

The distribution of two medically and agriculturally important cryptic rodent species, *Mastomys natalensis* and *M. coucha* (Rodentia: Muridae) in South Africa

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The medically and agriculturally important Natal multimammate mouse, *Mastomys natalensis* (A. Smith, 1834) and the multimammate mouse, *M. coucha* (A. Smith, 1836), are sibling species and cannot easily be distinguished morphologically. As a consequence, their respective distributional ranges across South Africa remain uncertain. Consequently, locality data of positively identified (karyotyped and/or electrophoretically determined) specimens from South Africa were collated from museum records, the literature, and recently collected material in an attempt to: 1) delimit geographic distributions using positively identified specimens; 2) predict the most likely areas of occurrence of the two sibling species using a variety of selected eco-geographic variables (EGVs) associated with verified locality data; and 3) assess both verified and predicted geographic distributions with reference to previously reported incidents of plague in South Africa. Both verified and predicted distributions are broadly similar and show a geographic separation along the eastern escarpment of South Africa that seems to be influenced by altitude and rainfall. *M. natalensis* occurs in the low altitude/high rainfall eastern coastal region, extending to northeastern South Africa, while *M. coucha* keeps to the high altitude/moderate rainfall central and northeastern South Africa. Although the two species were shown to be either sympatric or to occur in close proximity at four localities, additional research is needed to determine the zone of parapatry. Univariate and multivariate analyses showed statistically significant differences between eco-geographic characteristics of collecting localities associated with each of the two species in South Africa. The derived distributions indicate previously reported cases of plague in South Africa, to some extent, coincide with the distributional range of *M. coucha* rather than *M. natalensis*.

Key words: *Mastomys*, cryptic species, geographic distribution, plague, South Africa.

INTRODUCTION

Members of the genus *Mastomys* are small to medium-sized murid rodents and are widely distributed in Africa (Musser & Carleton 1993). Although most modern systematic reviews (e.g. Musser & Carleton 1993) of the genus recognize eight species, namely, *M. angolensis* (Bocage, 1890), *M. coucha* (A. Smith, 1836), *M. erythroleucus* (Temminck, 1853), *M. hildebrandtii* (Peters, 1878), *M. natalensis* (A. Smith, 1834), *M. pernanus* (Kershaw, 1921), *M. shortridgei* (St. Leger, 1933), and *M. verheyeni* Robbins & van der Straeten, 1989, the systematic status of the genus remains largely uncertain. This taxonomic problem is exacerbated by the presence of high levels of cytogenetic

diversity within the genus (Green *et al.* 1980; Duplantier *et al.* 1990; Granjon *et al.* 1997).

Some of the systematic problems within the genus *Mastomys* are well reviewed in a more recent systematic synthesis of the genus (Granjon *et al.* 1997) in which, for example, the authors argue about the inappropriate use of the name *hildebrandtii* for the more commonly used *hubertii* in West Africa. In addition, since the publication of the authoritative murid taxonomic synthesis by Musser & Carleton (1993), a new species, *M. awashensis*, has been described from Ethiopia, and it has been shown that *M. erythroleucus* represents a species complex, while *M. angolensis* belongs in the genus *Myomys* (Lavrenchenko *et al.* 1998; Volobouev *et al.* 2002).

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In southern Africa alone, three species, namely, *M. shortridgei*, *M. natalensis*, and *M. coucha* are recognized (Meester *et al.* 1986; Skinner & Smithers 1990; Musser & Carleton 1993; Granjon *et al.* 1997). While *M. shortridgei* has conventionally been regarded as a valid species, *M. natalensis* (*sensu lato*) was previously considered a single species until subsequent cytogenetic and protein electrophoretic studies revealed the presence of two electrophoretically distinct cytotypes ($2n = 32$ /'slow' haemoglobin electromorph and $2n = 36$ /'fast' haemoglobin electromorph) (Green *et al.* 1980; Gordon & Watson 1986). The two cytotypes have also been reported to differ in gross sperm and bacular morphology, reproductive behaviour, pheromones, and ultrasonic vocalizations (Skinner & Smithers 1990; Musser & Carleton 1993). All these differences together with the absence of hybrids in areas of sympatry strongly suggested reproductive isolation between the two chromosomal races (Gordon & Watson 1986). This led to the recognition of two cryptic species referred to the nominate species, *M. natalensis* for the $2n = 32$ cytotype and *M. coucha* for the $2n = 36$ cytotype (Meester *et al.* 1986; Skinner & Smithers 1990; Musser & Carleton 1993).

Despite the cytogenetic, electrophoretic, and a variety of other reported differences, the two cryptic species cannot easily be distinguished on qualitative external and/or cranial morphology (Gordon & Watson 1986). However, a subsequent study by Dippenaar *et al.* (1993) revealed subtle cranial morphometric differences between the two sibling species, but cautioned that such data need to be carefully evaluated before being applied due to the potential influence of geographic variation over the species' distributional ranges.

