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Niche-partitioning of three *Apodemus* species (Mammalia: Murinae) in an urban environment

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Abstract

Three species of the genus *Apodemus* (Wood Mouse *Apodemus sylvaticus*, Yellow-necked Mouse *A. flavicollis*, Herb Field Mouse *A. uralensis*) were studied in public parks and greeneries in the city of Vienna, Austria (1.76 million inhabitants). The study focused on niche-partitioning of these species along the urban gradient and at the habitat level. In 23 randomly selected parks at 59 different sites, 129 adult individuals were trapped during 2676 trap-units (total success rate 4.8 %). *A. sylvaticus* was most common (48.7 %), followed by *A. flavicollis* (43.3 %), and *A. uralensis* (8 %). The trapped individuals were unevenly distributed along the urban gradient (0–55 individuals/100 trap-units). Although *A. sylvaticus* and *A. flavicollis* overlapped broadly (38 % of parks), in urban areas *A. sylvaticus* was dominant, whereas in suburban habitats *A. flavicollis* was more common. *A. uralensis* was trapped in small numbers both at the periphery and city centre. Niche-partitioning was determined at macrohabitat level refering to park size, where medium-sized (>3.5 ha) and larger parks (>100 ha) were preferred over smaller ones. At microhabitat level partitioning occurred mainly based on variables defining predominantly intensive and extensive used parks.

Keywords: *Apodemus sylvaticus*, *Apodemus flavicollis*, *Apodemus uralensis*, habitat selection, urban gradient

Zusammenfassung

In der Großstadt Wien (1.76 Mill. Einwohner), Österreich, wurden drei Vertreter der Gattung *Apodemus* (Waldmaus *Apodemus sylvaticus*, Gelbhalsmaus *A. flavicollis*, Zwergwaldmaus *A. uralensis*) in öffentlichen Parks und Grünanlagen untersucht. Die Studie konzentrierte sich auf die Nischentrennung dieser Arten entlang des urbanen Gradienten. Auf 59 Probeflächen in 23 zufällig gewählten Parks wurden während 2676 Fangeinheiten (Erfolgsrate 4.8 %) insgesamt 129 Individuen gefangen; *A. sylvaticus* (48.7 %) war am häufigsten gefolgt von, *A. flavicollis* (43.3 %) und *A. uralensis* (8 %). Alle Arten waren entlang des urbanen Gradienten ungleich verteilt (0–55 individuals/100 trap-units). Obwohl *A. sylvaticus* und *A. flavicollis* deutlich überlappten (in 38 % der Parks), dominierte *A. sylvaticus* in urbanen Habitaten während *A. flavicollis* in suburbanen Habitaten häufiger anzutreffen war. *A. uralensis* wurde nur in geringen Zahlen entlang der Peripherie und nahe dem Stadtzentrum nachgewiesen. Die Nischentrennung erfolgte auf Makrohabitat-Ebene vor allem über die Parkgröße, wobei mittelgroße (>3.5 ha) und große Parks (>100 ha) gegenüber kleinen bevorzugt wurden. Auf Mikrohabitat-Ebene unterschieden sie sich vor allem in Merkmalen die intensiv und extensive genutzt Parks unterscheiden.

Introduction

Species tend to select characteristic vegetation profiles (the 'niche gestalt' of James 1971). At the simplest level, certain landscapes and vegetation types are associated with

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typical index species and often species can be roughly identified given a set of habitat types. But this is often not possible in closely related species or species with similar demands. Thus, habitat relationships become more substantial at finer scales (Fuller 2013). Animal species that are able to survive and persist in urban ecosystems are characterised by their high flexibility in habitat choice. They cover a diversification of ecological niches and are tolerant towards disturbance (Luniak 2004, Adams 2005, Angold et al. 2006). They are often pioneers, which are capable of expanding into city centres (Yalden 1980, Klausnitzer 1993, Reiter & Jerabek 2002).

