Habitat association of amphibians in East African bush- and grassland: an example from Meru National Park, Kenya

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The amphibian diversity in different vegetation communities was investigated in Meru National Park (Kenya), using transect sampling, drift-fences, pit-falls and opportunistic collection. Acacia wooded grassland had highest amphibian diversity (H’ = 2.071, D = 6.74), Acacia-Commiphora bushland ranked second (H’ = 1.858, D = 5.88) and Combretum wooded grassland ranked third (H’ = 1.581, D = 5.08). Acacia wooded grassland had the highest amphibian abundance (n = 173 individuals) and species richness (10 species). Combretum wooded grassland had eight species with less abundance (n = 113 individuals), while the Acacia-Commiphora bushland had seven species only, with higher abundance (n = 144 individuals). Detrended Correspondence Analysis showed the plots, which occur close together with similar species composition. Correspondence Analysis was performed to investigate the association of amphibian species with plant assemblages. There was a positive linear correlation between amphibian species richness and plant species diversity in all vegetation communities. However, as the Spearman Rank Test could not establish any significant correlation between plant and amphibian diversities in the respective habitats, the amphibians recorded in the present study area cannot be used as surrogate organisms to evaluate environmental changes.

KEY WORDS: Anurans, species richness, abundance, Afrotropics.

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INTRODUCTION

For more than a decade, amphibian population decline has been reported from many regions all over the world. It has been suggested that these animals can respond with population change to various environmental stressors and that the worldwide status of this vertebrate group is critical (Stuart et al. 2004). Amphibian species are often regarded as surrogate organisms for environmental conditions (e.g. Heyer et al. 1994, Kati et al. 2004).

Amphibian population decline is mainly known from semi-humid to humid regions in North, Central and South America, Europe and Australia (Stuart et al. 2004, http://www.amphibiaweb.org/declines/declines.html). In these ecosystems, especially in Neotropical rainforests, amphibian communities are species-rich, mainly as a result of species-specific association with a variety of different habitats (e.g. Duellman 1978, 1999). When many such habitat specialists co-occur, monitoring of amphibian diversity (i.e. species richness and abundance in particular habitats) is considered informative about the presence of environmental stressors.

Little is known about amphibian population decline in Africa (but see Schick 2004), especially in semi-arid and arid regions. Two of us (D.V. Wasonga and S. Lötters) are involved in establishing long-term monitoring of amphibian diversity in East Africa (Lötters et al. 2001, http://www.biota-africa.org). In addition to studying rainforests, we have focused on semi-arid bush- and grassland. These ecosystems are relatively poor in amphibian species. Moreover, the relatively few frogs and toads appear to be more generalists than specialists and display relatively large distributions (cf. Lötters et al. in press). For these reasons, it may be expected that there is little correlation between habitat quality and the presence or abundance of species and that amphibians in semi-arid bush- and grassland cannot be used as surrogate organisms for environmental change. To analyse this, we studied amphibian species richness and abundance in different habitats of Meru National Park, Kenya.

THE STUDY AREA

Meru National Park is located in the Eastern Province of Kenya, about 360 km northeast of Nairobi. It lies on the Equator between latitudes 0°10’ to 0°20’N and longitudes 38°0’ to 38°25’E (Fig. 1). The park covers an area of about 870 km² of lowlands. The altitude varies from 300 m above sea level in the southeastern corner where the River Tana forms part of the park boundary to over 850 m above sea level along the western boundary near the Nyambeni Hills. The elevation follows a steadily ascending gradient from southeast to northwest.

Average annual rainfall in the area is around 720 mm with a bimodal pattern. The short rains in November are much more intense than those from March to May (Ament 1975). The network of rivers flows across the park in a southeasterly direction to join the Tana River ensures an almost adequate water supply for the herbivore population across the park and maintains the vegetation regime (unpublished personal observations). Most rivers in the north...
are perennial, while the Tana and Ura are perennial in the south. The soils in the north are formed of Pleistocene-Recent lava, produced from the volcanoes of the Nyambenis. Towards the south, the Precambrian rock of the basement system can be seen.