Although both *M. natalensis* and *M. coucha* are widely distributed in their combined geographic range in South Africa (Meester *et al.* 1986; Skinner & Smithers 1990; Musser & Carleton 1993), their respective distributional ranges still remain uncertain. Some members of the genus have been implicated in the epidemiology of plague (Hallett *et al.* 1970; Isaäcson *et al.* 1981), Rift Valley fever (Swanepoel *et al.* 1978), schistosomiasis (Gear *et al.* 1966). Multimammate mice also may cause extensive damage to crops and stored grain (Poulet 1980; Fiedler 1988; Leirs *et al.* 1996). Consequently, there is a need for a more reliable delimitation of geographic ranges of these problem rodents.

The present study attempts to delimit the geo-

graphic distributions of *M. natalensis* and *M. coucha* in South Africa based on locality data derived from positively identified specimens. We also attempt to predict the most likely areas of occurrence of the two species in South Africa using some eco-geographic variables (EGVs) associated with the verified locality data. The geographic distributions derived from both verified locality data and predicted distributions are in turn assessed with reference to previously reported incidents of plague in South Africa.

MATERIALS & METHODS

Data sources

Primary data emanated from karyotyped and/or electrophoretically identified specimens in the Transvaal Museum (TM), Pretoria, and the Durban Natural Science Museum (DM), Durban. These data sources were augmented with karyotyped and/or electrophoretically identified records obtained from Hallett (1977) and Smit *et al.* (2001).

Locality data

Locality data from the various sources ranged from quarter-degree square resolution to Global Positioning System (GPS)-generated geographic coordinates. Where locality names only were available, a gazetteer that specifically included degrees, minutes, and seconds to conform with GPS-derived readings was used to identify the geographic coordinates for the locality. Locality data derived from positively identified specimens were digitized onto a map of South Africa (Schulze *et al.* 1997) using IDRISI32 (Eastman 2001).

Eco-geographical data

The prediction of the most likely areas of occurrence for *M. natalensis* and *M. coucha* in South Africa was based on the selection of suitable EGVs. Consequently, the following was the rationale behind the selection of seven EGVs considered in the prediction model in this study:

1. Altitude: represents an invariant feature of the physical landscape with a major influence at the macro-, meso-, and micro-climatic scales (Schulze *et al.* 1997).
2. Mean annual precipitation: characterizes the long-term quality of water available in southern Africa (Schulze *et al.* 1997) and is considered critical to the geographic distributions of *M. natalensis* and *M. coucha* in the subregion (Bronner *et al.* 1988; Dippenaar *et al.* 1993).

3. Mean annual temperature: represents a basic climatic parameter with a direct effect on all forms of life, and is frequently used as an index of the energy status of the environment (Schulze *et al.* 1997).
4. Daily mean minimum temperature for July: July being the coldest month may represent a tolerance parameter that may be influential in the distribution of *M. natalensis* and *M. coucha*.
5. Coefficient of variation of precipitation: with an inverse relationship with mean annual rainfall may also represent a tolerance parameter.
6. Mean primary production: represents a quantification of long-term and basic environmental status under rain-fed conditions (Schulze *et al.* 1997), and incorporates rainfall, energy status of the atmosphere, vegetation, and soil characteristics (Rozenzweig 1968).
7. Potential evaporation: represents the capacity of air to take up water, its associated energy for heat up-take used in the process, and the degree of turbulence in the lower atmosphere. This creates an atmospheric demand fully met by wet soils and actively growing vegetation leading to a complete ground cover that may be influential in the distribution of the two cryptic species (Schulze *et al.* 1997).

Independence and pseudo-replication of locality data points

Locality data points for each species were superimposed on EGV maps to derive associated EGV values for spatial analysis. However, an important aspect in this digital mapping process included a consideration of the minimum distance between locality data points. This was considered necessary in order to minimize the effect of autocorrelation from closely located data points that could violate the postulate of their independence (Guisan *et al.* 2000). Consequently, to accommodate for independence and to reduce the effect of pseudo-replication, a locality data point was only considered if it occurred on an individual (30 × 30 m) raster image value.

Analysis of eco-geographic variables

Patterns of variation between eco-geographical data associated with collecting localities for each of the two sibling species were evaluated univariately using Kruskal-Wallis analysis of variance (ANOVA; Sokal & Rohlf 1981; Zar 1996), and included the computation of standard descriptive statistics. Patterns of variation were also assessed using a

priori multivariate analyses based on unweighted pair-group arithmetic average (UPGMA) cluster analysis and principal components analysis (PCA) of standardized (Sneath & Sokal 1973) eco-geographical data. UPGMA cluster analysis was based on euclidean distances, whereas PCA was computed from product-moment correlation coefficients among variables (Sneath & Sokal 1973). All statistical analyses were based on the seven selected EGVs and were accomplished using algorithms included in STATISTICA (Statsoft 1995).

Prediction of most likely areas of occurrence

The prediction of the most likely areas of occurrence of the two species was based on spatial analysis using a multi-criteria evaluation procedure and fuzzy set theory (Malczewski 1999; Guisan *et al.* 2000; Eastman 2001). A fuzzy set attempts to evaluate the vagueness in a class of elements that do not have well-defined boundaries between entities that either partly or do not belong to a class (Klir & Yuan 1995; Malczewski 1999). The procedure attempts to define descriptive variables such as small, medium, and large in terms of a base variable, the values of which are real numbers in a specific range (e.g. temperature, precipitation, and moisture) (Malczewski 1999). Consequently, the values of basic EGV statistics were used to construct sigmoidal curves, the functions of which were in turn used to define EGV ranges for each of the two sibling species in this study. These ranges consisted of:

1. Minimum EGV value;
2. The first point of inflection at the -95% confidence interval (CI);
3. The second point of inflection at the +95% CI; and
4. Maximum EGV value.