Flexible generalists have a crucial advantage over specialists in their life history strategies. Among rodents, mice of the genus *Apodemus* possess advantageous pre-adaptations to colonise such urban ecosystems (Frynta et al. 1994). The urban space is a heterogeneous environment with many different possible habitat types for niche-building. In contrast to natural habitats, degree and intensity of anthropogenic disturbance are essential factors which determine species' occurrence. Common mowing of lawns, use of pesticides and planting of exotic plants are some of such anthropogenic disturbances (Dickman & Doncaster 1987). Urban stress seems to have a remarkably stronger influence on the structure and dynamics of small mammal populations than other stress factors in forest habitats (Chernousova 2010).

In the city of Vienna, three sympatric *Apodemus* species have been recorded in different densities. Among them, Yellow-necked Mouse *Apodemus flavicollis* and Wood Mouse *A. sylvaticus* are similar in size and mean weight of 33.4 g and 28.4 g respectively. Only Herb Field Mouse *A. uralensis* is markedly smaller, weighing only 20.5 g on average (Mitter et al. 2013). The biological characteristics and demands of the species in question give them each a different potential for settling in big cities. The most common species, *A. sylvaticus,* is considered a pioneer species which is able to colonise 'artificial' habitats even within a year. In this short time after re-cultivation, it can establish viable populations (Halle 1993) even in city centres (Frynta et al. 1994, Frynta & Vohralík 1994, Feiler & Tegegn 1998). *A. flavicollis* is common as well, and is known to be very mobile, but during its dispersal it prefers forested habitats over open habitats (Montgomery 1989a, b; Vukicevic et al. 2006). The 'steppe' species *A. uralensis* is least common (Mitter et al. 2013). In Austria it is documented for 'dry' habitats (Bauer 1960), wet fields and meadows (Steiner 1966) and humid riparian forests (Spitzenberger & Steiner 1967).

The present study is focused on (1) the distribution pattern of these three sympatric *Apodemus* species along the urban gradient, defined by the distance to the city centre, as well as (2) on possible habitat related differentiations among them in the urban environment of the city of Vienna, Austria.

Material and methods

Study area

The study area consisted of a variety of parks and greeneries in the city of Vienna (415 km² and 1.76 million inhabitants; 48° 12′ N, 16° 22′ E). Vienna is the largest and most populated city in Austria, and is situated at the north-eastern foothills of the Alps and at the north-western range of the Vienna Basin. Pannonian influences meet continental

Fig. 1: Example of an intensively used 'Baroque' garden (Laaer Berg) – Photo: G. Mitter.

climate and both are enriched by the mild city climate (WICHMANN et al. 2009). Over the study area, altitude ranges between 155–270 m a.s.l., precipitation rises from 515 mm in the east to 740 mm in the west and mean temperatures vary between 9.6°C in the west and 10.4°C in the east (WICHMANN et al. 2009, BERGER & EHRENDORFER 2011). Vienna is a 'green' city. Less than the half of its total area is sealed by buildings, and the remaining areas are composed of 'green' habitat elements. Large parts of the western periphery (Wienerwald) and the south-east (Lobau-riparian forest of the Danube, Prater) are covered by forest. Additionally, there are several extensively used parks in the inner city districts. Besides large park areas, e.g. the park surrounding Schönbrunn palace or the Augarten (50–>150 ha), Vienna also has many smaller parks, some only with a size of a few hundred square metres. Green areas cover between 3–13 % of the inner city districts and up to 70 % of the western districts (http://www.wien.gv.at/umwelt/parks/anlagen/). Having a lower proportion of green areas, the city centre also has the highest degree of sealed soil. For the design of this study, we tried to cover a wide range of public parks and greeneries, both regarding their distance from the city centre as well as their size and habitat composition (intensively and extensively used). Intensively used parks often included so-called 'Baroque' gardens (Fig. 1), whereas extensive areas often resembled forests (Fig. 2).

