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SHORT COMMUNICATION

Ranging behavior of European rabbits (*Oryctolagus cuniculus*) in urban and suburban landscapes

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Abstract
Various mammals, particularly carnivores, reportedly establish smaller home ranges in urban compared with rural areas. This may be because urban environments provide optimal resources within a small area, negating the requirement to range further, or because habitat fragmentation constrains ranging behavior. Comparable information on urban populations of herbivorous mammalian species (such as European rabbits) is scarce. To fill this knowledge gap, we radio-tracked 13 individuals (seven females and six males) equipped with radio collars in a suburban and an urban study site in the city of Frankfurt am Main in Germany during the reproductive season (March to September) of 2012. The study sites differed in levels of habitat fragmentation. We report the smallest home ranges ever described for this species, with mean 95% minimum convex polygons (MCPs) covering 0.50 ha, while no consistent differences between sites were uncovered. We occasionally tracked individuals crossing streets underground (in burrows), suggesting that streets may restrict the ranging behavior of rabbits—and possibly other burrowing species—to a much lesser extent than previously thought. We conclude that heterogeneous landscape structures, made up of a diverse mosaic of buildings, parks, and gardens, provide sufficient food and shelter in close proximity to burrows at both study sites. Therefore, our data support the hypothesis that optimal resources constrain ranges in this case rather than habitat fragmentation.

Keywords Habitat fragmentation · Home range · Urbanization · Urban ecology · Minimum convex polygons (MCPs)

Introduction

Key factors influencing individuals' ranging behavior are the distribution of resources (such as food or access to breeding sites), as well as the density and distribution of conspecifics, heterospecific competitors, and predators (Adkins and Stott 1998; Prange et al. 2003, 2004; Ryan and Partan 2014). For several species, urban ecosystems provide higher and more constant food availability,

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both in the form of human waste and through deliberate feeding (Niemelä 1990; Kowarik 2011; Šálek et al. 2015). In conjunction with reduced predation pressure (birds: Møller 2008; fox squirrels: McCleery et al. 2008; but see "predation paradox": Shochat et al. 2006 for contrasting results), longer vegetation and reproductive period factors (Partecke et al. 2004; Ditchkoff et al. 2006) as well as reduced migratory behavior (in birds: Jokimäki and Suhonen 1998; Møller 2008) result in higher populations densities (Prange et al. 2003; Shochat et al. 2006; Rodewald and Gehrt 2014) and thus, heightened intra-specific competition for space and resources (Hutchings et al. 2002; Schley et al. 2004; Ziege et al. 2016).

Tucker et al. (2018) related the Human Footprint Index (HFI) to radio tracking data of 803 individuals across 52 different mammalian species. The HFI is an index with a global extent that combines multiple proxies of human influence. It was calculated based on the extent of built environments, crop and pastureland, human population density, nighttime lights, railways, roads, and navigable waterways (for more details see Venter et al. 2016 and Tucker et al. 2018). An HFI value of zero represents natural environments (e.g., the Brazilian Pantanal) and values of up to 50 represent anthropogenically transformed environments with high human densities (e.g., New York City; Tucker et al. 2018). The authors reported that ranging distances in areas with a comparably high HFI (up to 35) were on average one-half to one-third of those found in conspecifics that live in areas with a low HFI (< 10).

Most studies on home range use of urban wildlife have focused on carnivorous species, such as red foxes, bobcats (*Lynx rufus*), or stone martens (*Martes foina*; reviewed in Šálek et al. 2015). Our present study was designed to provide novel insights into the question of how a medium-sized, herbivorous mammalian species—the European rabbit (*Oryctolagus cuniculus*, L. 1758)—might change its home range use in urban environments. