Distribution patterns of land snails in Ugandan rain forests support the existence of Pleistocene forest refugia

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ABSTRACT

Aim We investigated whether the biogeographical patterns expected if the East African fauna was affected by cycles of contraction to refugia and expansion of ranges, as has been previously hypothesized, can be found in the land snail fauna of rain forests in Uganda.

Location The Albertine Rift region and the Lake Victoria forest belt in Uganda.

Methods Snails and slugs were sampled in 60 plots in 13 rain forests, and small species were extracted from 5-L leaf litter samples. Relative species richness was calculated by rarefaction. The influence of putative determinants of species richness was examined by bivariate correlation and multiple regression. Clustering and nestedness were tested by Monte Carlo simulations with a null model that considers the range size distribution, the species richness distribution of the forests, and the spatial autocorrelation of the occurrences of each species. Biotic elements were determined by model-based Gaussian clustering.

Results A total of 169 land snail species were recorded from 13 Ugandan rain forests. Relative species richness increases with rainfall and altitude, and decreases with evaporation and distance from the putative East Congolian refugia. Mean annual rainfall and distance from the putative East Congolian refugia were included in the best multiple regression model. The distribution areas of the Ugandan land snails are significantly clustered. Two montane, two lowland and a northern biotic element were found. The mean range extension increases with increasing distance from the putative East Congolian refugia. Moreover, the ranges of the Ugandan land snails are significantly nested. The centre of the sets of nested subsets is in the Virunga Mountains, close to the putative East Congolian refugia.

Main conclusions The decrease of diversity with increasing distance from the putative East Congolian refugia, the clustering and nestedness of ranges, and the range size increase with increasing distance from the refugia indicate that the East African land snail fauna was affected by cycles of contraction to refugia and expansion of ranges. The significant clustering and nestedness cannot be explained by current environmental conditions. Given the environmental history, it can be supposed that the lowland elements expanded post-glacially, whereas the ranges of the montane species are probably currently contracting.

Keywords Biogeography, biotic elements, land snails, nestedness, Rapoport effect, refuge theory, species diversity, Uganda, vicariance.
INTRODUCTION

Refuge theory assumes that the recent distribution of organisms is influenced by past, usually Pleistocene, environmental changes that resulted in the contraction of ranges into refugia or the expansion of ranges from refugia (Haffer, 1969, 1982, 1997; Mayr & O’Hara, 1986). Refugia are areas that are less affected by environmental changes than the surrounding regions, so that organisms that become extinct elsewhere can survive there. Moreover, it has often been assumed that the contraction of ranges into refugia resulted in speciation by vicariance (Haffer, 1969, 1982, 1997; Mayr & O’Hara, 1986). The existence and importance of Pleistocene refugia in the northern continents, which were heavily affected by Pleistocene glaciations, is universally accepted. However, the existence and role of refugia in the tropics remains controversial (Nichol, 1999; Smith et al., 2005; Noonan & Wray, 2006).

Usually the existence of refugia has been inferred only from the recent distributions of species richness and endemic species. However, several other patterns in the distribution of organisms are expected to emerge if retraction to refugia and expansion from refugia are processes that affect recent biogeography. Such patterns include the clustering of ranges (Hausdorf & Hennig, 2004), the nestedness of ranges (Hultén, 1937; Daubenmire, 1975; Hausdorf & Hennig, 2003a), and an increase of average range extension with increasing distance from the refugia (a Rapoport effect: Pfenniger, 2004; Hausdorf, 2006).

We investigated whether the patterns expected if the fauna was affected by cycles of contraction to refugia and expansion of ranges can be found in the land snail fauna of rain forests in the Albertine rift region in Uganda. We did not consider the potential role of refugia in speciation. Land snails are good model organisms for historical biogeography because they are poor active dispersers that might reflect historical patterns better than mammals or flying insects. The Albertine rift region is especially suitable for such a study because Pleistocene refugia and post-glacial recolonization of adjacent areas have been proposed for this region (Hamilton, 1976; Diamond & Hamilton, 1980; Struhsaker, 1981; Crowe & Crowe, 1982; Rodgers et al., 1982; Kingdon, 1990; Maley, 1996, 2001; Tattersfield, 1996; Grubb, 2001; Linder, 2001) and because it is one of the centres of high biodiversity in Africa (Pomeroy, 1993).

