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Source: Journal of Vertebrate Biology, 69(2)

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/jvb.20006

Journal of
Vertebrate Biology

Open Acces

J. Vertebr. Biol. 2020, 69(2): 20006
DOI: 10.25225/jvb.20006

SPECIAL ISSUE: AFRICAN SMALL MAMMALS

Multimammate mice of the genus *Mastomys* (Rodentia: Muridae) in Ethiopia – diversity and distribution assessed by genetic approaches and environmental niche modelling

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Received 19 January 2020; Accepted 18 February 2020; Published online 27 April 2020

Abstract. Multimammate mice of the genus *Mastomys* are widespread in sub-Saharan Africa and occur in a wide range of open habitats. Representatives of this genus are the most common African rodents, the main vertebrate agricultural pests and vectors of human pathogens. In Ethiopia, the biogeographically most complex eastern African country, several species have been reported, but their distribution has never been described because of their cryptic morphology. Here we present genetically identified species from 377 Ethiopian *Mastomys* specimens and analyse their distributional patterns. The genus, represented by four species, inhabits most of the country, with the exception of the highest mountains and dry areas, such as the Afar triangle and the Somali region. For the first time we document *M. kollmannspergeri* from a single locality in the northernmost part of Ethiopia. Three previously recorded species are more widespread – *M. erythroleucus* was found at 32 localities, *M. natalensis* at 13 localities and the Ethiopian endemic species *M. awashensis* at 18 localities. Phylogenetic analysis of mitochondrial cytochrome *b* gene sequences indicates that only one of the six phylogroups of *M. natalensis* and one of the four phylogroups of *M. erythroleucus* are represented in Ethiopia. Haplotype network analysis indicates two subclades of Ethiopian *M. erythroleucus* separated by the Ethiopian Rift Valley. Using presence records, we constructed distribution models for the species and analysed the level of overlap. The predicted distribution shows most overlap between *M. awashensis* and *M. natalensis*, which is in agreement with empirical data as both species were found in sympatry at four localities. A medium level of overlap was predicted between *M. natalensis* and *M. erythroleucus* and both species were found co-existing at two localities. This study not only presents the first detailed distribution of cryptic *Mastomys* species, but also clearly identifies multimammate mice as model taxa for future evolutionary studies (e.g. the evolution of co-existence or host-parasite interactions) and indicates the regions suitable for such studies.

Key words: co-existence, overlap, suitability, commensal, sibling species, species distribution modelling, sympatry

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Introduction

Multimammate mice of the genus *Mastomys* are widespread and common murid rodents in sub-Saharan Africa. They occur in a wide range of habitats, avoiding only deserts, continuous tropical rainforests and high mountains (Monadjem et al. 2015). Representatives of this genus are often abundant, making them major vertebrate agricultural pests across the continent (Leirs 1994). Moreover, multimammate rats are reservoirs and vectors of human pathogens (Isaäcson et al. 1981, Gratz 1997, Lecompte et al. 2006, Meheretu et al. 2013), including plague and Lassa fever (Green et al. 1978, Fichet-Calvet et al. 2007). The latter is caused by arenaviruses, some of which have recently been found to be specific to particular rodent species and even intraspecific clades (Gryseels et al. 2017, Goüy de Bellocq et al. 2020). From an epidemiological point of view it is, therefore, important to know the precise distribution of these rodent hosts, especially if they display cryptic diversity, as is the case with numerous murid groups and *Mastomys* in particular.

Recent mammalogical compendia usually report eight species of the genus *Mastomys*: *M. natalensis*, *M. erythroleucus*, *M. awashensis*, *M. coucha*, *M. huberti*, *M. kollmannspergeri*, *M. pernanus* and *M. shortridgei* (Musser & Carleton 2005, Happold 2013, Wilson et al. 2017), even though multilocus phylogenetic studies indicate that *M. pernanus*, characterized by significantly smaller body size, is probably closer to the genus *Hylomyscus* than *Mastomys* (Lecompte et al. 2002). Apart from *M. pernanus*, all other species are characterized by morphological similarity and are distinguished mainly by the combination of cytogenetic and molecular traits (Granjon et al. 1997). This is the main reason why there is a general lack of precise distributional data in many regions, despite the high abundance of multimammate mice in rodent communities. More intensive investigation of *Mastomys* species distribution has been performed in West Africa (Hubert & Adam 1985, Duplantier et al. 1996, Denys et al. 2012). It was found that the distribution of some species may overlap, but they differ in habitat preference. For example, in south-eastern Senegal, *M. natalensis* lives strictly in human habitations, *M. huberti* in natural and cultivated wetlands, while *M. erythroleucus* is opportunistic preferring savannah-like habitats (Duplantier et al. 1990, 1996, 1997, Brouat et al. 2007). However, in Nigeria habitat preferences are different; *M. erythroleucus* lives around and inside villages, while *M. natalensis* prefers more natural environments. In semi-desert in the north of the country, where *M. erythroleucus* is absent, *M. natalensis* can also settle in human habitations (Dobrokhotov 1982).

Similar data are much scarcer in eastern Africa where *M. natalensis* seems to be the dominant multimammate mouse species (Leirs 1994, Makundi & Massawe 2003, Makundi et al. 2007, Massawe et al. 2011). In Ethiopia, biogeographically the most complex eastern African country (e.g. Linder et al. 2012), it was traditionally believed that two widespread sub-Saharan species, *M. natalensis* and *M. erythroleucus*, may co-occur, but their distribution was not determined due to their similar morphology (Lavrenchenko et al. 1992, Yalden et al. 1996). Later studies by Lavrenchenko (1995) discovered that in the Alvero River Valley both species live in sympatry. As in south-eastern Senegal, *M. erythroleucus* was found both in natural biotopes and in human buildings, while *M. natalensis* was strictly synanthropic. A further study by Lavrenchenko et al. (1998), based on genetic data, genital morphology and karyotypes, described a new species, *M. awashensis*. This species was originally thought to be endemic to the Awash Valley (type locality), but accumulating genetic data suggest a wider distribution in Ethiopia (Colangelo et al. 2010, Lavrenchenko et al. 2010) and possibly in neighbouring countries, e.g. Eritrea.

Preliminary data suggest that two or even three *Mastomys* species may co-exist in sympatry in Ethiopia (Lavrenchenko et al. 1992, 1998). However, barcodes were too few to reliably assess the distributional patterns. The absence of clearly expressed morphological differences between *Mastomys* species (Granjon et al. 1997) suggests that sympatric species would be expected not to overlap in their ecological niches through different habitat preferences (= "microallopatry"). Ethiopia, where up to three congeneric species co-occur, thus provides an ideal setting in which to test this hypothesis. The aims of this study were: (1) to genetically identify available *Mastomys* material from Ethiopia and to characterize the distribution of individual species; (2) to assess the level of their distributional overlap; (3) to use presence records for the construction of species distribution models and identification of the bioclimatic factors affecting their distribution. More generally, this study may help in understanding the ecological and evolutionary processes determining the distribution of sibling species in the heterogeneous conditions of the Ethiopian hotspot of endemism.