Floristically, Meru National Park belongs to the Somali-Masai Regional Centre of Endemism (White 1983). The vegetation composition within the park can be broadly divided into three communities (Ament 1975). Acacia wooded grassland (AWG) covers the eastern part of the Nyambeni lava flows and the volcanic alluvial soils along the northeastern boundary of the park. Dominant tree species include Acacia tortilis (Forsk.) Hayne and A. senegal (L.) Willd., mainly on the low strewn ridges, but are replaced by Hyphaene coriacea Gaertn. in the low swampy areas beside the rivers. The second type is Combretum wooded grassland (CWG), which covers the western part of the park. Here Combretum apiculatum Sond. is dominant, while Combretum molle G. Don and Combretum collinum Fresen. are also common. Ziziphus sp. and Harrisonia abyssinica Oliv. occur in scattered clumps, while Lawsonia inermis L. is common near rivers. Sehima nervosa (Rotter) Stapf is the dominant grass species. Scattered patches of Chrysopogon plumulosus Hochst. and Aristida adscensionis L. also occur in recently burned areas. There are some swampy patches, where Acacia seyal var. fistula (Schweinf.) Oliv. and A. drepanolobium Sjöstedt are present along with the grass Chloris gayana Kunth. The third vegetation type is Acacia-Commiphora bushland (ACB), which is dominant where the basement rock is exposed in the southern region of the park. The trees and shrubs are taller and there is a better grass cover near the western boundary where Acacia mellifera (Vahl) Benth., A. nilotica (L.) Del., A. brevispica Harms and A. ataxacantha D.C. are common. Further southeast, Acacia senegal (L.) Willd. and A. reficiens Wawra appear to become dominant. In many places, there are dense understorey bush of Bauhinia taitensis Taub., Grewia villosa Willd. and Combretum aculeatum Vent. Other minor habitat types include riverine forests, inselbergs, groundwater forest and swamps. The latter are commonly found in the most northerly triangle of the park.
The vegetation inside and outside the park is sharply contrasting in some areas especially to the east and south where there is extensive agriculture. An electric fence has been erected along the full length of the western boundary.

Land-use patterns in this area are wide ranging. The park is among the 60 sites designated as Important Bird Areas (IBAs) in Kenya (Bennun & Njoroge 1999). Meru National Park is part of the Meru Conservation Area. The Borana pastoralists occupy the northern section. The Tharaka pastoralists and subsistence farming community occur in the south.

METHODS

All three vegetation communities in the study area were sampled using non-randomly chosen localities within randomly chosen areas (Fig. 1), from October 2002 to January 2003. The spacing of sampling sites was largely determined by security concerns and accessibility, while attempts were also made to minimize off-road driving.

The transect method of sampling amphibians as described by previous authors was employed (e.g. Heyer et al. 1994). In accordance with sampling at other localities in East and West Africa (Lotters et al. 2001, Rödel & Ernst 2004), in each study site, a 600 m rectangular transect was established starting from a random point in each study site. A width of 2 m along the transect length was used for sampling. GPS readings were taken for each transect location. A team of two persons working for 2 hr per search night (i.e. 4 man-hours) made three visits to each site. The sites were sampled in a random rotational sequence to minimize bias. The first round of sampling covering all sites was carried out just before the rains during October 13-21, 2002 but was accompanied by light showers. The second round of sampling began at the start of heavy rains from October 27 to November 4, 2003. The last sampling was carried out a few weeks after the rains stopped during January 22-30, 2003.

For each of the anurans encountered, the scientific name was recorded (based on reference specimens at the National Museums of Kenya, Nairobi, which have been identified by different amphibian experts in the past). The numbers of individuals recorded were tallied for each sampling round with respect to each vegetation community. In addition, toes were clipped before release to avoid double counting of specimens.