MATERIALS AND METHODS

Study area and sampling

We sampled 60 plots, each 20 m × 20 m, in 13 forests within protected areas along the Albertine Rift Valley and in the forest belt around Lake Victoria in Uganda (Fig. 1, Table 1). Plots were selected so that diverse aspects within a forest were covered and according to accessibility. The number of plots varied among forests, as some sites considered in the sampling plan could not be visited because of heavy rainfall during the study period or because of political instability. Most plots were in primary forest that had no more than limited selective cutting. However, the plots in the Mabira and Bugoma forests were situated in recreation forest and in heavily encroached forest patches, respectively, and sampling in Maramagambo Forest was carried out in colonizing forest. Sampling was carried out in March and April 2006, during the rainy season, when snails and slugs are most active. A combination of visual searching and sorting a standardized volume of litter is the most efficient method for land snail inventories, if repeated visits to sites are not possible (Emberton et al., 1996; Cameron & Pokryszko, 2005). Thus, we collected all living slugs and snails as well as their empty shells for 2 h at each plot, and in addition collected c. 5 L of surface leaf litter and soil into plastic bags for later sampling. The litter samples were dried, fractioned by sieving, and sorted. More details of the sampling plots and lists of the sampled species will be published elsewhere (Wronski & Hausdorf, in preparation).

The material will be kept in the Zoological Museum at the University Hamburg in Germany. A reference collection has been deposited at the Zoological Museum of Makerere University, Kampala, in Uganda.

Measuring species richness

In order to survey the land snail fauna of a forest exhaustively it is certainly insufficient to sample a few plots (Cameron & Pokryszko, 2005). Therefore, we standardized species richness to account for the number of sampled specimens in a forest. We used the approach proposed by Prendergast et al. (1993) to calculate relative species richness. First, the number of specimens was rarefied for each pair of forests to the lower number collected in one of the forests using EcoSim ver. 7 (Gotelli &
A pairwise measure of relative species richness, corrected for sampling effort, of forest A compared with forest B is calculated as the number of species expected in A divided by that expected in B for the same number of specimens. The overall index of relative species richness for a forest is then calculated as the geometric mean of all such pairwise values.

### Putative determinants of species richness

We tested seven abiotic variables as potential determinants of species richness (Table 2), namely mean annual rainfall, mean monthly evaporation (averaged over the year; calculated estimates from meteorological data and corrected evaporation-pan data), mean annual maximum temperature (the three climatic parameters were taken from the Atlas of Uganda, Uganda Department of Land and Surveys, 1967), forest area (mainly from Howard et al., 2000), soil pH (from Langdale-Brown et al., 1964), mean altitude (measured with GPS), and shortest distance from the putative East Congolian refugia (Fig. 1) as shown in the reconstructions of Hamilton (1976): fig. 1 and Maley, 1996: fig. 5, 2001: fig. 5) (see also Jolly et al., 1997), using bivariate correlation and multiple regression analyses. We chose the best multiple regression model among all subsets of variables based on the Akaike information criterion, as well as on leave-one-out cross-validation (squared loss) (Hastie et al., 2001).

### Tests for clustering of distribution areas

We applied the test for clustering proposed by Hausdorf & Hennig (2003b) and Hennig & Hausdorf (2004) to the species × forests matrix. As dissimilarity measure between the ranges of the examined taxa we used the geco coefficient (Hennig & Hausdorf, 2006), which takes the geographic distances between the occurrences of the taxa into account and is robust against incomplete sampling:

\[
d_C(A,B) = \frac{1}{2} \left( \frac{\sum_{a \in A \cap B} \min_{b \in B} \delta(a,b)}{|A|} + \frac{\sum_{b \in B \cap A} \min_{a \in A} \delta(a,b)}{|B|} \right).
\]

A, B ⊆ R denote the distribution areas of two taxa and are subsets of the set of geographic units of the study region R. 

### Table 2  Bivariate relationships between relative land snail species richness and abiotic variables of forests. n = 13 for all analyses.