The spatial analysis in IDRISI32 was based on a multi-criteria evaluation (MCE) module that requires an allocation of a weight to each variable used in the analysis in order to reflect its relative importance (Eastman 2001). Among the various weighting methods (Guisan *et al.* 2000), this study was based on the EGV loadings derived from the PCA to allocate a weight in order to estimate each EGV's relative importance.

Species distributions and plague outbreak

The geographic distributions of the two sibling species derived from both verified locality data and predicted distributions were assessed with reference to historical incidents of plague in South

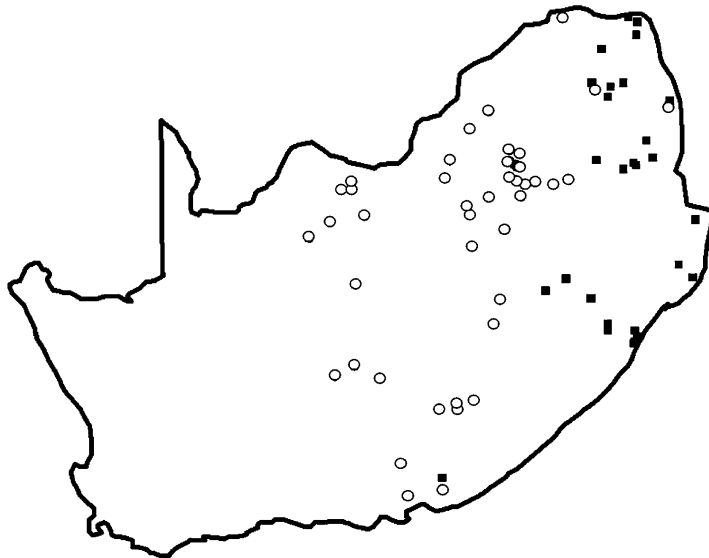


Fig. 1. Geographic distribution of *Mastomys natalensis* (■) and *M. coucha* (○) in South Africa based on cytogenetically and/or electrophoretically identified specimens.

Africa. The broader area affected by plague outbreaks in South Africa was estimated from records of previously reported cases of plague obtained from Davis (1964).

RESULTS

Geographic distributions based on positively identified specimens

Data from 3669 specimens were processed. A total of 3577 records were obtained from the Transvaal Museum's mammal collection, 253 of which included positively (karyotypically and/or electrophoretically determined) identified specimens from 61 localities in South Africa. The Durban Natural Science Museum mammal collection yielded 35 positively identified specimens from five localities. Hallett (1977) yielded 15 positively identified specimens from 15 localities, while Smit *et al.* (2001) yielded 42 specimens from two localities. Collation of all locality data based on positively identified specimens (Appendix I) yielded 77 localities in South Africa of which 31 were for *M. natalensis* and 46 were for *M. coucha*.

The geographic distributions of *M. natalensis* and *M. coucha* show a distinct pattern of segregation along the eastern escarpment of South Africa that seems to be largely influenced by altitude and rainfall (Fig. 1). *M. natalensis* occurs along the low altitude/high rainfall eastern coastal region, extending up to the northeastern corner of South

Africa. By contrast, *M. coucha* occurs in the high altitude/moderate rainfall central and northeastern parts of South Africa. The verified locality data showed the two cryptic species to be either sympatric or to occur in close proximity at four localities (Fig. 1). These localities include Pretoria and Satara (Kruger National Park) in the north-eastern part of South Africa as well as Grahams-town and the Addo Elephant Park in the Eastern Cape Province.

Assessment of eco-geographical data

Standard descriptive statistics for the seven selected EGVs for each species are summarized in Table 1. Kruskal-Wallis ANOVA showed highly statistically significant differences ($P < 0.001$) between the seven selected EGVs associated with collecting localities for *M. natalensis* and *M. coucha* in South Africa (Table 2).

A phenogram derived from a UPGMA cluster analysis based on euclidean distances showed two discrete clusters, designated A and B, which broadly coincide with an assemblage of collecting localities associated with each of the two cryptic species in South Africa (Fig. 2). With the exception of 10 (indicated by arrows on the phenogram) of the 77 analysed localities, cluster A comprises a grouping of collecting localities for *M. natalensis*, whereas cluster B consists an assemblage of collecting localities for *M. coucha* in South Africa. Of the exceptional localities, five localities repre-

Table 1. Standard statistics of seven eco-geographic variables associated with collecting localities of cytogenetically and/or electrophoretically identified specimens of *Mastomys natalensis* and *M. coucha* in South Africa. \bar{X} = arithmetic mean; S.D. = standard deviation; n = sample size; Range = observed range of variation.

