblyodipsas polylepis*	Acontophiops lineatus*	Nucras caesicaudata
Amblyodipsas micropthalma*	Microacontias lineatus*	Nucras holubi
Xenocalamus sabiensis*	Microacontias litoralis*	Nucras livida
Xenocalamus transvaalensis*	Typhlosaurus aurantiacus*	Nucras tessellata
Xenocalamus bicolor*	Typhlosaurus cregoi*	Pedioplanis burchelli
Lamprophis fiskii	Typhlosaurus gariepensis*	Pedioplanis lineooccellata
Lamprophis fuscus	Typhlosaurus lineatus*	Pedioplanis laticeps
Lamprophis inornatus	Typhlosaurus lomiae*	Pedioplanis namaquensis
Lycophidion pygmaeum	Typhlosaurus meyeri*	Tropidosaura cottrelli
Pseudaspis cana*	Typhlosaurus vermis*	Tropidosaura gularis
Dipsina multimaculata	Lygosoma sundevalli*	Cordylus giganteus
Rhamphiophis rostratus	Scelotes anguineus*	Gerhosaurus flavigularis
Prosymna bivittata	Scelotes arenicolus*	Gerhosaurus nigrolineatus
Prosymna frontalis	Scelotes bidigittatus*	Gerhosaurus typicus
Prosymna janii	Scelotes bipes*	Agama aculeata
Prosymna stuhlmannii	Scelotes bourquini *	Agama armata
Prosymna sundevallii	Scelotes caffer *	Agama hispida
Aspidelaps scutatus	Scelotes capensis*	Chondrodactylus angulifer
Elapsoidea boulengeri*	Scelotes fitzsimonsi *	Colopus wahlbergii
Elapsoidea sundevalli *	Scelotes gronovii *	Pachydactylus austeni
Homoroselaps dorsalis*	Scelotes guentheri*	Ptenopus garrulus*

Amphibians

Arthroleptis stenodactylus	Breviceps gibbosus*	Hemisus marmoratus*
Amietophrynus gariepensis	Breviceps macrops*	Hildebrandtia ornata*
Amietophrynus garmani	Breviceps montanus*	Pyxicehalus adspersus*
Amietophrynus gutturalis	Breviceps mossambicus*	Pyxicephalus edulis*
Poyntonophrynus vertebralis	Breviceps namaquensis*	Tomopterna cryptotis*
Schismaderma carens	Breviceps rosei*	Tomopterna krugerensis*
Vandijkophrynus angusticeps	Breviceps sopranus*	Tomopterna marmorata*
Breviceps acutirostris*	Breviceps sylvestris*	Tomopterna natalensis*
Breviceps adspersus*	Breviceps verrucosus*	Tomopterna tandyi*
Breviceps bagginsi*	Hemisus guineensis*	Tompoterna delalandii*
Breviceps fuscus*	Hemisus guttatus*	

and 74 (± 15 % of total) of those species can be classed as "strictly fossorial" (Table 1). Of the 116 amphibian species known from South Africa (Minter et al. 2004), 32 (± 28 %) were classed as fossorial with, 25 of those species (± 22 % of total) classed as "strictly fossorial" (Table 1).