<table>
<thead>
<tr>
<th>Variable</th>
<th>r</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean annual rainfall (mm)</td>
<td>0.694</td>
<td>0.008</td>
</tr>
<tr>
<td>Mean annual maximum temperature (°C)</td>
<td>−0.359</td>
<td>0.057</td>
</tr>
<tr>
<td>Mean monthly evaporation (mm)</td>
<td>−0.571</td>
<td>0.041</td>
</tr>
<tr>
<td>Mean altitude (m)</td>
<td>0.598</td>
<td>0.031</td>
</tr>
<tr>
<td>Acidity (pH)</td>
<td>−0.491</td>
<td>0.088</td>
</tr>
<tr>
<td>Area (km²)*</td>
<td>0.141</td>
<td>0.645</td>
</tr>
<tr>
<td>Distance from refugia (km)*</td>
<td>−0.563</td>
<td>0.045</td>
</tr>
</tbody>
</table>

*log₁₀-transformed.
is the number of geographic units of \( A \). \( d_R \) can be defined as the geographic distance between geographic units. \( u \) is a monotone increasing transformation with \( u(0) = 0 \). For geographical distances we used the following transformation \( u \) that weights down the differences between large distances:

\[
u(d) = u_f(d) = \left\{ \begin{array}{ll}
\frac{d - d_R}{d_R} & : d \leq f \ max d_R \\
0 & : d > f \ max d_R
\end{array} \right. \quad 0 \leq f \leq 1.
\]

That is, \( u_f \) is linear for distances smaller than \( f \) times (we set \( f = 0.1 \)) the diameter (maximum geographical distance) of the considered region \( R \), and larger geographical distances are treated as ‘very far away’, encoded by \( u_f = 1 \). The geco coefficient is a generalization of the Kulczynski dissimilarity, which is obtained with \( f = 0 \) and \( u_f(0) = 0 \) (see Hennig & Hausdorf, 2006).

Clustering of ranges means that dissimilarities between ranges of the same cluster are small, whereas the distances between ranges of different clusters are large. The variation of distances of a homogeneously distributed set of ranges is expected to be lower, as there is no clear distinction between ranges that belong together and ranges that should be separated. Therefore, we use the ratio between the sum of the 25% smallest and the sum of the 25% largest geco distances between the ranges of the examined taxa as test statistic \( T \). This statistic is expected to be smaller for clustered data than for homogeneously data.

We investigated whether the observed degree of clustering of ranges can be explained completely by the range size distribution, the varying number of taxa per forest, and the spatial autocorrelation of the occurrences of each taxon using a Monte Carlo simulation to approximate the distribution of the test statistic under the null hypothesis.

The null model used in the Monte Carlo simulation should simulate the case in which all inhomogeneities of the data can be attributed to varying range sizes, to varying numbers of taxa per geographic unit, and to the spatial autocorrelation of the occurrences of a taxon. We applied a null model in which all ranges are generated independently according to the same probabilistic routine. This routine yields ranges in such a way that the distribution of the number of forests per range approximates the actual distribution of the number of forests per range, the richness distribution of the forests approximates the actual richness distribution of the forests, and the tendency to form disjunct areas is governed by a parameter that is estimated from the real data set. Computational details have been described elsewhere (Hausdorf & Hennig, 2003a; Hennig & Hausdorf, 2004).

If there is significant clustering of distribution areas, biotic elements – i.e. clusters of taxa with similar ranges – are determined using model-based Gaussian clustering with a noise category as implemented in the software \textsc{mclust} (Fraley & Raftery, 1998; see also Hausdorf & Hennig, 2003b), because this method provides decisions about the number of meaningful clusters and the number of points that cannot be assigned adequately to any biotic element (noise category). Model-based Gaussian clustering operates on a data set where the cases are defined by variables of metric scale. We therefore performed a non-metric multidimensional scaling (NMDS; Kruskal, 1964) on the matrix of geco distances. Furthermore, \textsc{mclust} requires an initial estimation of noise, that is, points that do not fit in any cluster, which was carried out using the software \textsc{nnclean} (Byers & Raftery, 1998) as suggested by Fraley & Raftery (1998). As tuning constant (the number of nearest neighbours taken into account) for \textsc{nnclean} we chose \( k = \) number of species \( 40^{-1} \), rounded up to the next integer. Four NMDS dimensions were used.