Among all areas, 23 parks were randomly selected (size variation 1.1–600 ha) with a total of 59 different patches. In the large parks with diverse habitat types (e.g. Augarten, Stadtpark, Schönbrunn, botanical garden), several different trapping patches were selected per park. These sites were situated between 0.6–9 km from the city centre

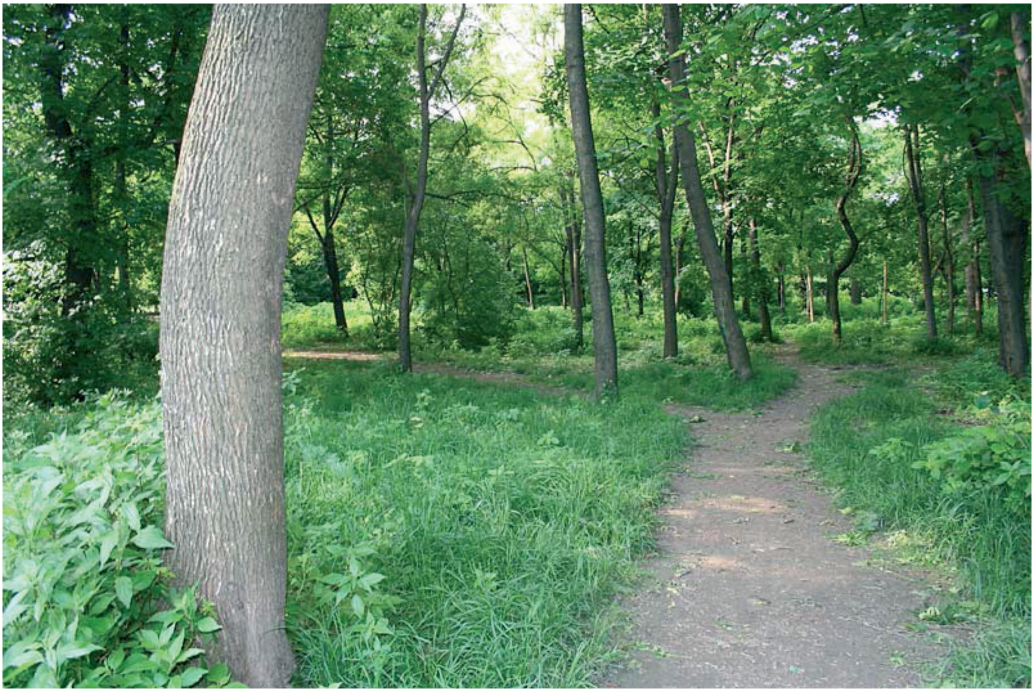

Fig. 2: Extensively used parks often look like forests (Augarten) – Photo: G. Mitter.

(St. Stephen´s Cathedral). A total of 23 habitat variables were used to characterise the particular park type at each patch (Table 1). These habitat variables were measured in an area of 2 000 m^2 around the trapping area.

Live-trapping and species identification

Mice were trapped using Rödl-type live traps (Janova et al. 2010). The trap dimensions were 24 cm (length) × 6 cm (width) × 6 cm (height). Depending on the specific habitat type at every site, 10–20 traps were laid out at regular distance intervals of 10 m. Distinctive structures like ditches, slopes and prominent trees were used preferentially, as they represent good trapping sites for small mammals (Steiner 1966). We used the 'minimum number alive' method (Krebs 1996) to calculate rodent densities. Each site was sampled for 48 hours and each trap was controlled two times a day, in the morning and in the evening hours. During 2676 trapping units, 129 adult *Apodemus* individuals were caught, among them 55 *A. sylvaticus,* 49 *A. flavicollis* and 9 *A. uralensis*. The study period extended from May to September 2010. Trapping order of parks was determined randomly to avoid a possible bias. Traps were baited with high-energy peanut butter (78 % fat, 9 % carbohydrates und 13 % proteins).