Material and Methods

Sampling and species identification

Multimammate mice were collected in the framework of the Joint Ethio-Russian Biological Expedition (JERBE) (1986-2018) and the Czech-Ethiopian expeditions (2012-2018). For specimens collected in the early years of the JERBE activity, species identification was carried out using cytogenetic methods. Individual *Mastomys* species of eastern Africa are well distinguished by their karyotypes: *M. awashensis* – 2n = 32, FNa = 54; *M. erythroleucus* – 2n = 38, FNa = 50-56; *M. natalensis* – 2n = 32, FNa = 52-54 (Green et al. 1980, Granjon et al. 1997, Lavrenchenko et al. 1998). Two species with 32 chromosomes, *M. natalensis* and *M. awashensis*, differ by the number of metacentric and submetacentric elements, C-banding pattern and the form of the Y-chromosome (see Lavrenchenko et al. 1998). Another diagnostic method was based on differences in the relative mobility of haemoglobin electromorphs (see details in Dobrokhotov 1982, Robbins et al. 1983, Lavrenchenko et al. 1992). More recent samples were barcoded at the mitochondrial cytochrome *b* gene (cyt*b*), which is a suitable marker for identification of *Mastomys* species (Lecompte et al. 2002, Colangelo et al. 2010). DNA was extracted using a standard phenol-chloroform method or commercial kits. Cyt*b* sequences (1140 bp) were amplified using primers and a protocol described by Lecompte et al. (2002). To determine the phylogenetic position of Ethiopian samples within the genus, 30 cyt*b* sequences of all *Mastomys* species possibly occurring in Ethiopia were retrieved from GenBank (Table S1). Nucleotide sequences were edited and aligned using Bioedit 7.0.5.3 (Hall 1999). A phylogenetic tree was constructed using Bayesian inference in MrBayes version 3.2.6 (Ronquist & Huelsenbeck 2003). For the detection of partitions and a choice of appropriate models of sequence evolution we used PartitionFinder version 2.1.1 (Lanfear et al. 2012).

Table 1. List of localities with genetically identified *Mastomys* species. Localities closer than 3 km were merged. Species identification was performed by sequencing the mitochondrial cyt*b* gene (S), PCR assay (P), cytogenetic analysis of karyotypes (K), and electrophoresis of haemoglobin (H). (No. of localities correspond to Fig. 1).

Species	Locality	No.	Coordinates		Alt. (m)	Identification by
			Lat.	Long.		
M. kollmanspergeri	Mai-Temen	14	14.0945	37.4575	967	S(1)
M. awashensis	Gojeb River	1	7.2545	36.7980	1068	S(6), P(3)
	Shebe	2	7.4782	36.5334	1730	S(1)
	Gibe NP 1	3	8.2331	37.5887	1099	S(3)
	Gibe NP 2		8.2338	37.5823	1156	
	Lake Koka	4	8.4651	39.1606	1613	K(7)
	Didessa River	5	8.6943	36.4149	1296	S(1)
	Awash NP	6	8.8453	40.0119	970	K(4)
	Babile Elephant Sanctuary 1	7	9.0586	42.2796	1216	S(8), P(1)
	Babile Elephant Sanctuary 2		9.1478	42.2624	1260	
	Dhati-Welel NP 1	8	9.2249	34.8662	1474	S(8)
	Dhati-Welel NP 2		9.2393	34.8653	1397	
	Dhati-Welel NP 3		9.2449	34.8644	1392	
	Ankober 1	9	9.5548	39.7818	1879	S(3)
	Ankober 2		9.5554	39.7657	2134	
	Kombolcha	10	11.0526	39.6481	2380	S(2)
	Gumara River 1	11	11.7525	37.9068	2128	S(3), H(3)
	Gumara River 2		11.7797	37.7313	1878	
	Adi Mancarre	12	12.5492	39.6431	1523	S(4)
	Adi Aba Musa		12.6393	39.5383	2525	
	Kube		12.6551	39.5816	1783	
	Simien Mts NP	13	13.1858	37.9671	3145	S(1)
	Mai-Temen	14	14.0945	37.4575	967	S(1)

M. erythroleucus	Megado	15	3.9190	38.2572	1127	S(2)
	Gamado		3.9549	38.2550	1527	
	Borena NP 1	16	4.4103	38.2720	1535	S(13), P(18)
	Borena NP 2		4.4732	38.2738	1605	
	Borena NP 3		4.5467	38.2790	1673	
	Borena NP 4		4.5525	38.2744	1648	
	Arero forest	17	4.8099	38.8646	1658	S(2), P(5)
	Arero village		4.8260	38.8203	1620	
	Yabelo Wildlife Sanctuary 1	18	4.9535	38.2196	1491	S(15), P(12)
	Yabelo Wildlife Sanctuary 2		4.9624	38.2067	1549	
	Yabelo Wildlife Sanctuary 3		4.9627	38.2128	1529	
	Omo river	19	4.9940	36.0915	380	K(1)
	Darra	20	5.2833	37.4666	1058	S(15)
	Dabba		5.4053	37.4450	1209	
	Mande 1		5.5333	37.4166	1301	
	Mande 2		5.5333	37.3833	1476	
	Mago NP	21	5.7773	36.4396	946	S(1)
	Lake Chamo	22	5.7875	37.5953	1116	S(5), P(6)
	Nechisar NP 1	23	5.9490	37.6635	1279	S(10)
	Nechisar NP 2		5.9697	37.6539	1369	
	Nechisar NP 3		5.9770	37.5869	1171	
	Arba Minch		6.0260	37.5659	1208	
	Arba Minch University		6.0674	37.5661	1237	
	Bulcha Forest	24	6.2182	38.1973	1945	S(2)
	Koi river	25	6.6552	35.1939	871	S(1)
	Bishan-Vaka	26	7.2911	35.2688	1357	S(8), P(14)
	Adamy-Tulu	27	7.8462	38.6941	1658	S(3)
	Alvero river	28	7.9319	34.2896	444	K(12), H(45)
	Gore 1	29	8.0917	35.4819	1781	S(2)
	Gore 2		8.0959	35.4892	1665	
	Gambella	32	8.2174	34.5627	456	S(1)
	Lake Koka	4	8.4651	39.1605	1613	K(15), H(12)
	Didessa River	5	8.6943	36.4149	1296	S(1)
	Alatish NP 1	30	12.1997	35.6666	568	S(9)
	Alatish NP 2		12.2992	35.7634	579	
	Alatish NP 3		12.3457	35.7388	573	
	Alatish NP 4		12.4953	35.6366	533	
M. natalensis	Jimma	31	7.7010	37.0715	1683	S(1)
	Alvero river	28	7.9319	34.2897	444	K(5), H(10)
	Gibe NP	3	8.2338	37.5823	1156	S(6)
	Gambella NP	33	8.3178	33.6451	417	S(2)
	Lake Koka	4	8.4651	39.1604	1613	K(2), H(2)
	Ambo	34	8.9687	37.8972	2191	K(4)
	Dhati-Welel NP 1	8	9.2234	34.8772	1437	S(20), P(2)
	Dhati-Welel NP 2		9.2393	34.8653	1397	
	Dhati-Welel NP 3		9.2449	34.8644	1392	
	Dhati-Welel NP 4		9.2449	34.8652	1397	
	Amanuel	35	10.4212	37.5635	2338	S(2)
	Bahar-Dar	36	11.6123	37.3773	1792	S(4), P(4)
	Gumara river 1	11	11.7801	37.7523	1896	S(4), P(3)
	Gumara river 2		11.7826	37.7540	1937	
	Dega-Istephanos island	37	11.8831	37.3216	1804	S(4), P(12)
	Alatish NP	30	12.2665	35.7256	580	S(1)