**Tests for nestedness of distribution areas**

The cases in which the occurrences of a species in the 13 forests form a subset of the occurrences of another species, that is, the number of supersets, is used as a test statistic for nestedness following Hausdorf & Hennig (2003a). Several other test statistics for nestedness have been proposed (for a review see Wright \textit{et al.}, 1998). All these test statistics assume that there is only a single set of nested subsets; however, the number of supersets is also appropriate as a test statistic, if there is more than one set of nested subsets (see also the discussion in Hausdorf & Hennig, 2007). This is especially possible if a larger region is considered (as in the present study) and there are several separate centres of endemism (e.g. the Pyrenees, the Alps and the Carpathian Mountains in the study of Hausdorf & Hennig, 2003a). For \( n \) species, all \( n \times (n - 1)/2 \) pairs are screened for supersets. If two ranges are identical, this is not treated as if one species range was a superset of the other. The distribution of the test statistic under the null hypothesis is approximated by a Monte Carlo simulation. Using the null model outlined in the description of the test for clustering, we investigated whether the observed degree of nestedness of ranges can be explained completely by the range size distribution, the varying number of species per forest and the spatial autocorrelation of the occurrences of each species. Conventional null models that have been used for tests for nestedness (for a review see Wright \textit{et al.}, 1998) do not consider well-known ecological patterns. Thus, the null hypothesis is often rejected in tests of nestedness, although the observed degree of nestedness is the result of other well-known ecological patterns and processes (Hausdorf & Hennig, 2007; Moore & Swihart, 2007). Here we use a null model that considers the spatial autocorrelation of the occurrences of each species, because spatial autocorrelation is a prominent pattern (Legendre, 1993), especially at a biogeographical scale, and its neglect might result in the rejection of the null hypothesis in cases in which the observed degree of nestedness can be explained by the spatial autocorrelation alone.

We used the index of nestedness (Hausdorf & Hennig, 2003a) to visualize the spatial distribution of the sets of nested subsets. The index of nestedness \( (n) \) is defined as the average of the \( p_i \) values of all species present in sample \( j \), where \( p_i \) is the number of supersets, that is, the cases in which the occurrences of a species \( i \) form a subset of the occurrences of another species. Again, identical ranges are not counted as subsets or
supersets of each other. The index of nestedness increases towards the geographic centres of the sets of nested subsets.

Tests for Rapoport effects

A correlation between range extension in the direction away from the refugia and the distance from the refugia would be a Rapoport effect in the wide sense as defined by Stevens (1996). To test for such an effect, arithmetic means of the range extensions in the direction away from the refugia of all species occurring in the same distance zone in any direction away from the refugia [width 0.2 \( \log_{10} \) distance from refugia (km)] are plotted against distance from the refugia, and the range extension of each species in the direction away from the refugia is plotted against the midpoint of the range. Distances and range extensions have been log-transformed.

Software

Most calculations were made with the statistical software R. The tests for nestedness and clustering as well as the method for the delimitation of biotic elements were implemented in the program package PRACCLUS, which is an add-on package for R. These programs are available at http://cran.r-project.org.

RESULTS

Relationship between species richness and environmental parameters

In total we recorded 168 land snail species in the 13 investigated rain forests in the Albertine Rift Valley and the Lake Victoria forest belt in Uganda (Fig. 1). The most species-rich families were Streptaxidae (43 species), Subulinidae (38 species) and Urocyclidae (29 species). Bivariate correlation analyses revealed that the relative species richness of Ugandan forests for land snails significantly increases with mean annual rainfall and altitude (actually, the relationship with altitude is hump-shaped with an increase up to c. 2000 m altitude and a decrease at higher altitudes) and decreases with mean monthly evaporation and distance from the putative East Congolian refugia (Table 2, Fig. 2a). Moreover, there is an only marginally non-significant negative correlation with mean annual maximum temperature and soil pH. Species richness measured as the number of species in zones in a direction away from the refugia cannot be explained by varying sampling intensity. In the five distance zones considered, 14, 9, 22, 5, 10 plots (in order of increasing distance from the putative refugia) were sampled, respectively. Thus, we would expect a maximum of the number of species at medium distances from the refugia based on sampling intensity alone, rather than a monotonous decline with increasing distance from the refugia.

The best multiple regression model according to the Akaike information criterion (AIC) as well as according to leave-one-out cross-validation (squared loss) includes mean annual rainfall and distance from the putative East Congolian refugia (\( R^2 = 0.5777 \), F-statistic: 6.839 on 2 and 10 d.f., \( P = 0.0134 \)). The AIC of the best model with the two mentioned variables is lower (−41.26) than that of the best model with one (−41.26; mean annual rainfall) or three (−41.28) variables. The squared loss value is also smaller for two variables (0.0443) than for one (0.0448) or three (0.0778) variables.