Eco-geographic variable	<i>Mastomys natalensis</i>				<i>Mastomys coucha</i>			
	\bar{X}	S.D.	n	Range	\bar{X}	S.D.	n	Range
Altitude	661.8	490.0	31	16.0–1783.0	1329.4	376.33	46	182.0–1903.0
Mean annual precipitation	827.3	277.9	31	214.0–1292.0	576.5	147.44	46	303.0–987.0
Mean annual temperature	19.2	2.3	31	14.0–23.0	16.4	2.14	46	12.0–22.0
Daily mean minimum temp. for July	14.1	2.7	31	8.0–18.0	9.5	2.29	46	8.0–18.0
Coefficient of variation of precipitation	23.2	6.1	31	15.0–36.0	28.8	3.26	46	21.0–35.0
Mean primary production	8.2	2.7	31	2.2–12.8	5.7	2.05	46	1.8–9.7
Potential evaporation	1894.0	210.0	31	1274.4–2254.8	2268.5	329.33	46	1669.4–2890.8

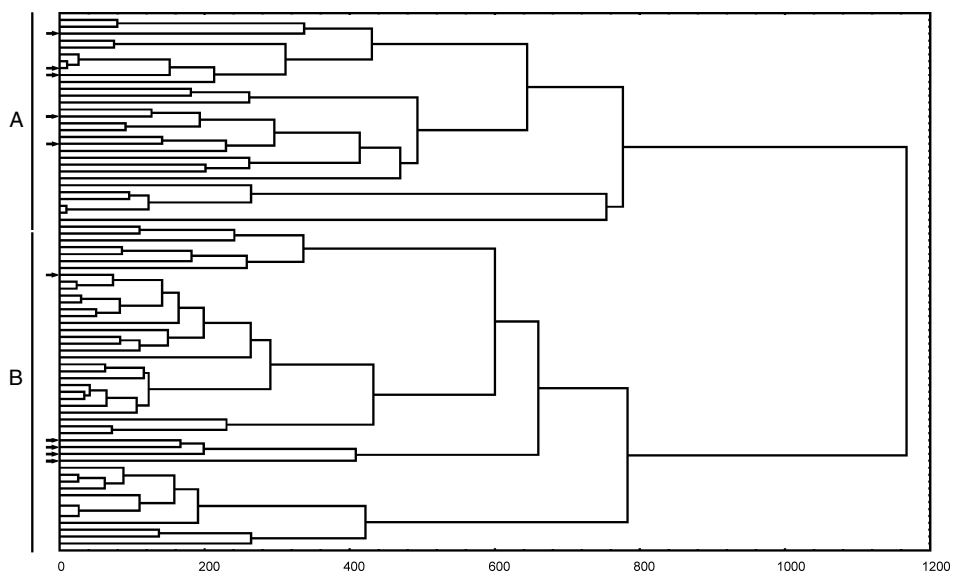
sented collecting localities for *M. natalensis*, while the remaining five represented those for *M. coucha*. All five exceptional collecting localities for *M. coucha* and one for *M. natalensis* broadly coincide with areas of potential geographic overlap between the two cryptic species in South Africa. Of the remaining collecting localities for *M. natalensis* that do not conform to the general trend, three localities are in the northeastern Drakensberg.

As in UPGMA cluster analysis, a PCA scattergram of the first two of the seven derived components broadly indicates two species-linked collecting locality assemblages (Fig. 3) that largely separate on the first PCA axis. Although there are

Table 2. H -values from a Kruskal-Wallis analysis of variance (ANOVA) of eco-geographic variables associated with collecting localities of cytogenetically and/or electrophoretically identified specimens of *Mastomys natalensis* and *M. coucha* from South Africa.

Eco-geographic variable	$H_{1,77}$
Altitude	25.58***
Mean annual precipitation	17.04***
Mean annual temperature	22.26***
Daily mean minimum temp. for July	32.46***
Coefficient of variation of precipitation	17.12***
Mean primary production	17.52***
Potential evaporation	24.44***

*** $P < 0.001$.

**Fig. 2.** Euclidean distance phenogram derived from an unweighted pair-group arithmetic average cluster analysis based on eco-geographic variables associated with collecting localities of cytogenetically and/or electrophoretically identified specimens of *Mastomys natalensis* (A) and *M. coucha* (B) from South Africa. Arrows indicate localities of uncertain placement in multivariate space.