Three heated and one cold chain were employed (nchains = 4) with the runs initiating from random trees; two independent analyses (nruns = 2) were conducted with 5 million generations each; the trees and parameters were sampled every 2000 generations. Results were checked for convergence using Tracer version 1.6 (Drummond & Rambaut 2007). For each run, the first 20% of sampled trees were discarded as burn-in. For rapid genotyping and species identification of larger numbers of Ethiopian *Mastomys* without sequencing, we also developed a simple molecular PCR assay, allowing the discrimination of the three species based on cyt*b* fragment length (Martynov & Lavrenchenko 2018). A cyt*b* haplotype network was constructed on the basis of a subset of nucleotide sequences from 83 specimens and trimmed to 688 bp to avoid missing data. Haplotypes were generated using DNAsp version 5.10.01 (Librado & Rozas 2009), the median-joining network was produced in PopART (downloaded on 15.5.2016 from http://popart.otago.ac.nzhttp://popart.otago.ac.nz). The level of genetic divergence between mitochondrial groups was estimated using the number of base substitutions per site (uncorrected *p*-distances) in MEGA version 7.0 (Kumar et al. 2016). In total, using the methods described above, we genetically identified 59 specimens of *M. awashensis*, 230 *M. erythroleucus*, 88 *M. natalensis* and one *M. kollmannspergeri* from Ethiopia (Table 1).

Species distribution modelling

Ecological niche modelling can predict species distributions based on various factors (e.g. bioclimatic variables) and is a rapidly developing approach used for understanding geographical biodiversity patterns (Lyet et al. 2013, Feuda et al. 2015, Vences et al. 2017). We modelled the potential distribution of three Ethiopian *Mastomys* species by using a maximum entropy approach in MaxEnt version 3.4.1 (Phillips et al. 2006, Phillips & Dudík 2008). This algorithm combines the geographic coordinates of particular species occurrences with environmental parameters and characterizes the ecological niche. The resulting model can be used to predict species' distributions (Hernández et al. 2006). For ecological niche modelling we used the following data layers: 19 bioclimatic variables from the WorldClim database (http:www.worldclim.org; version 2.0), Global Aridity Index and Potential Evapotranspiration Climate Database v2 (http://www.cgiar-csi.org/), Percent Tree Cover and Land Cover (Table S3) (https://globalmaps.github.io/). We used layers with 30 arc seconds spatial resolution and the WGS 84 datum. For all analyses, a region of sub-Saharan Africa was cut from the layers between 21° and –35° latitude, –18° and 52° longitude. To create the models in MaxEnt software for each species 75 % of the occurrence localities were used as training data, and the remaining 25 % were reserved for testing the resulting model. In order to exclude possible errors in the ecological niche model associated with training and testing data, a bootstrap with 500 replications with random seeding was used. Other settings were default. Model quality was measured using the area under the curve (AUC) derived from receiver operating characteristic (ROC) plots. AUC values of 0.5 indicate no greater fit than expected by chance, 0.75 are considered useful and 1.0 show a perfect model fit (Hanley & McNeil 1982, Swets 1988, Elith 2000, Jiménez-Valverde 2012).

We estimated bioclimatic variables that are most important for species distribution with the Jackknife test (Elith et al. 2011). Each variable was excluded in turn, and a model created with the remaining variables. In the next step a model was created using each variable separately. Finally we constructed a model using all variables. ENMtools version 1.4 (Warren et al. 2010) was used to measure predicted range overlaps between three Ethiopian *Mastomys* species (suitability threshold for presence: 0.2) (Fitzpatrick & Turelli 2006). Overlap values are in the range from 0 (no overlap) to 1 (absolute overlap). The transformation of GIS-layers into the work formats, excluding the areas necessary for research and visualisation of distribution models for each species, was carried out using QGIS 3.4 (Palomo et al. 2017).

Results

Diversity and distribution of multimammate mice in Ethiopia

The genus *Mastomys* is widespread in Ethiopia, especially across the western and southern part of the country. It is absent only from the highest mountains (e.g. the Bale and Arsi Mountains) and dry areas like the Afar triangle and the Somali region of the eastern part of the country (Fig. 1). All cyt*b* sequences of *Mastomys* from Ethiopia unequivocally (posterior probability PP > 0.95) clustered with one of the four mitochondrial clades of the phylogenetic tree, which corresponded to four species (Fig. 2). Detailed exploration of the results of phylogenetic analysis shows that only phylogroup A-III of *M. natalensis* (sensu Colangelo