Tests for clustering of distribution areas

The test statistic \( T \) of the tests for the clustering of distribution areas, the ratio of the sum of the 25% smallest geco distances to the sum of the 25% largest distances between the species ranges, is significantly smaller than would be expected under the null model (\( P = 0.001 \)). The test indicates that the
distribution areas of the Ugandan land snail species are significantly clustered.

Biotic elements, groups of species with similar ranges, were determined with model-based Gaussian clustering. Although the clustering is significant, 90 of the 168 Ugandan land snail species were included in the noise component. The remaining species were assigned to the following five biotic elements (Fig. 3): an element restricted to the montane forests above c. 1500 m altitude (Bwindi, Echuya, Mgahinga; 34 species), another montane element centred in Mgahinga forest (18 species), a widespread lowland element that occurs up to c. 1700 m altitude (11 species), another widespread lowland element restricted to altitudes below 1500 m (seven species), and a northern element found only in Semliki, Mabira and Budongo (nine species).

Tests for nestedness of distribution areas

There are 4495 cases in which the range of a Ugandan land snail species is a subset of the range of another species. The observed number of supersets is significantly higher than those obtained in 1000 Monte Carlo simulations (2978–4899 supersets were observed, mean 3945.97). Thus, the test indicates that the ranges of the Ugandan land snail species are significantly nested ($P = 0.031$). The centre of the sets of nested subsets is in the Virunga Mountains (Mgahinga forest) in the south-west of the study area (Fig. 4), close to the putative East Congolian refugia. Nestedness remains significant if the montane elements are omitted ($P = 0.039$; there are 2234 supersets in the real data, whereas 1357–2482 were counted in 1000 Monte Carlo simulations, mean 1884.90).

Tests for Rapoport effects

The mean range extension of land snail species increases with increasing distance from the putative East Congolian refugia (Fig. 5a). There is also a significant positive correlation between the range extension of land snail species in the direction away from the putative East Congolian refugia and the midpoint of the range in the study area in Uganda (Fig. 5b; Spearman’s rank correlation coefficient $r_s = 0.803$, two-sided, $P = 0.000$).

DISCUSSION

If the fauna of an area was affected by cycles of contraction to refugia and expansion of ranges, diversity should decrease with increasing distance from refugia, ranges of organisms should be clustered (Hausdorf & Hennig, 2004) and nested (Hultén, 1937; Daubenmire, 1975; Hausdorf & Hennig, 2003a), and range size should increase with increasing distance from the refugia (the Rapoport effect; Plenninger, 2004; Hausdorf, 2006).

Actually, the relative species richness of Ugandan land snails decreases significantly with increasing distance from the putative East Congolian refugia (Table 2, Fig. 2). Such a correlation has also been found for Ugandan anthropoid primates (Struhsaker, 1981) and ferns (Lwanga et al., 1998) and for East African forest mammals (Rodgers et al., 1982). The distance from the putative East Congolian refugia is also included in the best multiple regression model.

The ranges of land snails in the study region in Uganda are significantly clustered, as predicted by the refuge theory. A biotic element analysis identified five clusters that can be grouped into montane and lowland elements, as is the case for most other African organisms (Hamilton, 1976). A cluster analysis of the land snail fauna revealed two montane elements centred in the Virunga Mountains in the south-west of the study area, two widespread lowland elements, and a northern...
The percentage of species that could not be classified in biotic refugia (Hamilton, 1976; Kingdon, 1990; Maley, 1996, 2001). The clustering of ranges cannot simply be explained by current environmental conditions, because the species richness of the sites is considered in the null model. The differentiation of lowland and montane elements fits the hypothesis that there were separate lowland and montane refugia (Hamilton, 1976; Kingdon, 1990; Maley, 1996, 2001). The percentage of species that could not be classified in biotic elements and that were included in the noise component, that is, species that apparently have idiosyncratic distribution patterns, is higher (54%) than in comparable studies of north-west European (Hausdorf & Hennig, 2004) and Mediterranean (Hausdorf & Hennig, 2006) land snails. This might be an artefact arising from the fact that knowledge of the distribution of land snails in Uganda is less complete than that in north-west Europe and the investigated Mediterranean regions.