To supplement amphibian encounters from transects and opportunistic collection, straight-line drift fence and pit-fall trapping techniques were used (Karns 1986, Heyer et al. 1994). This complementary effort mainly targeted anurans whose life history strategy involves burrowing habit (e.g. Hemisus). Due to the intensity of the work involved, only one trap station was established in each of the three vegetation communities. A 20 m drift fence (see Heyer et al. 1994) made of polythene flashing 50 cm above the ground and 5 cm below the surface was erected. Ten pitfalls (each of 20 l buckets) were placed, flush with the ground surface, alternately on either side of the fence at 2 m intervals. Traps were checked shortly after sunrise and about 3 to 4 hr after sunset. Two trap nights were conducted in each trap station per visit.

Vegetation sampling techniques

In the areas where amphibian sampling transects were located, a transect divided into 15 stratified random plots (each measuring 20 × 10 m), was laid, with a block of five plots per amphibian sampling location. This was repeated in each vegetation community (i.e. Acacia wooded grassland, Combretum wooded grassland and Acacia-Commiphora bushland) following Ament (1975) giving a total of 45 plant sampling plots. The overall stratification was similar to that applied in amphibian sampling. The amphibian and plant samples were progressively assigned with plots 1-5 corresponding to amphibian sampling point 1, plots 6-10, sampling point 2 and so on. Within each plot, a modified Braun-Blanquet cover abundance scale
was used to assign various plant species cover/abundance rating, following the method of Mueller-Dombois & Ellenberg (1974). Species were rated as 5 (any number of individuals, with a cover of more than 75% of plot area); 4 (any number of individuals, with a cover of 50-75% of plot area); 3 (any number of individuals, with a cover of 25-50% of plot area); 2 (any number of individuals, with a cover of 5-25% of plot area); 1 (numerous individuals, but with a total cover of less than 5% of plot area); r (few individuals with small cover); and + (solitary individual with small cover). For statistical processing, the last two scales were assigned values of 0.5 and 0.1, respectively. Plant species, based on collected material, were identified at the East African Herbarium, Nairobi. Braun-Blanquet cover abundance was recorded for 122 plant species in the 45 plots.

Data analyses

Amphibian abundance and species richness were expressed in terms of number of individuals and species observed, respectively. Diversity indices relating species richness and abundance were computed for each sampling plot and also pooled for the overall vegetation community. Both the Shannon-Weaver index \(H'\) and the inverse of Simpson's index \(D\) were applied. In addition, Shannon's evenness index \(E\) was computed (Peet 1974, Magurran 1988, Krebs 1999).

The software CANOCO, version 4.0 (Braak 1987), was used to analyse vegetation data collected from plots in the entire study area. Detrended Correspondence Analysis (DCA) was applied to the vegetation data to determine the vegetation assemblages in the study area. In the DCA ordination procedure, the location of each sampling plot is indicated as the centroid of sample scores, based on variations of species composition (Braak 1987, 1988). The mean values of the Braun-Blanquet ratings for each species were used in this procedure. Since explicit environmental data was not included in the present study, an indirect gradient analysis was applied to the vegetation data. The cover abundance scale was used as a species score indicating patterns of species occurrence to visualize community variation between the plots.

Correspondence Analysis was performed to examine the correlation of plant species presence and abundance with amphibian species richness. The row (species) and column (plant assemblages) scores were plotted in two-dimensional space using canonical standardization. The relationship is indicated by the relative positions of both variables on the biplot, constructed from output dimensions with the highest eigenvalues. The first dimension accounts for the most inertia (high eigenvalue) and the level of importance reduces from the left to right side of the axis. On the basis of presence/absence and numbers of amphibian data, assemblage V (comprising plots 21, 28, 30) was excluded from the analysis. The significance of the relationship was investigated with the Spearman Rank Test, using the nine sampling points (transects) for amphibians and the respective sampling blocks for plants.

RESULTS

In total 430 individuals of 11 amphibian species belonging to seven genera and families (all belonging to the order Anura) were observed during the present investigation in Meru National Park (Table 1). Most of these species are terrestrial in habit, but aquatic, fossorial and arboreal lifestyles also occur (Table 1). Acacia wooded grassland had the highest species abundance and richness, with a total of 173 individuals of 10 species. Eight species (113 individuals) were recorded from Combretum wooded grassland, while Acacia-Commiphora bushland had seven species (144 individuals). Two species, Hemisus marmoratus and Phrynomantis bifasciatus, were exclusively recorded in the Acacia wooded grassland. All the Hemisus
were captured from pitfall trap station in the *Acacia* wooded grassland near Murera gate (Fig. 1). *Amietophrynus gutturalis* and *Ptychadena cf. mascareniensis* were both absent from *Acacia-Commiphora* bushland.

<table>
<thead>
<tr>
<th>Species – Overall lifestyle</th>
<th>Number of specimens observed in each transects per vegetation community</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Acacia wooded grassland</td>
</tr>
<tr>
<td>----------------------------</td>
<td>-------------------------</td>
</tr>
<tr>
<td><em>Amietophrynus maculatus</em> (Hallowell 1854), family Bufonidae – Terrestrial</td>
<td>1 2 0 6 5 2 8 9 4</td>
</tr>
<tr>
<td><em>Amietophrynus garmani</em> (Meek 1897), family Bufonidae – Terrestrial</td>
<td>5 6 5 0 0 0 5 4 7</td>
</tr>
<tr>
<td><em>Amietophrynus gutturalis</em> (Power 1927), family Bufonidae – Terrestrial</td>
<td>2 7 3 4 3 4 0 0 0</td>
</tr>
<tr>
<td><em>Ptychadena porosissima</em> (Steindachner 1867), family Ptychadenidae – Terrestrial</td>
<td>10 12 17 4 5 2 6 8 7</td>
</tr>
<tr>
<td><em>Ptychadena cf. mascareniensis</em> (Duméril &amp; Bibron 1841), family Ptychadenidae – Terrestrial</td>
<td>7 3 4 4 6 7 0 0 0</td>
</tr>
<tr>
<td><em>Ptychadena anchietae</em> (Bocage 1867), family Ptychadenidae – Terrestrial</td>
<td>3 2 3 1 3 4 16 13 12</td>
</tr>
<tr>
<td><em>Phrynobatrachus natalensis</em> (Smith 1849), family Phrynobatrachidae – Terrestrial</td>
<td>4 1 3 2 3 2 6 2 3</td>
</tr>
<tr>
<td><em>Hemisus marmoratus</em> (Peters 1854), family Hemisotidae – Fossorial</td>
<td>27 0 0 0 0 0 0 0 0</td>
</tr>
<tr>
<td><em>Hyperolius glandicolor</em> Peters 1878, family Hyperoliidae – Arboreal</td>
<td>13 10 14 12 9 20 4 4 5</td>
</tr>
<tr>
<td><em>Phrynomantis bifasciatus</em> (Smith 1847), family Microhylidae – Terrestrial to fossorial</td>
<td>8 0 0 0 0 0 0 0 0</td>
</tr>
<tr>
<td><em>Xenopus borealis</em> Parker 1936, family Pipidae – Aquatic</td>
<td>0 0 3 0 2 4 17 0</td>
</tr>
<tr>
<td>Total individuals</td>
<td>173</td>
</tr>
<tr>
<td>Total species</td>
<td>10</td>
</tr>
</tbody>
</table>
Amietophrynus garmani did not occur in Combretum wooded grassland while Xenopus borealis, the only aquatic species, was not recorded in Acacia wooded grassland (although water was available). Five species (Amietophrynus maculatus, Hyperolius glandicolor, Phrynobatrachus natalensis, Ptychadena porosissima and