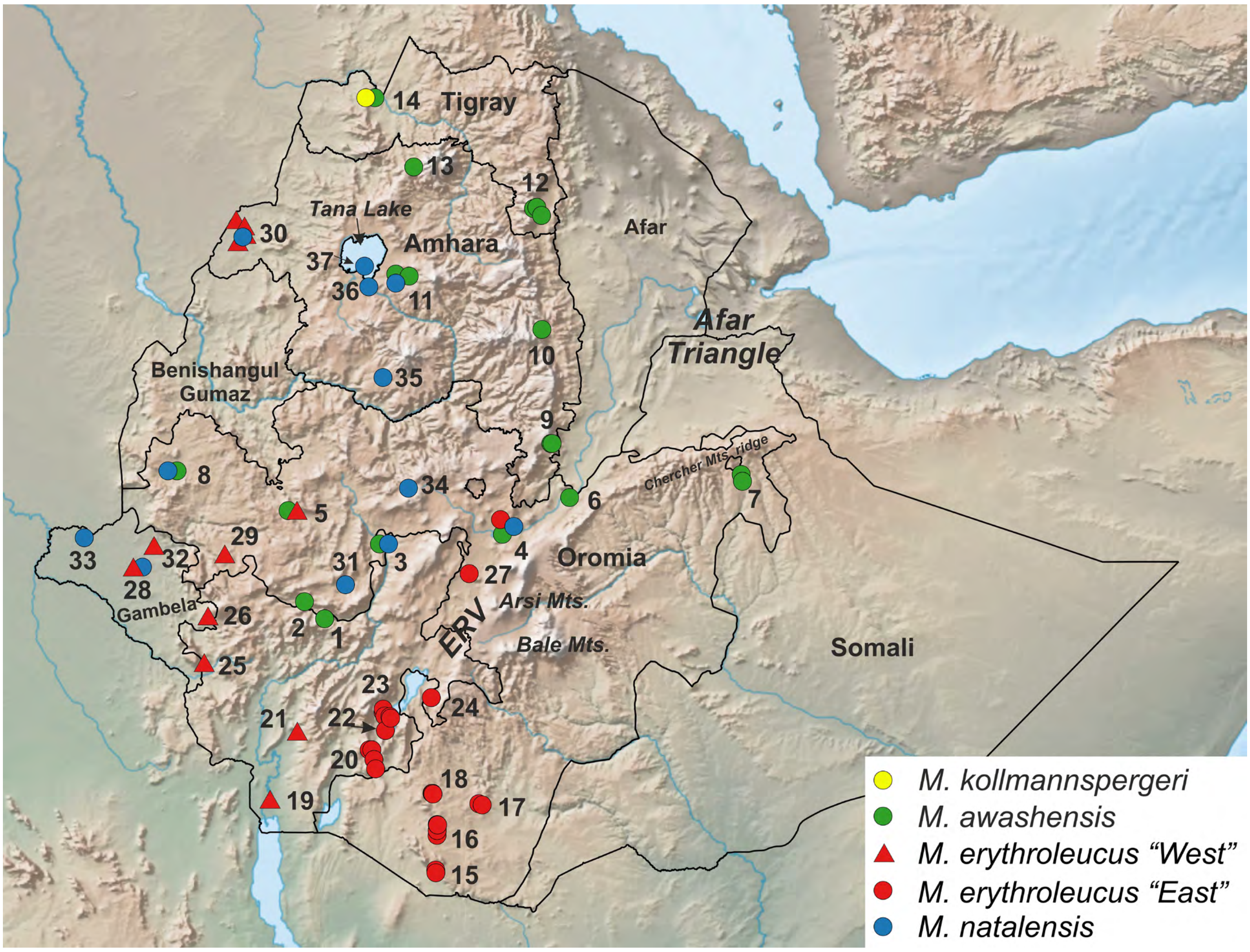

Fig. 1. Distribution of four *Mastomys* species in Ethiopia based on genetic identification of species. The numbers of localities correspond to Table 1 (ERV – Ethiopian Rift Valley).

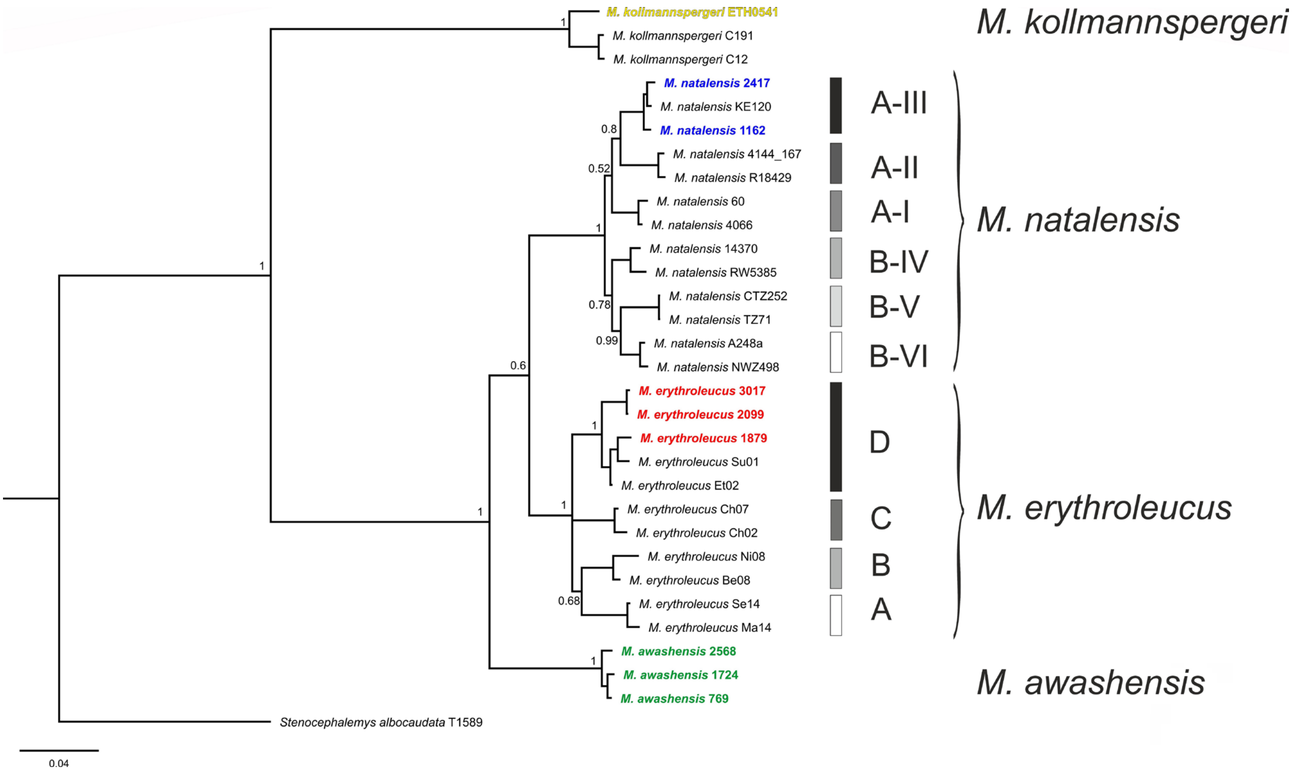

Fig. 2. Bayesian phylogenetic tree of four *Mastomys* species occurring in Ethiopia. The numbers above branches represent posterior probabilities of nodes. The abbreviations A-I to B-VI and A-D indicate intraspecific lineages of *M. natalensis* (sensu Colangelo et al. 2013) and *M. erythroleucus* (sensu Brouat et al. 2009), respectively. Ethiopian *Mastomys* are in bold and in colour.