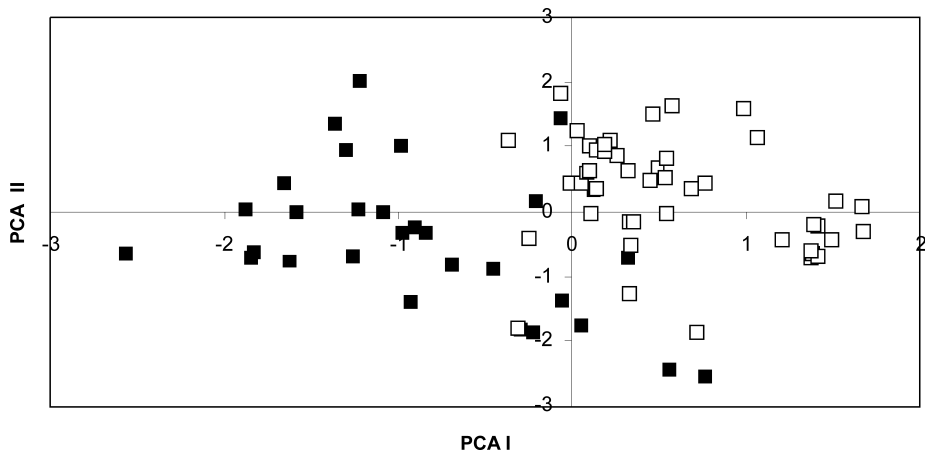


Fig. 3. Axes I and II from a principal components analysis based on eco-geographic variables associated with collecting localities of cytogenetically and/or electrophoretically identified specimens of *Mastomys natalensis* (■) and *M. coucha* (□) from South Africa.

some overlaps, these assemblages largely consist of clusters of collecting localities for *M. natalensis* and *M. coucha* in South Africa. Similar to the phenogram, the overlapping localities largely coincide with areas of potential geographic overlap between the two cryptic species in South Africa.

The first principal component, which accounts for 51% of the variance, shows that mean annual precipitation, coefficient of variation of precipitation, mean primary production, and potential evaporation account for the separation (Table 3). The second component, which is dominated by altitude, mean annual temperature, and daily mean minimum temperature for July accounts for 38% of the variance (Table 3). A consideration of principal component axes III–VII did not reveal any geographically discernible pattern with reference to the selected EGVs. Consequently, the

relative EGV loadings derived from the first two PCA axes (Table 3) were used to allocate a weight (Table 4) to estimate each EGV's relative importance in the MCE module as part of the procedure for predicting the most likely areas of occurrence of the two sibling species in South Africa.

Predictions of species distributions in South Africa

Predictions of the most likely areas of occurrence (indicated in dark shades) for both *M. natalensis* (Fig. 4) and *M. coucha* (Fig. 5) broadly coincide with the geographic distributions derived from verified locality data (circles). Apart from reflecting the generally wide distributions of the two sibling species in South Africa, the predicted distributions (Figs 4 & 5), suggest a possible zone of overlap along the eastern escarpment.

Table 3. Loadings of variables on the first two components from a principal components analysis of seven eco-geographic variables associated with cytogenetically and/or electrophoretically identified specimens of *Mastomys natalensis* and *M. coucha* in South Africa.

Eco-geographic variable	Principal components axes	
	I	II
Altitude	0.493	0.833
Mean annual precipitation	-0.888	0.388
Mean annual temperature	-0.310	-0.913
Daily mean minimum temp. for July	-0.580	-0.799
Coefficient of variation of precipitation	0.893	-0.378
Mean primary production	-0.851	0.386
Potential evaporation	0.742	-0.206
% Trace	51.0	38.0

Table 4. Highest loadings of variables (regardless of statistical sign) on either the first or the second components (*cf.* Table 3) from a principal components analysis of seven eco-geographic variables (EGV) associated with cytogenetically and/or electrophoretically identified specimens of *Mastomys natalensis* and *M. coucha* in South Africa. The sum of these EGV loadings standardized to unity was used to allocate a weight to estimate each EGV's relative importance for the multi-criteria evaluation spatial analysis module in IDRISI32 (Malczewski 1999; Guisan *et al.* 2000; Eastman 2001).

Eco-geographic variable	Highest PCA I/II loading	Relative weighted score
Altitude	0.833	0.141
Mean annual precipitation	0.888	0.150
Mean annual temperature	0.913	0.154
Daily mean minimum temp. for July	0.799	0.135
Coefficient of variation of precipitation	0.893	0.151
Mean primary production	0.851	0.144
Potential evaporation	0.742	0.125
Total	5.919	1.000

Species distributions and incidence of plague in South Africa

Geographic distributions based on both verified locality data and predicted distributions show that previously reported cases of plague, to an extent, coincide with the distributional range of *M. coucha* rather than *M. natalensis* in South Africa (Fig. 6). Exceptional areas include the northeastern parts of South Africa that have records of *M. coucha* but no historical records of plague as reported by Davis (1964), and the western parts that have no

records of *M. coucha* but have previously reported incidents of plague.

DISCUSSION

The geographic distributions of *M. natalensis* and *M. coucha* in South Africa based on both verified locality data and predicted distributions show a distinct pattern of segregation along the eastern escarpment. Although other potentially influential factors may be involved, this distributional pattern seems to be largely influenced by alti-