Reptile species richness in South Africa is not uniformly distributed over the country and ranges from 25 to 97 species per QDS. Higher species richness is evident from the north-eastern Mpumalanga and eastern Limpopo provinces (Fig. 2). 'Strictly fossorial' reptile species richness ranges from 0 to 25 species per QDS and showed a similar pattern of distribution to that of the entire South African reptile fauna (Fig. 2). The central grassland regions,
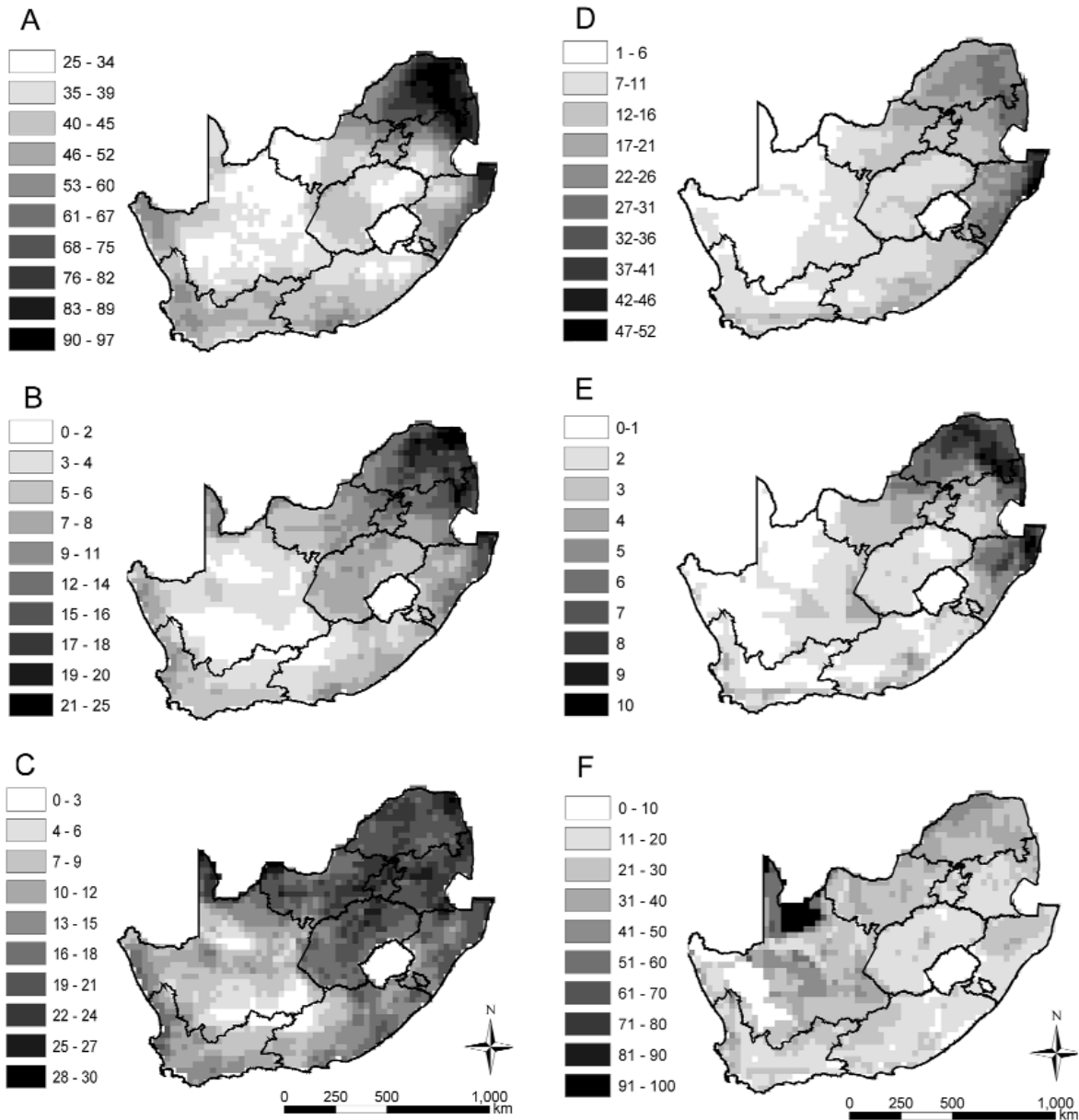

Figure 2. Predicted Reptile Species Richness, Fossorial Reptile Species Richness, and Percentage Fossorial Reptile Species Richness in South Africa at QDS resolution.

Table 2: Quantitative fossorial herpetofaunal survey results collected from 47 excavations, using two survey methods in KwaZulu-Natal, South Africa.