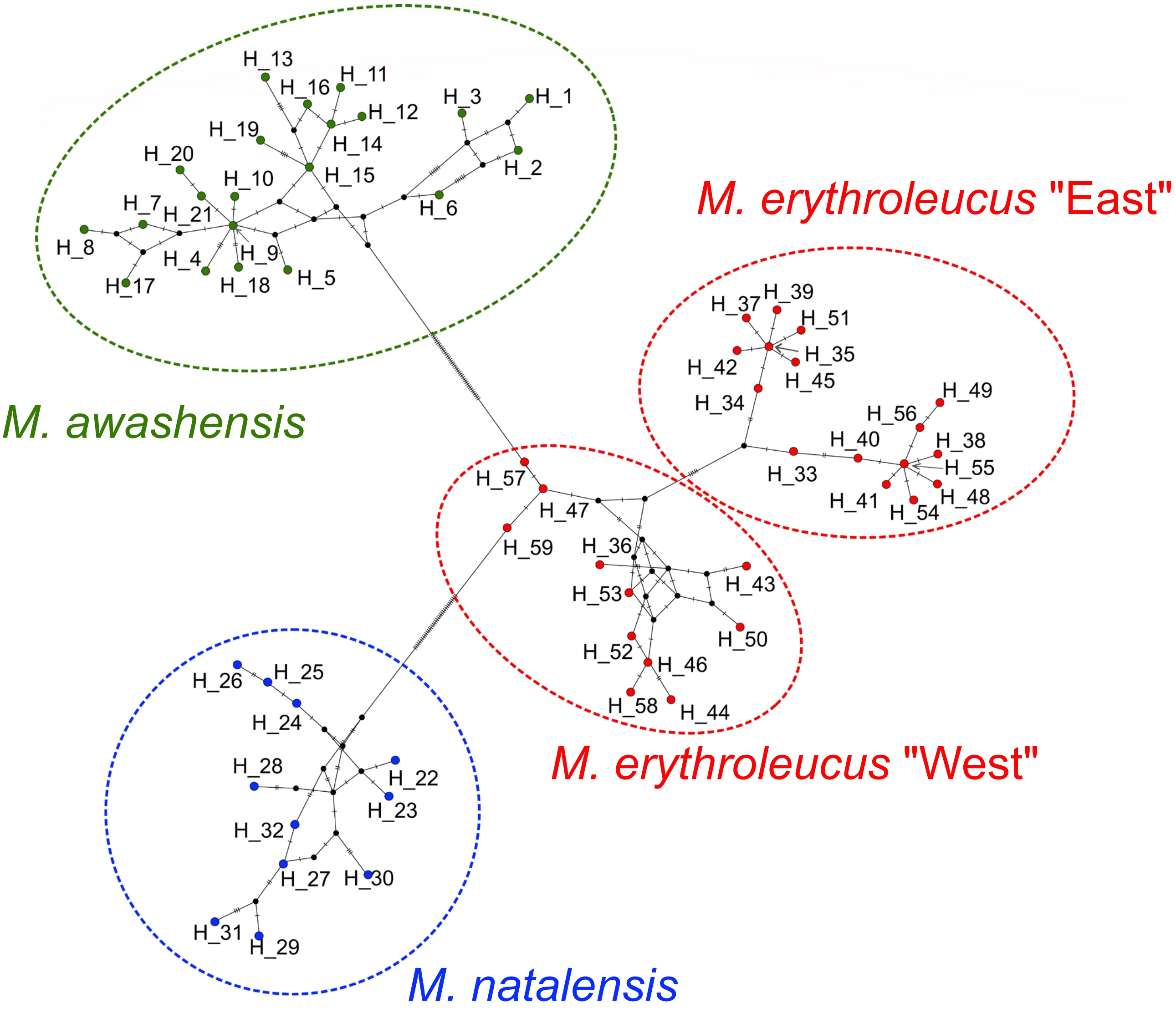

Fig. 3. Median-joining network for Ethiopian *Mastomys*. The abbreviations H_1 to H_59 correspond to haplotypes in Table S1 in the Supplementary information.

et al. 2013) and phylogroup D of *M. erythroleucus* (sensu Brouat et al. 2009) are represented in Ethiopia (Fig. 2). Haplotype network analysis (Fig. 3) indicates two subclades of phylogroup D of *M. erythroleucus* in Ethiopia (differing by up to 2.5% at cyt*b*), geographically separated from each other by the western side of the Ethiopian Rift Valley (ERV). The "West" subclade is distributed in the western part of the country, while the "East" is in the bottom of the ERV and in the southeastern part of the country (Fig. 1). When combined with additional species identification methods, we documented the presence of *M. awashensis* at 18 localities, *M. erythroleucus* at 32 localities, and *M. natalensis* at 13 localities (Fig. 1; see details in Table 1). The fourth species, *M. kollmannspergeri*, was identified based on a single cyt*b* sequence that significantly clustered with sequences of this species from northern Cameroon and Chad (Fig. 2), and represents a new species for Ethiopia.

The four Ethiopian *Mastomys* species have partly overlapping distributions (Fig. 1). The Ethiopian endemic species *M. awashensis* is widely distributed on the north-western plateau of the Ethiopian highlands, the ERV near Lake Koka and in the Awash NP. In the south-eastern plateau it was documented only from the Babille Elephant Sanctuary (see also Lavrenchenko et al. 2010). It occurs at the highest elevations of any *Mastomys* species, ranging from 967 at Mai-Temen to 3145 m a.s.l. in the Semien Mountains NP (Fig. 4). *Mastomys erythroleucus* is common in the southern part of the country (Fig. 1). Additionally, the species was recorded from two localities (vicinities of Lakes Koka and Ziway (Adamy-Tulu)) in the central part of the ERV. The

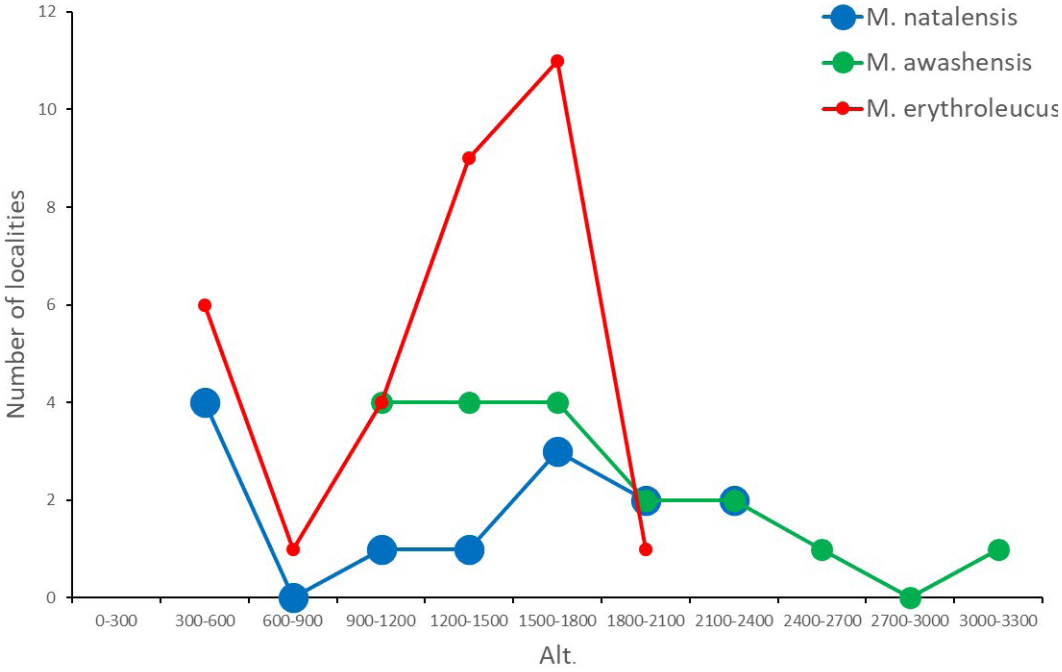

Fig. 4. The distribution of elevation profiles of Ethiopian *Mastomys*. Altitudinal range groups by steps of 300 m. The vertical axis shows the number of localities in each group. Note that the fourth species, *M. kollmannspergeri*, was found only at a single locality at 967 m a.s.l.