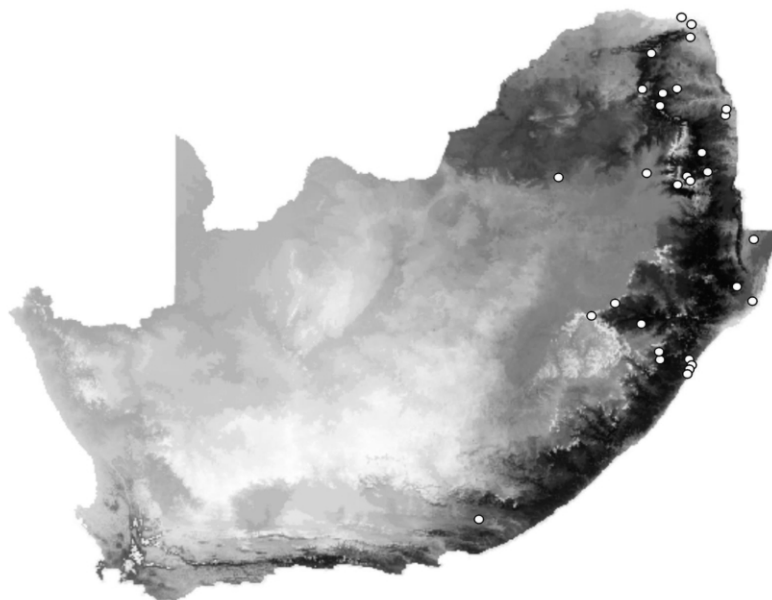


Fig. 4. The most likely areas of occurrence (darker shading) of *Mastomys natalensis* in South Africa predicted from eco-geographic variables associated with collecting localities of cytogenetically and/or electrophoretically identified specimens (O) using a multi-criteria evaluation spatial analysis module in IDRISI32 (Malczewski 1999; Guisan *et al.* 2000; Eastman 2001).

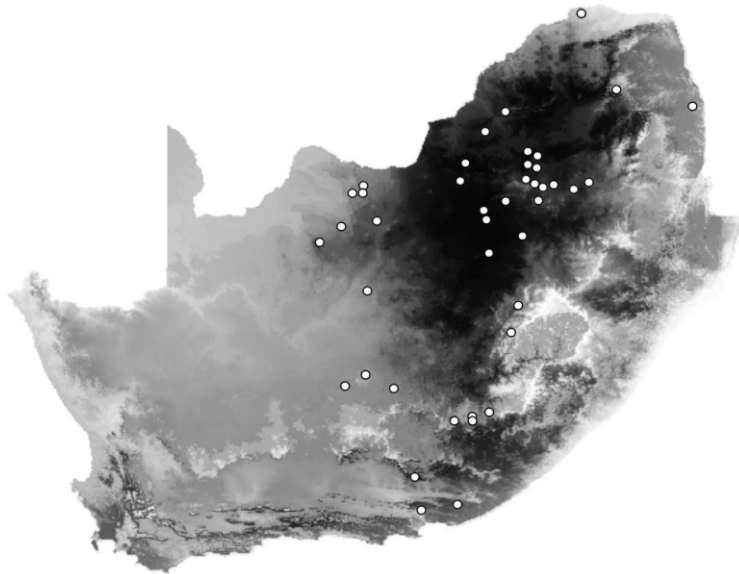


Fig. 5. The most likely areas of occurrence (darker shading) of *Mastomys coucha* in South Africa predicted from eco-geographic variables associated with collecting localities of cytogenetically and/or electrophoretically identified specimens (○) using a multi-criteria evaluation spatial analysis module in IDRISI32 (Malczewski 1999; Guisan *et al.* 2000; Eastman 2001).

tude and rainfall as suggested by previous studies (Bronner *et al.* 1988; Dippenaar *et al.* 1993). *M. natalensis* occurs along the low altitude and high rainfall eastern coastal region, extending up to the northeastern corner of South Africa, while

M. coucha occurs in the high altitude and moderate rainfall areas in the central and northeastern parts of South Africa.

Distributions based on both positively identified specimens and predicted distributions are similar.

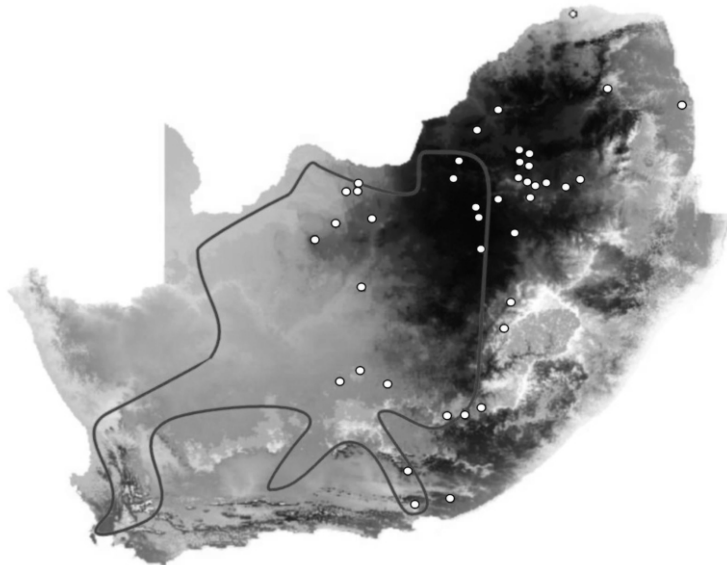


Fig. 6. The broader area (enclosed) historically affected by plague outbreaks in South Africa estimated from records of previously reported cases of plague obtained from Davis (1964). The area is superimposed on the geographic distribution of *Mastomys coucha* in South Africa based on both cytogenetically and/or electrophoretically identified specimens (○) as well as its predicted most likely area of occurrence (darker shading).