Method	Area (m²)	Volume (m³)	Mass (tons)	Land use	No. of sites	Specimens
1	35	11.9	19.64	Grassland	7	
1	30	10.2	16.83	Sugarcane	6	
1	45	15.3	25.25	Forest	9	*Breviceps mossambicus, Scelotes mossambicus*
1	30	10.2	16.83	*Eucalyptus*	6	*Breviceps mossambicus*
Sub-total	140	47.6	78.55		28	3 specimens (2 species)
2	99	99	163.35	Grassland	11	*Breviceps mossambicus*
2	27	27	44.55	Sugarcane	3	*Amietophrynus gutturalis* x 2
2	27	27	44.55	Forest	3	*Scelotes mossambicus*
2	18	18	29.7	Eucalyptus	2	
Sub-total	171	171	282.15		19	4 specimens (3 species)
Total	**311**	**218.6**	**360.7**		**47**	**7 specimens (3 species)**

the Limpopo valley along the north-eastern edge of the country, and areas bordering the Kalahari in the northwest showed the greatest proportion of fossorial reptiles (Fig. 2). Proportional richness in northern KwaZulu-Natal was also high but decreased with increasing latitude.

Amphibian species richness is not uniformly distributed across South Africa and ranges from 0 to 52 species per QDS (Fig. 2). Areas of high amphibian species richness occur in the north-eastern regions of the country and especially in northern KwaZulu-Natal (Fig. 2). This pattern broadly correlates with areas of high rainfall, as previously noted by others (Poynton 1964; Alexander et al. 2004). "Strictly fossorial" amphibian species richness was highest in the northeastern regions and ranged from 0 to 10 species per QDS (Fig. 2). Fossorial amphibian species appear to make up a greater proportion of the entire amphibian community in the northern and western regions of South Africa.

The Mtunzini area, where our study site was located, is predicted to host approximately 70 reptile species and 43 amphibian species. Of these, 13 reptile species (18.6 %) are fossorial in their habits, as are 8 amphibian species (18.6%). These predictions correspond with the known reptile and amphibian distribution records in the literature and from field surveys conducted in the area (Maritz 2007). The high absolute fossorial richness of the area (13 reptile species; 8 amphibian species) and the large percentage of the total herpetofaunal community that shows fossorial habits (18.6 % in both groups) places the study area in the top 15 % most fossorial reptile species rich and top 6 % fossorial amphibian species rich grid squares in South Africa.

Fossorial herpetofaunal surveys.—Fossorial herpetofaunal surveys yielded very low capture rates, suggesting low population densities of fossorial herpetofauna in the sampled area. Only seven individual animals were captured despite 360.7 metric tons of soil being processed from 47 sites. Three species were recorded, namely the lizard Scelotes mossambicus (two individuals), and the frogs *Amietophrynus gutturalis* (two individuals) and *Breviceps mossambicus* (three individuals) (Table 2). Measures of fossorial herpetofaunal

density across the study site were 0.019 ± 0.010 individuals.m^{-2} (mean $\pm$ SE). The estimated fossorial herpetofaunal density of the 47 sites showed a frequency distribution that differed significantly from normal (Kolmogorov-Smirnov: d = 0.50, $P < 0.01$) (Fig. 3). All individuals were captured from soil that came from within 100 mm of the surface.

Density measures from the different survey methods did not differ significantly for capture rates per unit area (Mann-Whitney U Test: U = 246.0, $P = 0.66$, Fig. 4). The 47.3 m^3 of soil processed using Method 1 produced only two specimens at density of 0.021 ± 0.016 individuals.m^{-2} (mean $\pm$ SE). Similarly, Method 2 produced only three specimens from 171 m^3, yielding density measures of 0.016 ± 0.009 individuals.m^{-2} (mean $\pm$ SE).

Since no difference was detected between density estimates from the two survey methods, we pooled the survey data to investigate whether land use influenced fossorial herpetofaunal density in a detectable manner. No difference was found between fossorial herpetofaunal density estimates from the four categories of land use (Kruskal-Wallis ANOVA: H(3,47) = 1.079, $P = 0.78$, Fig. 5). Fossorial herpetofaunal density estimates ranged from $0.006 \pm$

Table 3: Results from the Generalized Linear/Nonlinear Model (GLZ) showing the effect of texture (from soil particle size distribution), mean soil compaction, and land use on fossorial herpetofaunal density.