distribution of *M. erythroleucus* at the north-western plateau is sporadic, but it was relatively abundant in the Alatish NP (Fig. 1). This species was found within an elevational range from 380 m a.s.l. in the River Omo Valley to 1945 m a.s.l. in the Bulcha Forest on the slopes of the ERV (Fig. 4). *Mastomys natalensis* is widespread at the north-western plateau. It was found in a single locality (Lake Koka) at the bottom of the ERV and was never documented in the south-eastern plateau of the Ethiopian highlands. The elevational range of the species varies from 417 m a.s.l. in the Gambela NP to 2191 m a.s.l. in Ambo (Fig. 4). The area near Lake Koka is exceptional because three Ethiopian *Mastomys* species co-occur there. The fourth species, *M. kollmannspergeri*, was found at a single locality (Mai-Temen 967 m a.s.l.) in the northeast of the country (Fig. 1), reaching here its eastern distributional limit.

Species distribution modelling

All models obtained using MaxEnt had high mean AUC values (0.996 ± 0.001 for *M. awashensis*, 0.994 ± 0.002 for *M. erythroleucus*, and 0.987 ± 0.007 for *M. natalensis*), indicating good performance of the model. Based on the results of the Jackknife test (Table S2) there are no specific bioclimatic variables that strictly limit the distribution of particular species, but their combination appears to be important. Nevertheless, it is possible to define variables that best describe the model species distribution. The environmental variables with highest gain when used in isolation are Isothermality (BIO2/BIO7) (*100) (AUK = 0.9082), Mean Temperature of Wettest Quarter (AUK = 0.8666) and Temperature Seasonality (standard deviation *100) (AUK = 0.8467) for *M. awashensis*, Temperature Seasonality (standard deviation *100) (AUK = 0.8788), Precipitation of Driest Quarter (AUK = 0.8664) and Aridity Index (AUK = 0.8599) for *M. erythroleucus*, Precipitation of Coldest Quarter (AUK = 0.8755), Mean Temperature of Wettest Quarter (AUK = 0.8440) and Aridity Index (AUK = 0.8409) for *M. natalensis*. The environmental variables that most significantly decrease the gain when omitted and, therefore, have the most information that is not present in other the variables are Min Temperature of Coldest Month (AUK = 0.9826) for *M. awashensis*, Precipitation of Coldest Quarter (AUK = 0.9783) for *M. erythroleucus* and Precipitation of Coldest Quarter (AUK = 0.9595) for *M. natalensis*. The predicted distributions under the current climate conditions for *M. awashensis*, *M. erythroleucus* and *M. natalensis* are shown in Fig. 5, and they clearly suggest that the arid Afar and Somali regions are not suitable for any *Mastomys* species. The most suitable conditions for *M. awashensis* are predicted at medium elevation in the most north-eastern part of the north-western plateau, but also in the ERV around Lake Koka and Awash NP, along the Chercher Mountain ridge, as well as in a small part of Eritrea. The distribution of *M. erythroleucus* is

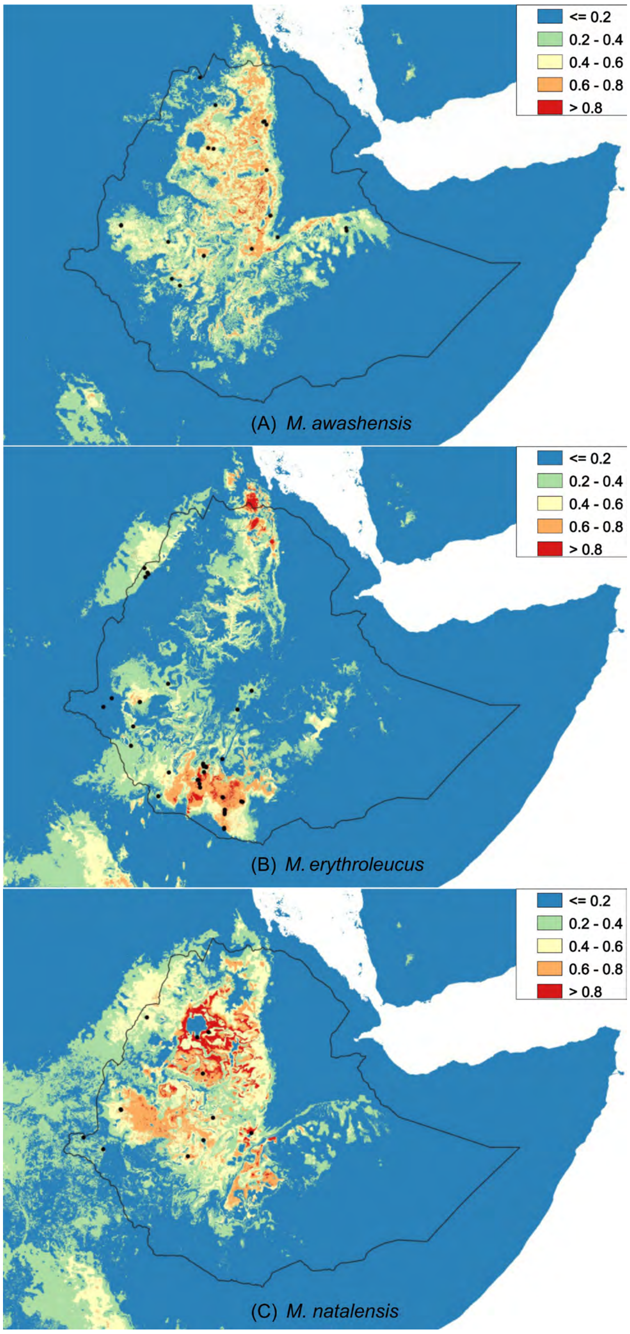

Fig. 5. Ecological niche models for present-day conditions for (A) *M. awashensis*, (B) *M. erythroleucus*, and (C) *M. natalensis*. Colours (from blue to red) represent suitability of environmental conditions and black dots depict locations of specimens used to generate models.

predicted mainly in the south of the country. For this species, suitable habitats may also occur in the eastern part of the Tigray region, in a narrow area of central Eritrea near the border with Ethiopia, where this species is absent (or possibly replaced by *M. kollmannspergeri*, though further research is required). On the other hand, the model indicates low/medium suitability for the broad belt including the Alatish NP and the Dinder NP on the border with Sudan, though we demonstrated the occurrence of *M. erythroleucus* in this area. There are almost no suitable conditions in the highlands and the northern part of the ERV. The predicted distribution for *M. natalensis* largely overlaps with that of *M. awashensis*. The highest probability of its occurrence was found at medium elevation around Lake Tana, but also in other parts of the north-western plateau, especially in its westernmost part, and in the central part of the ERV around Lakes Koka, Ziway, Abijatta and Shalla. The model also predicts suitable conditions at the south-eastern plateau around the Arsi and Bale Mountains, but currently there is no confirmed record of the species from this area.