It is possible that this conclusion could be considered a circular argument in that eco-geographic parameters of the known localities were used to predict the distribution where there are no positively identified specimens. Nevertheless, we consider that the approach ultimately advances a hypothesis that can be used to iteratively seek specimens from within the projected range to test the hypothesis.

Distributions based on verified locality data showed the two species to be either sympatric or to occur in close proximity around Pretoria and Satara (Kruger National Park) in the north, as well as Grahamstown and Addo Elephant Park in the southeastern part of the Eastern Cape Province. In contrast, the predicted distributions strongly suggest a continuous zone of overlap along the eastern escarpment. To some extent, this predicted zone of overlap seems to be supported by multivariate analyses where overlapping localities in UPGMA cluster analysis and PCA largely coincided with areas of potential geographic overlap between the two cryptic species. However, additional data from this potential zone of overlap are needed to determine the specific zone of parapatry between the two cryptic species in South Africa.

Although altitude and rainfall may be influential in the distributions of the two sibling species in South Africa, the PCA provided an insight into the relative importance of the selected EGVs. Important EGVs included altitude, mean annual precipitation, mean annual temperature, daily mean minimum temperature for July, coefficient of variation of precipitation, mean primary production, and potential evaporation. Of interest is that mean annual precipitation and coefficient of variation of precipitation show an inverse relationship since areas of high rainfall have low rainfall variability and vice versa (Schulze *et al.* 1997). It may, therefore, be inferred that *M. natalensis* prefers areas of high annual rainfall but with low variability, while *M. coucha* prefers areas of low annual rainfall but with high variability, or alternatively, it could be a case of avoidances rather than preferences of specific areas by the two sibling species in South Africa. However, questions relating to the finesse and the ecological relevance of the difference between avoidance of some areas or a preference for others needs to be investigated further.

Of additional interest is that potential evaporation was one of the eco-geographic variables

identified by PCA to be influential in the distribution of the two cryptic species in South Africa. Given the high average potential evaporation value associated with collecting localities for *M. coucha*, which is almost double that of collecting localities for *M. natalensis*, it is possible that *M. coucha* is affected more by desiccation. This, together with the lower mean annual temperature associated with collecting localities for *M. coucha* suggest that the species is more likely to be affected by drought than *M. natalensis*. This, however, requires further investigation, particularly under controlled laboratory conditions.

Given these likely preferred conditions, it is interesting to note that the delineated distributional ranges of the two sibling species in South Africa are associated with specific vegetation types. The predicted distributional limits of *M. natalensis*, for example, seem to coincide with the savanna/grassland (Rutherford & Westfall 1986; Low & Rebelo 1996) transitional zone. Interestingly, Smit *et al.* (2001) noted that *M. natalensis* seems to occupy the warm, moist savanna regions, while the grassland regions appear to predominantly support *M. coucha*. In so far as altitude is concerned, the central part of South Africa, which represents the central plateau, seems to be dominated by *M. coucha*. A similar preference for high altitude by *M. coucha* exists in the central and northern highlands of Zimbabwe (Gordon 1978).

An important aspect of this study included an interpretation of the distributions of *M. natalensis* and *M. coucha* derived from both verified locality data and predicted distributions with reference to previously reported incidents of plague in South Africa. Davis (1964) indicated that the interior plateau within the escarpment has previously been affected by plague. Taxa implicated in such outbreaks include rodents of the subfamily Gerbillinae and fleas of the subfamily Xenopsyllinae, which act as a host to the plague parasite, *Yersinia pestis* (Davis 1964).

However, among members of the subfamily Gerbillinae, it is only the Namaqua gerbil, *Desmodillus auricularis* and the highveld gerbil, *Tatera brantsii*, whose distributions broadly coincide with areas that have historically been affected by plague outbreaks. Consequently, Davis (1964) suggested that *M. natalensis* (*sensu lato*) may act as the important link between gerbils and humans. Nevertheless, it should be noted that plague is a vector-transmitted disease, so that at least the vectors (fleas) must also be present, and moreover,

the presence of plague in other rodents, especially *Tatera*, is well documented in South Africa.

Following the discovery of the two sibling species within *Mastomys* and their delimited geographic boundaries in this study, it seems that apart from other taxa, *M. coucha* may also play a role in plague outbreaks in South Africa. Since the discovery of the two sibling species, Isaacs *et al.* (1981) demonstrated that *M. coucha* is susceptible, while *M. natalensis* is resistant to *Y. pestis* infection. However, it is of particular interest that *M. coucha* occurs in some parts of South Africa that have no historical records of plague, while it is absent in other areas (where gerbils occur) where incidents of plague have previously been reported. This suggests that either a complex of taxa are involved in the epidemiology of plague in South Africa, or that populations of *M. coucha* in areas with no records of plague do not attain infectious levels. Of particular relevance, however, care needs to be taken when addressing questions relating to why areas with no plague exist because it may not necessarily follow that the absence of evidence is evidence of absence. In addition, it is possible that stochastic processes may play a role in causing a pathogen to appear (or disappear) in an area, leading to instantaneous and to some extent, stochastic conditions to determine whether an infection persists locally.