	Degrees of freedom	Log-Likelihood	Chi ^{2}	P
Texture	1	-4.03	0.01	0.91
Compaction	1	-4.02	0	0.98
Land use	3	-4.05	0.46	0.93

0.006 individuals.m^{-2} (mean $\pm$ SE) for Grasslands to 0.043 ± 0.034 individuals.m^{-2} (mean $\pm$ SE) for Forests.

None of the selected factors (soil texture, mean soil compaction, or land use) used in the Generalized Linear/Nonlinear Model successfully predicted fossorial herpetofaunal density (Table 3).

DISCUSSION

Our spatial analyses of herpetofaunal species richness indicates that fossorial herpetofaunal species richness is not uniformly distributed across South Africa, nor is the percentage of fossorial herpetofaunal species that makes up
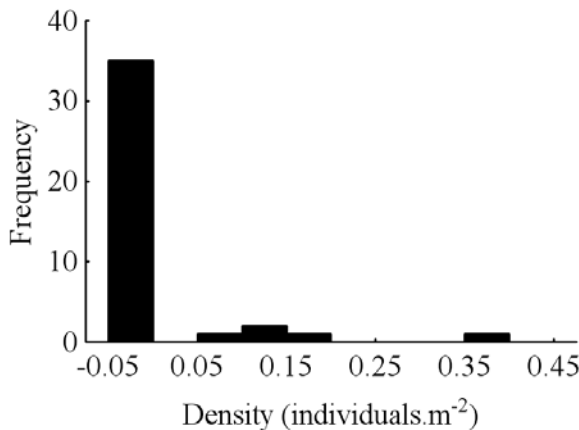

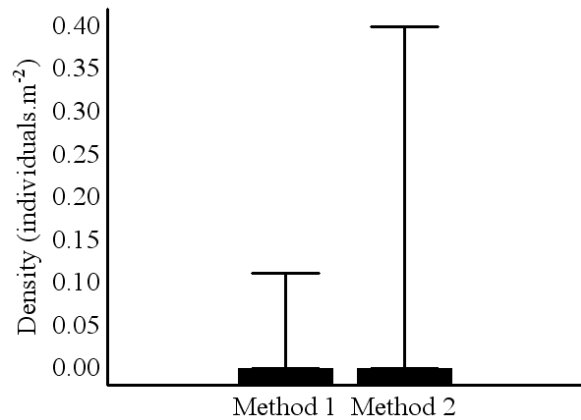Figure 3. Frequency distribution of estimated densities across all sites (N = 47).

Figure 4. Comparison of mean density estimates produced from Method 1 (N = 28) and Method 2 (N = 19) used to survey fossorial herpetofauna. Error bars indicate 95 % confidence limits.

the herpetofaunal assemblage uniformly distributed. Generally, richness of the fossorial reptile species follows a pattern similar to richness of reptiles in general, with peaks in the northern and eastern parts of the country. However, the pattern shown for the proportion of fossorial species making up the reptile assemblage is surprising: our expectation was that fossorial species richness would predominate in the arid west, because low rainfall generally results in more friable, sandy soil with little humus (Watts & Dexter 1998). Instead, fossorial species make up a higher percentage of the total assemblage in the northern and eastern parts, and generally appear to be correlated with areas of higher rainfall. Fossorial amphibian species richness showed a similar pattern to overall amphibian species richness, generally correlating with areas of high rainfall. It is apparent that fossorial amphibian species make up larger proportions of the total amphibian community in the arid north and northwestern regions. This result is logical given that amphibian species richness is low in the areas and arid environments provide a strong selective pressure for fossorial habits as an escape from desiccation.