Predicted distributions for particular *Mastomys* species partly overlap. The most similar are models for *M. awashensis* and *M. natalensis* (0.743). This finding is in accordance with available records of these species (Fig. 1). We documented the co-existence of both species at four localities: Gibe NP, Lake Koka, Dhati-Welel NP and the River Gumara (Table 1). There is a medium degree of overlap between *M. natalensis* and *M. erythroleucus* models (0.595). Both species co-exist at two localities: River Alvero Valley and Lake Koka. The smallest overlap in environmental requirements is observed between *M. awashensis* and *M. erythroleucus* (0.501). Nevertheless, these two species were found in sympatry at two localities with an average level of suitability: the eastern shore of Lake Koka and the Didessa River Valley.

Discussion

The highest diversity of multimammate mice is in Ethiopia

In this study we used a combination of genetic approaches to describe the diversity and distribution of multimammate mice in Ethiopia. We provide evidence of four *Mastomys* species in Ethiopia, more than any other African country. Such diversity is apparently associated with the heterogeneous natural conditions. The two major blocks of the Ethiopian Highlands, separated by the ERV, provide a significant elevational gradient in ecological conditions (the elevation in Ethiopia ranges from –125 to 4533 m a.s.l). Further, savannahs surrounding the highlands are divided into at least two major biogeographical types: Sudanian in the northwest and Somali-Masai in the ERV and south-east (Linder et al. 2012). This makes the country an outstanding hotspot of biodiversity, not only for numerous highland endemics, but also for taxa living in open savannah-like ecosystems. Until the end of the last century, all Ethiopian *Mastomys* were considered a single species (called e.g. "*Praomys natalensis*" by Yalden et al. 1976). With increasing use of (cyto)genetic methods, the number of species has increased. Lavrenchenko et al. (1989) and Orlov et al. (1989) found *Mastomys* with 2n = 32 chromosomes in Ethiopia, and Yalden et al. (1996) in their revised Ethiopian check-list of mammals report two species of multimammate mice (called *Praomys erythroleucus* with 2n = 38, and *P. hildebrandtii* with 2n = 32). Later, Lavrenchenko et al. (1998) described a new Ethiopian species, *M. awashensis*, distinguished on the basis of its genital morphology, spermatozoal structure, allozyme electrophoresis and unique features of its 2n = 32 karyotype. Finally, we provide here the first evidence for the occurrence of a fourth species, *M. kollmannspergeri*, which is known from Sudanian savannahs in central Africa, with one (presumably isolated) locality in Sudan (Dobigny et al. 2008). This record means that the distribution range of *M. kollmannspergeri* is expanded to the northeast by 380 km.

Two species of Ethiopian *Mastomys*, *M. natalensis* and *M. erythroleucus*, are among the most widespread rodent species in sub-Saharan Africa. Both have pronounced intraspecific phylogeographical structure with six described lineages in *M. natalensis* (AI-AIII in Sudanian and BIV-BVI in Zambezian savannahs; Colangelo et al. 2013) and four lineages in *M. erythroleucus* (all of them in Sudanian savannah; Brouat et al. 2009). The parapatric distribution of particular lineages and the presence of narrow zones of hybridization at their zone of contact (e.g. Gryseels et al. 2017) suggest that their evolutionary history was influenced by Pleistocene climatic changes. During unsuitable (humid) periods their populations were fragmented (e.g. by riverine or montane forests; see Colangelo et al. 2013) and differentiated in allopatry in discrete savannah refugia. In phases when the savannah ecosystem expanded, their populations also increased and currently we can observe secondary contacts of differentiated lineages, sometimes located along large rivers (Brouat et al. 2009), or mountains (e.g. Eastern Arc Mountains; Colangelo et al. 2013). In Ethiopia, both species reach the north-eastern margin of their distribution. All genotyped individuals of *M. natalensis* belong to the clade A-III, which has hitherto been known only from south-western Kenya (Colangelo et al. 2013), and we have, therefore, significantly extended the known distribution of this species northwards (compare with the map in Colangelo et al. 2013 and Denys et al. 2017). Similarly, all Ethiopian individuals of *M. erythroleucus* had mtDNA of the easternmost lineage D, previously known only from one locality in southern Ethiopia and one in Sudan (Brouat et al. 2009). This lineage is further divided into "West" and "East" subclades, geographically separated by unfavorable mountain ridges at the west margin of the ERV and at the bottom of the ERV, which likely acted as a barrier to gene flow during humid periods of the Pleistocene when was filled by large palaeolakes (a similar phylogeographic pattern is also found in other savannah rodents, e.g. gerbils of the genus *Gerbilliscus*; Aghová et al. 2017). Visual inspection of distributional patterns (Fig. 1) and ecological niche models (Fig. 5) suggest that the two species overlap in Ethiopia to only a limited extent. While *M. erythroleucus* is common in the relatively arid southernmost part of the country (plus the Alatish NP in north-western Ethiopia), *M. natalensis* is widespread in the lower to middle elevations of the north-western highlands. More intensive sampling in western Ethiopia (e.g. Benishangul-Gumuz region) is still needed to assess the real level of their distributional and ecological overlap.

The third species, *M. awashensis*, was originally described as a narrow endemic in the River Awash Valley (Lavrenchenko et al. 1998). Genotyping of material collected in more recent surveys shows it is also found in eastern Ethiopia (Lavrenchenko et al. 2010) and Tigray (Colangelo et al. 2010), suggesting that it is more widespread than previously thought. Here we report numerous additional localities, especially from the west-central highlands, where it was found in sympatry with both species discussed above (Fig. 1). On the other hand, it seems to be the only multimammate mouse species occupying large parts of the northern highlands and eastern Ethiopia. We can speculate that the species differentiated in a long-term savannah refugium separated from other similar open habitats (inhabited by other *Mastomys* species) by mountain ranges. Such a refugium may have been located at the margin of the Afar lowlands, where other endemic taxa of savannah rodents were recently found, e.g. the genera *Gerbilliscus* (Aghová et al. 2017), *Acomys* (Aghová et al. 2019) and *Arvicanthis* (Bryja et al. 2019). Spreading deeper and higher into the highlands, especially along the river valleys, may have been facilitated by recent intensive deforestation of the landscape by humans. More detailed phylogeographic studies are needed to shed light on the evolutionary history of this taxon. Currently we consider it as endemic to Ethiopia, though it may also be present in neighbouring parts of Eritrea. The ecological niche model also predicts suitable environmental conditions for this species in northern Uganda and western Kenya, but it has never been confirmed in these countries. Its presence there seems unlikely because the belt of semi-desert savanna, inhospitable for all *Mastomys*, effectively separates southern Ethiopia and the predicted regions of Kenya and Uganda. While many species in the highlands are endemic to Ethiopia, this is a much rarer phenomenon among savannah taxa. In addition to *M. awashensis* there are only few such species, e.g. *Mus proconodon* (Bryja et al. 2014, Lavrenchenko & Bekele 2017), or savannah taxa from the margin of the Afar Triangle mentioned above.