Furthermore, the refuge theory predicts that the biota in regions more distant from a refugium will be subsets of the biota closer to the refugium. In fact, the ranges of the Ugandan land snails are significantly nested, and the centre of the sets of nested subsets is located in the Virunga Mountains (Fig. 4) close to the putative East Congolian refugia. Since the centre of the sets of nested subsets corresponds to the centre of the montane elements (Fig. 3), the nestedness pattern is probably the result of contraction or expansion of species belonging to the montane element.

Several of the species from south-western Uganda classified in the montane elements have widely disjunct distributions (see also Verdcourt, 1984a). For example, Streptostele teres Pilsbry, 1919 is known from the Ruwenzori Mountains and Mount Elgon (Verdcourt, 1983); Elgonocyclus kaptaweliensis (Germain, 1934) and Punctum ugandanum (E. A. Smith, 1903) are known from the Kenyan highlands (Verdcourt, 1982, 1988); and, furthermore, Micromazinia volkensi (Martens, 1895) and Trachycystis lamellifera (E. A. Smith, 1903) are also found in the Kenyan and Tanzanian highlands (Verdcourt, 1984a,b). It is likely that they were more widespread during the cool, arid glacial, when montane forests descended by 1000–1500 m (Bonnefille et al., 1990; White, 1993; Maley, 1996, 2001; Flenley, 1998; Kiage & Liu, 2006). Because of the aridity during the glacials, forest patches could develop only in particularly sheltered locations with sufficient humidity. Such isolated forest patches may have existed in the interlacustrine highlands of Uganda in areas of favourable topography (Jolly et al., 1997). The forest patches provided the opportunity for the stepping-stone dispersal of Afromontane species (not only land snails); for example, from the presumably larger montane forests in Eastern Congo to the smaller refugia in the highlands of Kenya and Tanzania. When the isolated patches of montane forest at lower elevations disappeared as a result of the temperature increases in the interglacials or the post-glacial, the ranges of Afromontane species became disjunct. Thus, the montane regions can be considered contemporary refugia, as has been emphasized by White (1993). An alternative explanation for the disjunct distribution patterns would be that they are the result of passive chance dispersal by birds or heavy storms. Although such long-distance dispersal of land snails is possible (Kirchner et al., 1997; Gittenberger et al., 2006), it is less likely than a stepping-stone dispersal of Afromontane species through more densely situated montane forest patches during the glacials.

Lowland rain forest was much more limited during the cool, arid glacial periods (Maley, 1996, 2001; Flenley, 1998) and spread post-glacially. In the study region, the centres of the sets of nested subsets are in the montane region at present (Fig. 4), because the currently ongoing process is the contraction of the species-rich montane elements, whereas the lowland and lower montane elements have already spread across the study region. Nevertheless, nestedness is still significant if the montane
elements are omitted from the analysis, indicating that the lowland fauna was also affected by cycles of contraction and expansion of ranges.

We can conclude that the decreasing species richness and increasing range size of Ugandan land snails with increasing distance from the putative East Congolian refugia and the significant clustering and nestedness of the ranges of Ugandan land snails indicate that the East African land snail fauna was affected by cycles of contraction and expansion of ranges. In accordance with previous studies showing that patterns of endemism can be only partly predicted from contemporary factors (Linder, 2001; Jetz et al., 2004; Rahbek et al., 2007), our results indicate that the significant clustering and nestedness of land snail species ranges in Uganda cannot be explained by current environmental conditions that might be sufficient to explain the distribution of species richness alone. There are distinct montane and lowland elements with presumably different histories in the Ugandan land snail fauna. Given the environmental history, it can be supposed that the lowland elements expanded post-glacially, whereas the ranges of the montane species are probably currently contracting.

ACKNOWLEDGEMENTS

We are grateful to G. Isabirye-Basuta and J. Baranga for their support of our project, to A. Apio and P. Barugahare for assisting in fieldwork, to C. Hennig for statistical advice, and to M. Griesbach for linguistic corrections. We thank the Uganda Wildlife Authority, the National Forest Authority of Uganda and the Uganda National Council for Science and Technology for research permission, and the German Research Council (445 UGA-18/1/06) for funding this study.

REFERENCES


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Editor: Melodie McGeoch