A potential explanation for peaks in richness in the central northern parts may be the distribu-
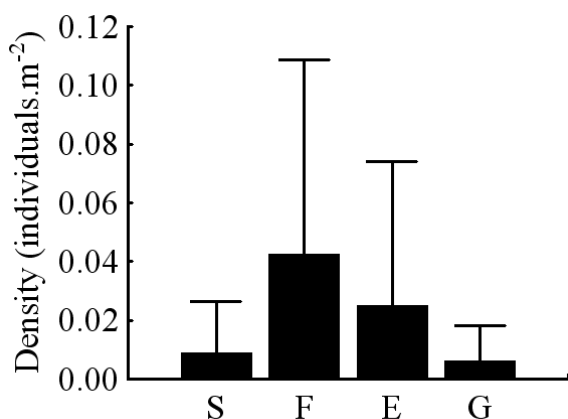

Figure 5. Mean estimated fossorial herpetofaunal density from four categories of land use. S - Sugarcane; F - Forest; E - *Eucalyptus*; G - Grassland. Error bars indicate 95 % confidence limits.

tion of soil and sand types and the ease with which different substrates allow for a burrowing lifestyle. These areas are dominated by the aeolian Kalahari sands, which are conducive for sand-swimming. Similarly, the high richness and percentages of fossorial species on the northeastern coastal plain is associated with aeolian deposits in this area.

Fossorial herpetofaunal density (0.019 ± 0.010 individuals.m^{-2}) and diversity (three species) were lower than expected. Measey et al. (2003) estimated Gegeneophis ramaswamii density at between 0.51 and 0.63 individuals.m^{-2}, depending on season (Using data presented in Measey's Table 1, we calculate the average to be 0.62 individuals.m^{-2}). Pooley et al. (1973) found fossorial herpetofaunal density to be 0.23 individuals.m^{-2}. Kuhnz et al. (2005) estimated Anniella pulchra density at 0.23 individuals.m^{-2} and J. Marais (pers. comm.) estimated Scelotes inornatus density at approximately 0.02 individuals.m^{-2}, although these estimates are taxon specific and representative of optimal habitat. It is clear that our density estimates are much lower than the other two known estimates made in South Africa (Pooley 1973; Marais pers. comm.), suggesting that these higher measures for specific species may represent above-average measures, because optimal sites are usually chosen for study. Our study site was chosen because it is due to be developed for mining, and our measures may represent densities that are more realistic for the region as a whole.

Differences between density estimates recorded during our study and those published (Pooley 1973; Measey et al. 2003; Kuhnz 2005; Measey 2006) could also result from several other causes that are not mutually exclusive. Actual densities across the sites could be patchy, or minor discrepancies in the survey methods could produce incomparable results. Measey (2006) surveyed sites in areas from which semi-quantitative surveys had yielded

target animals. Thus the quantitative surveys on which density estimates were based, were made only in areas known to host target animals, and thus are likely to represent the density of animals in those areas, and over-estimate density at larger scales that would include areas where the animals do not occur. Alternatively, if one performs quantitative surveys randomly (or in an evenly stratified design) across the entire site, the resultant density estimate is likely to be closer to the average density at the landscape scale.

Ultimately the choice of sampling regime is dependent on the objectives and spatial scale of the survey. If the researcher intends investigating density-related aspects of ecology relative to the organisms themselves or density at fine spatial scales, then sampling in areas perceived to represent optimal habitat, as proposed by Measey (2006), may be more appropriate. At the landscape level however, such density estimates lose value as they over-estimate density by an unknown magnitude.

Data collected during our study did not show differences in fossorial herpetofaunal density between sites under different land uses. Unfortunately, this may be the result of the poor capture rates achieved, which resulted in low statistical sensitivity. Despite the lack of statistical significance in this analysis, there does appear to be a trend towards higher densities in more closed habitats such as forests. It should also be noted that most of the secondary grasslands on the site have, at some stage, been under sugarcane and so may share a common factor that acts to depress fossorial herpetofaunal abundance (Maritz 2007). Finally, fossorial herpetofaunal density may not have varied under the different land-uses because of the minimal variation in substrate across the site.