We documented *M. kollmannspergeri* from a single locality (Mai-Temen) in the northeast of the country, where it was found in sympatry with *M. awashensis* (but not captured in the same trap line). *Mastomys kollmannspergeri* was originally described as a subspecies of *M. natalensis* from Ighazer (Niger) (Petter 1957). On the basis of chromosomal analysis of samples from the type locality, Chad and Southern Sudan, it was proposed that these specimens, referred to as *M.* cf. *kollmannspergeri*, should receive species designation (Viegas-Péquignot et al. 1987, Dobigny et al. 2002, Granjon et al. 2004). *Mastomys verheyeni* was described as a species with a narrow habitat surrounding Lake Chad in northeastern Nigeria and northern Cameroon (Robbins & Van der Straeten 1989, Lecompte et al. 2002, 2005). Further studies unequivocally showed that *M. verheyeni* is a junior synonym of *M. kollmannspergeri* (Denys et al. 2002, Dobigny et al. 2008). This species was reported from relatively few localities in the central part of the Sahelo-Sudanian savannah (Niger, northern Cameroon and Chad) and a single locality in eastern Africa in south-eastern Sudan (Dobigny et al. 2008). This is a new species for Ethiopia and the present record suggests that it may be more widespread in under-sampled regions of the eastern half of the Sahelo-Sudanian savannah belt.

Co-existence of multiple species of *Mastomys*

A notable finding of the present study is evidence for the co-existence of multimammate mice species as well as divergence in ecological niche occupancy. Dobrokhotov (1982) showed that *M. erythroleucus* and *M. natalensis* are sympatric in most of Nigeria. However, *M. erythroleucus* lives exclusively in the houses and outbuildings of humans, while *M. natalensis* is known only from natural biotopes (secondary forests, agricultural land and untouched savannah). In the north of Nigeria, in a semi-desert savannah where *M. erythroleucus* is absent, *M. natalensis* also lives in human buildings. Thus, populations of both species, occupying different ecological niches, and apparently do not co-occur with each other. In Sierra Leone the habitat preferences of these species are the opposite to those observed in Nigeria: *M. erythroleucus* dominates the natural biotopes, and *M. natalensis* prefers a commensal lifestyle (Bellier 1975, Hubert 1977). A similar situation is observed in Senegal, where *M. natalensis* lives strictly in human habitations, while *M. erythroleucus* is opportunistic but prefers savannah-like habitats, and a third species, *M. huberti*, inhabits natural and cultivated wetlands (Duplantier et al. 1990, 1996, 1997, Brouat et al. 2007). In Coastal Guinea, in Mankountan, *M. erythroleucus* is found both in wet rice fields and in houses, *M. huberti* prefers wet rice fields, where it co-exists with *M. erythroleucus*, but it never enters human buildings (Denys et al. 2012). In northern Cameroon, both *M. erythroleucus* and *M. kollmanspergeri* inhabit savannah and fields but are rarely found inside houses (in Kossa and Doué, respectively). In contrast, most *M. natalensis* were trapped inside houses, and only few were found outdoors (Dobigny et al. 2011). In Tanzania, *M. natalensis* shows both commensal and free-living populations and it was shown that commensalism could quickly lead to genetic differentiation (Gryseels et al. 2016).

Several *Mastomys* species can live in sympatry in Ethiopia. However, their co-existence shows a different character to that seen in West Africa, where one species is usually commensal, while another lives in natural savannah-like habitats. In Ethiopia, all three widespread species prefer natural habitats, but this observation can be biased by the relatively low intensity of sampling in human habitations. The only case of clear habitat separation was observed in the Alvero River Valley, where *M. natalensis* lives strictly in human settlements while *M. erythroleucus* occurs both in buildings and in savannah habitat (Lavrenchenko 1995). In nearby localities near Lake Koka, both *M. natalensis* and *M. erythroleucus* co-exist in natural biotopes and the results of distributional modelling predict a high level of suitability for both species in this area. A detailed study of commensal *Mastomys* in Ethiopia has not yet been conducted. Our pilot data show that *M. erythroleucus* can inhabit both the savannah and human settlements in southern Ethiopia (Arero Forest and Borena NP). *M. awashensis* demonstrates a lesser tendency towards commensalism. This species is rare in crop fields but is documented in household compounds in three hamlets in the Tigray region (Meheretu et al. 2013). This pattern is similar to the situation in West Africa, where *M. natalensis* and *M. erythroleucus* can be commensal, and *M. huberti* expresses a preference for natural habitats.

Ethiopia has the highest number of *Mastomys* species of any African country, one of which is endemic (*M. awashensis*). Further research based on a geographically extended data set will help to reduce the gaps in our understanding of the distribution of multimammate mice in Ethiopia and demonstrate their co-existence and level of commensalism. This information is of particular importance, because *Mastomys* rodents are important agricultural pests, and each of the sibling species can be a specific reservoir for pathogens potentially harmful to humans. Furthermore, detailed information on the distribution of *Mastomys* species will be necessary for the adoption of the most promising species-specific pest-control methods (e.g. Massawe et al. 2018).

Acknowledgements

This study was supported by the Russian Foundation for Basic Research (project no. 18-04-00563-a) and the Czech Science Foundation (project no. 18-17398S). All fieldwork complied with legal regulations in Ethiopia and sampling was carried out with the permission of the Ethiopian Wildlife Conservation Authority and the Oromia Forest and Wildlife Enterprise. For management of the JERBE expedition, we are grateful to Andrei Darkov (Joint Ethio-Russian Biological Expedition, Fourth Phase – JERBE IV). We thank D.S. Kostin, A.R. Gromov, D.Y. Alexandrov, A.A. Warshavsky, Yu. F. Ivlev, M. Kasso, R. Šumbera, A. Konečný, V. Mazoch, T. Aghová, P. Kaňuch, J. Krásová, M. Lövy, D. Mizerovská, K. Welegerima, and M. Uhrová for help with field sampling. Author contributions: A.A. Martynov, J. Bryja, Y. Meheretu, L.A. Lavrenchenko conceived and designed the study and collected most of the samples; A.A. Martynov and J. Bryja analyzed the genetic data; A.A. Martynov performed environmental niche modelling and wrote the first version of the manuscript. All authors contributed to the final version of the paper. All authors read and approved the final manuscript.

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Supplementary online material

Table S1. List of samples used to determine the phylogenetic position of Ethiopian *Mastomys* and construct the haplotype network. The abbreviations A-I to B-VI and A-D indicate intraspecific lineages of *M. natalensis* (sensu Colangelo et al. 2013) and *M. erythroleucus* (sensu Brouat et al. 2009), respectively.

Table S2. Results of jackknife analysis for three *Mastomys* species. Numbers represent AUC values when a model was created using only the particular variable separately/a model was created with the remaining variables.

Table S3. Categories of land cover.

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