Identification of living *Apodemus* species is difficult (Steiner 1966, Götz 1991, Spitzenberger 2001) as teeth formula can't be used. So besides classical identification literature (Feiler & Tegegn 1998, Jenrich et al. 2010), an identification catalogue was prepared using study skins from the Museum of Natural History Vienna, which showed the individual variation in colour and pattern of the taxa in the study area.

Statistical analysis

Non-parametric tests were used for statistical analyses, as most habitat variables were not normally distributed. Relationships between trapping success and habitat data were tested with regression analyses, whereas Mann-Whitney U-Test was used for group comparisons. Cluster analyses were applied to detect whether habitat variables could be combined into clusters. Before starting this process, data were converted to an ordinal scale. Data were usable for cluster analysis, because they contained no outlier or extreme values. Two types of park sites (cluster 1, cluster 2) could be identified by this method. The correlation matrix showed a similar result to the Spearman correlations. We used Spearman correlations to evaluate the distribution of *Apodemus* species at different park sites. Kruskal-Wallis test was used to assess whether either of the *Apodemus* species showed a preference for one of the clusters. The same test was taken to check whether the different species were more abundant in some parks than in others. All statistical analyses were carried out in SPSS 19.0.

Results

Distribution along the urban gradient

Distribution patterns of the three *Apodemus* taxa along the urban gradient showed noticeable differences. One remarkable such difference was the trapping frequency along the urban gradient, which varied between 0 and 55 individuals / 100 trap units. Three peaks were apparent: the first in the intensively used parks in and adjacent to the city centre (distance to centre 1–1.3 km). The second in semi-natural parks around that circle (distance 1.7–1.9 km), and the third in the large park areas with intensively and extensively used habitat elements (distance 5–6 km). The capture rate declined towards the periphery in *A. sylvaticus* (r_s = - 0.789, $p < 0.01$) and was more or less constant in the other two species (*A. flavicollis*: r_s = 0.277, n.s.; *A. uralensis*: r_s = 0.540, n.s.). Occurrence of both *A. sylvaticus* and *A. flavicollis* overlapped broadly. Close to the city centre, *A. sylvaticus* was dominant (65–100 %), while *A. flavicollis* (74–100 %) dominated towards the periphery. *A. uralensis*, which was previously confirmed only for the south-eastern parts of Vienna, occurred sympatrically with the two other species. Generally, medium-sized (> 3.5 ha) and large parks (> 50 ha) were preferred over small ones (< 3.5 ha). In *A. sylvaticus*, a significant correlation between number of trapped individuals and park size was confirmed (r_s = - 0.869, $p < 0.01$), but not so in *A. flavicollis* (r_s = 0.304, n.s.) and *A. uralensis* (r_s = 0.512, $p < 0.08$). Generally, in medium-sized parks *A. sylvaticus* was dominant, while *A. flavicollis* dominated in large ones (Mann-Withney U-Test = 4.6, $p < 0.05$). Positive relationships between body weight and park size were found in *A. flavicollis* (r_s = 0.516, $p < 0.029$) and in *A. sylvaticus* (r_s = 0.633, $p < 0.034$). In smaller parks (< 50 ha), mean body weight was lower than in more extensive green areas, especially compared to the size-category > 100 ha. Sample size was too small in *A. uralensis* to show any relationship (r_s = 0.200, $p < 0.4$, n.s.). No relationship was detected between body weight and the urban gradient (*A. flavicollis:* r_s = 0.16, $p < 0.29$, n.s.; *A. sylvaticus:* r_s = 0.27, $p < 0.3$, n.s.; *A. uralensis:* r_s = -0.394, $p < 0.303$, n.s.).

Table 1: Cluster analysis of habitat variables in Viennese public parks and greeneries. Significant variables are shown in bold (see text). Variables assigned to cluster 1 (intensively used parks) are underlain with pale grey, those assigned to cluster 2 (extensively used parks) with dark grey.