The presence of grasses, forbs, and exotic vegetation and disturbance of the soil are known to negatively influence the distribution of

Anniella pulchra (Kuhnz et al. 2005). Additionally, several authors (Hinde et al. 2001; James & M'Closkey 2003; Masterson et al. 2008) have shown that habitat structure can be an important driver of terrestrial herpetofaunal diversity and abundance. While changes in surface structure may influence fossorial herpetofauna less than they do their terrestrial counterparts, subsurface structure (rocks, tree roots, etc.), may influence the occurrence of fossorial herpetofauna. Such substructure is often transformed by agricultural practices. Food availability may vary with land use, particularly if certain land uses employ pesticides (e.g., Sugarcane: Johnson 1987), and thus, may drive changes in fossorial herpetofaunal diversity and density. Finally, the management of tracts of land under different land uses may result in changes in fossorial herpetofaunal diversity or abundance. Numerous authors have shown that management, through the alteration of habitat structure or the addition of chemicals, can alter diversity or abundance of herpetofauna (e.g., Ford et al. 1999; Hailey 2000; Jones et al. 2000; James & M'Closkey 2003).

Our data suggest that fossorial herpetofauna may be patchy in their occurrence. A frequency plot of fossorial herpetofaunal density across the study site (Fig. 3) indicates a non-uniform or highly aggregated distribution of animals (Zar 1996). Of the five excavation sites that yielded specimens, two (40 %) produced more than one individual, which would not be expected for a low density, uniformly distributed pattern of occurrence. Kuhnz et al. (2005) found non-uniform distribution of Anniella pulchra, providing further evidence of a non-uniform distribution of fossorial herpetofauna.

Unfortunately, because of the low capture rates achieved in our survey, our analysis of the factors that may influence fossorial herpetofaunal density is not sensitive and, thus, the lack of significant predictors is not surprising.

Table 4: Comparison of fossorial herpetofauna survey methods used in this study. Method 1 involved small-scale excavations proposed by Measey et al. (2003). Method 2 involved large-scale excavations using earthmoving machinery.

Factor	Method 1	Method 2
Ecological footprint	Footprint limited to immediate site of excavation	Excavations results in large area being scarred by movement of earthmoving machinery
Size of equipment	Small equipment makes access in all habitats easy	Large equipment not practical in 'closed' habitats
Availability of equipment	Equipment easily available in remote locations	Equipment difficult to source in remote locations
Financial costs	Equipment cheap, can be operated by unskilled labour	Equipment hire expensive, requires skilled operator

Potential explanations for the non-significant result may also include our choice of factors. Alternatively, variation of soil characteristics within the substrate type may not actually influence fossorial herpetofaunal density. We recommend further standardized sampling from multiple sites, some of which should be located on other substrate types, as a means to address this question.

The two methods compared in this investigation produced very similar estimates of fossorial herpetofaunal density despite the fact that Method 2 surveyed a greater area (31 m^2 more) than Method 1. Table 4 provides a comparison of the two methods used in this investigation. The relative advantages and disadvantages make the choice of technique situation dependent. We think that while Method 2 gives investigators peace of mind in terms of the completeness of the sampling procedure through reduction of escape rates and the opportunity to sample to greater depths (although our data suggest that most organisms occur superficially in the soil profile), it carries major financial, environmental, and logistic drawbacks. We recommend the application of Method 1 for surveying fossorial herpetofauna but urge researchers to be explicit about the sampling regime used and to explicitly consider how the location of sampling sites is determined.

Finally, we recommend that quantitative fossorial herpetofaunal surveys become part of all herpetofaunal surveys. Resultant data will improve our understanding of how patterns of distribution and abundance change on spatial and temporal scales, vastly improving our ability to predict the occurrence of fossorial species and to perform accurate conservation assessments. Studies should be explicit about the scale at which they predict fossorial herpetofaunal density, as small scale surveys or biased sampling regimes may overestimate landscape scale fossorial herpetofaunal density.

ACKNOWLEDGEMENTS

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