Table 2.
Numbers of individuals and species of amphibians and their diversity indices recorded for three major vegetation communities in Meru National Park.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Acacia wooded grassland</th>
<th>Combretum wooded grassland</th>
<th>Acacia-Commiphora bushland</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of individuals</td>
<td>173</td>
<td>113</td>
<td>144</td>
</tr>
<tr>
<td>Number of species</td>
<td>10</td>
<td>8</td>
<td>7</td>
</tr>
<tr>
<td>Shannon-Weaver index, $H'$</td>
<td>2.07</td>
<td>1.58</td>
<td>1.86</td>
</tr>
<tr>
<td>Simpson's index, $D$</td>
<td>6.74</td>
<td>5.08</td>
<td>5.88</td>
</tr>
<tr>
<td>Shannon evenness index, $E$</td>
<td>0.90</td>
<td>0.89</td>
<td>0.96</td>
</tr>
</tbody>
</table>

Fig. 2. — DCA Ordination diagram of vegetation data in Meru National Park based on species composition sample scores. Numbers refer to sampling plots; oval shapes designate species assemblages I, II, III, IV, V.
were common to all three vegetation communities in the study area. A comparison of amphibian species diversity across the vegetation communities revealed that *Acacia* wooded grassland had the highest species diversity (H' = 2.07, D = 6.74) (Table 2). This was followed by *Acacia-Commiphora* bushland, while *Combretum* wooded grassland had the lowest diversity (H' = 1.581, D = 5.08). The same trend of species diversity was obtained from the Shannon-Weaver index, H' (richness and evenness measure) and the Simpson's index, D (dominance measure). The basic assumption for H', random sample of individuals from a large population was thus fulfilled. All the anurans tended to show a virtually even distribution in the three vegetation communities.

Fig. 2 shows the order of similarity of the habitat as determined by the groupings of the overall vegetation data by the DCA procedure. In the DCA Ordination diagram, adjacent plots denote similarity in species composition. Five species assemblages were identified from this clustering (Table 3). This table was generated from the closeness and or clustering of the study plots to each other and each cluster denotes an assemblage. On Axis 1, the DCA clusters are distinctly aligned into three major communities. The constituent plots in assemblage II, III, V, and I, IV correspond to *Acacia* wooded grassland, *Combretum* wooded grassland and *Acacia-Commiphora* bushland, respectively.

Associations were found between the amphibian species and the various species assemblages identified above. The results of the Correspondence Analysis (CA) are presented in Fig. 3. *Hemisus marmoratus* and *Phrynomantis bifasciatus* showed a clumped affinity to assemblage II (Fig. 3A, top left) and thus were excluded from the second CA leaving only nine species (Fig. 3B). The differences in the relative frequencies of these species are well discernible along the first dimension (Fig. 3B). Most of the observed variation (62.84%) is characterized by assemblage II and III lying within the *Acacia* wooded grassland and *Combretum* wooded grassland, respectively. The results show that *Amietophrynus gutturalis*, *Hyperolius glandicor* and *Ptychadena cf. mascareniensis* are more dissimilar in their habitat choice than the rest of the species. Within plant assemblage I, *Amietophrynus maculatus*, *Phrynobatrachus natalensis*, *Ptychadena anchietae* and *Xenopus borealis* display only a moderate association. *Ptychadena porosissima* is closely linked to assemblage II, whereas *Amietophrynus garmani* is more of an assemblage IV species.

Amphibian species diversity correlated positively with plant species diversity in all sampling plots except number 5 (Table 4). For instance, plot 7 had relatively