Habitat variable	**Mann-Whitney U**	**Wilcoxon W**	**Z**	**Grouping variable: cluster**[1]	**Rank means**	
					1	**2**
Park size (m^2)	227.5	1217.5	-1.908	0.056	27.7	36.8
Park sealed soil (%)	234	1224	-1.942	0.052	27.8	36.4
Park flowers (%)	231	351	-2.132	**0.033**	32.3	23.4
Park lawn (%)	115	235	-4.117	**0**	34.9	15.7
Park meadow (%)	259	379	-1.555	0.12	31.6	25.3
Park herbs (%)	127	1117	-3.838	**0**	25.4	43.5
Park lane (%)	113	233	-4.301	**0**	34.9	15.5
Shrub density (%)	295	415	-0.632	0.528	30.8	27.7
Shrub species total (n)	330	450	0	1	30.0	30.0
Shrub species native (n)	209	1199	-2.227	**0.026**	27.3	38.1
Shrub height (m)	264	1254	-1.179	0.238	28.5	34.4
Tree single (n)	97.5	217.5	-4.679	**0**	35.3	14.5
Tree group (n)	247.5	367.5	-2.129	**0.033**	31.9	24.5
Tree forest (n)	0	990	-7.616	**0**	22.5	52.0
Tree species total (n)	233	1223	-1.790	0.073	27.8	36.5
Tree species native (n)	243	1233	-1.625	0.104	28.0	35.4
Tree dbh <10 cm (n)	191	1181	-3.252	**0.001**	26.8	39.3
Tree dbh 10-30 cm (n)	173.5	1163.5	-2.839	**0.005**	26.4	40.4
Tree dbh 30-50 cm (n)	193	1183	-2.494	**0.013**	26.9	39.1
Tree dbh 50-70 cm (n)	225	1215	-2.003	**0.045**	27.6	37.0
Tree dbh 70-100 cm (n)	225.5	1215.5	-2.231	**0.026**	27.6	37.0
Tree dbh >100 cm (n)	264.5	1254.5	-2.035	**0.042**	28.5	34.4
Total tree numbers (n)	142.5	1132.5	-2.686	**0**	25.7	42.5

[1] Asymp. Significance (2-tailed)

Habitat selection in the city parks

Habitat structure in the city parks was described by means of cluster analysis. Two main habitat types (cluster 1, cluster 2) could be differentiated (Table 1). Cluster 1 characterised intensively used parks with a high lawn and flower proportion, low herb layer, prominent lane proportion, low number of native shrub species, more single or small groups of trees. All other parks and greeneries with opposite habitat characters fell into cluster 2. Park habitat-type and the trapping results were correlated by means of a Spearman correlation to test whether the three *Apodemus* species were sympatrically or

Table 2: Spearman correlation between habitat variables and *Apodemus* trapping numbers. Notification limit $r_s = 0.257$ ($p < 0.1$). Trends for positive and negative correlations above that limit are shown in italics and bold.

Habitat variables		**Notification limit**	
	A. flavicollis	***A. sylvaticus***	***A. uralensis***
A. flavicollis			
A. sylvaticus	0.531		
A. uralensis	0.253	0.355	
Park size (m²)	0.002	-0.095	0.097
Park sealed soil (%)	0.185	0.035	-0.002
Park flowers (%)	***0.325***	***0.264***	0.117
Park lawn (%)	-0.011	0.221	-0.057
Park meadow (%)	-0.106	-0.015	0.012
Park herbs (%)	0.084	-0.139	0
Park lane (%)	-0.168	-0.156	-0.067
Shrub density (%)	-0.026	-0.107	-0.131
Shrub species total	***0.261***	0.143	0.226
Shrub species native (n)	***0.334***	0.135	***0.258***
Shrub height (m)	0.190	0.219	0.171
Tree single (n)	-0.160	***-0.285***	-0.156
Tree group (n)	0.006	***0.334***	-0.048
Tree forest (n)	***0.259***	0.032	0.145
Tree species total	0.110	-0.168	0.084
Tree species native (n)	0.165	-0.110	0.019
Tree dbh <10 cm (n)	-0.076	-0.080	0.140
Tree dbh 10-30 cm (n)	0.190	***0.293***	0.012
Tree dbh 30-50 cm (n)	0.137	-0.097	-0.172
Tree dbh 50-70 cm (n)	0.136	-0.204	-0.080
Tree dbh 70-100 cm (n)	***0.262***	-0.184	0.067
Tree dbh >100 cm (n)	0.055	-0.067	0.036
Total tree numbers (n)	0.245	0.176	0.011
	0.400	***-0.400***	0.078