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Appendix 1

Cytogenetically and/or electrophoretically identified specimens of *Mastomys natalensis* and *M. coucha* from South Africa used in the study, and a gazetteer of their collecting localities given in decimal format. Data sources included the Transvaal Museum (TM), Pretoria, the Durban Natural Science Museum (DM), Durban, and records from Hallett (1977) and Smit *et al.* (2001).

Mastomys natalensis: (1) (22.30 S; 30.86 E) (TM 44226); (2) (22.43 S; 31.07 E) (TM 41651); (3) (22.72 S; 31.03 E) (TM 36669); (4) (23.05 S; 30.22 E) (TM 40774); (5) (23.83 S; 30.03 E) (TM 36671); (6) (23.83 S; 30.75 E) (Hallett 1977); (7) (23.92 S; 30.45 E) (Hallett 1977); (8) (24.17 S; 30.38 E) (Hallett 1977); (9) (24.25 S; 31.83 E) (TM 36655); (10) (24.38 S; 31.78 E) (TM 36655); (11) (25.18 S; 31.28 E) (TM 36656); (12) (25.58 S; 31.43 E) (Hallett 1977); (13) (25.63 S; 30.12 E) (TM 40911); (14) (25.70 S; 30.97 E) (TM 41749); (15) (25.73 S; 28.22 E) (TM 40394); (16) (25.77 S; 31.05 E) (TM 44306); (17) (25.86 S; 30.75 E) (TM 44367); (18) (27.04 S; 32.42 E) (TM 44668); (19) (28.07 S; 32.03 E) (TM 43340); (20) (28.38 S; 32.36 E) (TM 45336); (21) (28.41 S; 29.42 E) (TM 44437); (22) (28.42 S; 29.43 E) (TM 39207); (23) (28.68 S; 28.93 E) (DM 2404); (24) (28.85 S; 30.00 E) (DM 2403); (25) (29.47 S; 30.38 E) (DM 6755); (26) (29.60 S; 30.38 E) (TM 37767); (27) (29.60 S; 31.02 E) (TM 38706); (28) (29.75 S; 31.07 E) (Smit *et al.* 2001); (29) (29.87 S; 31.00 E) (TM 32389); (30) (29.92 S; 30.98 E) (TM 38666); (31) (33.03 S; 26.53 E) (DM 5061).

Mastomys coucha: (32) (22.33 S; 29.32 E) (TM 45434); (33) (24.02 S; 30.07 E) (TM 43335); (34) (24.40 S; 31.78 E) (TM 36670); (35) (24.50 S; 27.62 E) (TM 34279); (36) (24.93 S; 27.15 E) (TM 45491); (37) (25.40 S; 28.10 E) (TM 45211); (38) (25.50 S; 28.33 E) (TM 41008); (39) (25.65 S; 26.70 E) (TM 42045); (40) (25.68 S; 28.09 E) (TM 44187); (41) (25.75 S; 28.25 E) (TM 44927); (42) (25.78 S; 28.28 E) (TM 39263); (43) (25.78 S; 28.33 E) (TM 43337); (44) (26.02 S; 28.08 E) (TM 29029); (45) (26.06 S; 26.60 E) (TM 45500); (46) (26.10 S; 29.48 E) (TM 42408); (47) (26.12 S; 28.25 E) (Hallett 1977); (48) (26.15 S; 28.68 E) (TM 29190); (49) (26.17 S; 24.42 E) (TM 29186); (50) (26.22 S; 28.45 E) (TM 42447); (51) (26.23 S; 29.12 E) (DM 5408); (52) (26.33 S; 24.17 E) (TM 29202); (53) (26.33 S; 24.42 E) (TM 29004); (54) (26.50 S; 28.35 E) (TM 41856); (55) (26.52 S; 27.61 E) (Smit *et al.* 2001); (56) (26.72 S; 27.10 E) (TM 41857); (57) (26.92 S; 27.17 E) (TM 45017); (58) (27.08 S; 23.92 E) (Hallett 1977); (59) (27.28 S; 27.97 E) (Hallett 1977); (60) (27.43 S; 23.43 E) (Hallett 1977); (61) (27.44 S; 23.43 E) (TM 44467); (62) (27.45 S; 23.43 E) (TM 44466); (63) (27.67 S; 27.23 E) (TM 29193); (64) (28.52 S; 24.52 E) (Hallett 1977); (65) (28.88 S; 27.88 E) (TM 29002); (66) (29.45 S; 27.72 E) (TM 29228); (67) (30.43 S; 24.47 E) (Hallett 1977); (68) (30.65 S; 24.02 E) (TM 32356); (69) (30.73 S; 25.10 E) (TM 32356); (70) (31.25 S; 27.25 E) (TM 32321); (71) (31.33 S; 26.87 E) (TM 32319); (72) (31.45 S; 26.88 E) (TM 32320); (73) (31.45 S; 26.45 E) (TM 32367); (74) (32.72 S; 25.58 E) (TM 32323); (75) (33.32 S; 26.53 E) (TM 29207); (76) (33.45 S; 25.73 E) (TM 32359); (77) (25.73 S; 33.45 E) (Hallett 1977).