<table>
<thead>
<tr>
<th>Species assemblage</th>
<th>Constituent sampling plots</th>
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<tbody>
<tr>
<td>I</td>
<td>8  14  15  26  31  32  33  34  35  36  37  38  39  40  41</td>
</tr>
<tr>
<td>II</td>
<td>1  2  3  4  5  6  7  9  10  11  12</td>
</tr>
<tr>
<td>III</td>
<td>16  17  18  19  20  22  23  24  25  27</td>
</tr>
<tr>
<td>IV</td>
<td>42  43  44  45</td>
</tr>
<tr>
<td>V</td>
<td>21  28  30</td>
</tr>
<tr>
<td>Outlier plots</td>
<td>13  29</td>
</tr>
</tbody>
</table>
Fig. 3A-B. — Correspondence Analysis scatter plot illustrating variations of species distribution with plant assemblages: A, including all amphibian species; B, excluding *Hemisus marmoratus* and *Phrynomantis bifasciatus*.
Amphibian (anuran) species richness and abundance varied across the vegetation communities studied at Meru National Park. *Acacia* wooded grassland had the highest amphibian species richness and diversity (Tables 1-2), as well as the highest plant species presence and abundance (Table 4). This illustrates the importance of vegetation diversity in supporting diverse anuran assemblages of semi-arid regions (at least at our study site). The two diversity indices yielded similar results. As seen in Fig. 4, the species accumulation curves did not perfectly demonstrate an asymptotic trend in *Acacia* wooded grassland. These results strongly suggest that more species would have been recorded had the sampling period been extended. Indeed there was a differential sampling success at the various sampling localities. The result at 24 man-hours strongly suggested an asymptotic level for AWG and CWG. Yet an additional 8 and 12 man-hours would be required to demonstrate asymptotes for ACB/CWG and AWG, respectively.

Even though the species distributions appeared almost even (Shannon evenness index), our study showed that the anurans demonstrated some degree of association with vegetation assemblages. The only two burrowing frog species (*Hemisus marmoratus, Phrynomantis bifasciatus*) were recorded exclusively from plant assemblage II. In contrast, the only aquatic species (*Xenopus borealis*) was absent. The two former anurans may be regarded as specialists related to soil conditions (e.g. Rödel 2000). The use of pitfall traps in the present study was essential for the capture of *Hemisus marmoratus*, which is fossorial. All the specimens were recorded at the trap station adjacent to Murera stream at Murera gate (Fig. 1). However, it remains unclear
why *Xenopus borealis*, which can be regarded as a highly adaptive frog (S. Lötters, unpublished observations), was not found in the *Acacia* wooded grassland habitat. Even prolonged sampling would probably not have resulted in the presence of this frog (cf. Fig. 4), since it is our feeling that *Xenopus* can hardly be overlooked. These observations did not include exhaustive life history data for the species recorded.

The observed variation in species abundance between assemblages III, I and IV (corresponding to CWG and ACB respectively) can be explained by the spatial partitioning of the species of the same genus and through comparative ecological niches. All the three *Ptychadena* and *Amietophrynus* species (Table 1) can be regarded as generalists. However, our knowledge of the life history of Afrotropical anurans is limited (e.g. Rödel 2000, Lötters et al. in press) and, based on the spatial pattern of anurans, it is possible that each species possesses a slightly different ecological adaptability (or preference). Hence their occurrence and abundance among the three vegetation assemblages might be sensitive to habitat conditions. Slight environmental changes across the Meru National Park might result in different spatial patterns of the *Amietophrynus* and *Ptychadena* species.

The only arboreal frog (*Hyperolius glandicolor*) was most abundant in assemblages II and III (corresponding to the two wooded grassland communities), while *Phrynobatrachus natalensis*, considered a generalist due to its wide geographical distribution (e.g. Lötters et al. in press), was more or less equally distributed. It cannot be ruled out that the former responds to habitat changes associated with woodland. The *Phrynobatrachus* species is probably the least sensitive with respect to vegetation assemblage (cf. Table 1 and Fig. 3). As far as we know, this relatively small terrestrial anuran shows little overlap in lifestyle with other species in the Meru National Park (cf. Lötters et al. in press).

Some of the amphibian species in the park’s semi-arid bush- and grassland appear to be specialists (e.g. *Hemisus marmoratus, Phrynomantis bifasciatus, Xeno-

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**Fig. 4.** — Species accumulation curves in the different vegetation communities (AWG, *Acacia* wooded grassland; CWG, *Combretum* wooded grassland; ACB, *Acacia-Commiphora* bushland).
When they share similar ecological niches, they might act as surrogate species to evaluate environmental changes. However, as the Spearman Rank Test could not establish any significant correlation between plant and amphibian diversities in the respective habitats, we conclude that the amphibians recorded in the present study area cannot be used as surrogate organisms to evaluate environmental changes.

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