syntopically distributed. *A. flavicollis* and *A. sylvaticus* were shown to occur in 38 % of the parks sympatrically. But they were only marginally syntopic since, at microhabitat level, they differed markedly in some of the habitat variables (Table 2). Because of the unfavourable ratio between a high number of parks and low trapping success, no significant correlations were found. By setting the notification limit to $p < 0.1$, some trends could be identified: *A. flavicollis* preferred parks with high flower proportion, high shrub diversity in terms of absolute species and native species numbers, high forest-like elements and old trees with a diameter > 70 cm. Microhabitat of *A. sylvaticus* also consisted of a high flower proportion, but single trees were avoided in favour of groups of trees with small diameters (10–30 cm). Due to the small sample size, no clear picture could be drawn for the urban habitat demands of *A. uralensis*, with the exception of a possible correlation to a high proportion of native shrubs.

Table 3: Kruskal-Wallis test of preference for either of the habitat clusters and for park sites by the three *Apodemus* species. Significant differences are shown in bold.

		A. flavicollis	***A. sylvaticus***	***A. uralensis***
Cluster 1 or 2	χ^2	3.54	0.003	1.252
	df	1	1	1
	p <	0.060	0.958	0.263
Park site	χ^2	34.059	44.814	17.105
	df	22	22	22
	p <	**0.048**	**0.003**	0.758

Kruskal-Wallis tests were used to show whether the *Apodemus* species were more frequent in the anthropogenically influenced cluster 1 or in the widely undisturbed cluster 2 (Table 3). No significant results were found. Using the same test for park sites, however, significant differences were found for *A. flavicollis* and *A. sylvaticus*, explaining why *A. flavicollis* and *A. sylvaticus* were rarely found together in the same habitat complex. In general, a greater sample size would be beneficial to differentiate the interspecific microhabitat requirements of the three urban *Apodemus* species more clearly.

Discussion

Evolutionary and ecological success of a species, as well as individual survival, depends on the successful adaptation to varying environmental conditions (Scharfe & Schlund 1992). In the city of Vienna, a great variety of habitats offer a large number and different quality of ecological options. Therefore, wild animals such as representatives of the genus *Apodemus* can achieve high abundances. Opportunistic commensals are best preconditioned for using the biotic and abiotic advantages provided by artificially developed habitats (Pattisiall & Cundall 2009). Regarding their population dynamics, behaviour and feeding habits, they are highly flexible. Due to their differing biological characteristics and demands, species possess different abilities to settle in urban environments. At the moment it is not known whether the specific traits of the *Apodemus* species will be sufficient to settle permanently in the urban environment, which consists of many isolated habitat islands. One open question is whether the subpopulations of the three species are in genetic contact to each other through green corridors or if they are isolated in the long term.

Due to their adaptability, various species of the genus *Apodemus* are common in parks and greeneries throughout Vienna, with insular areas of higher abundance. Despite claims made by Jenrich et al. (2010), the species *A. flavicollis* and *A. sylvaticus* are not as widely distributed as generally assumed. The urban environment is a very specific, rapidly changing habitat (Ramalho & Hobbs 2012) that demands high adaptability. Whether niche-partitioning occurs based on intra- and interspecific competition (Chiakova & Frynta 1996, Montgomery 1978) or whether it is mainly conditioned by the ecological demands of the three species in question can currently not be determined with certainty based on the data available.

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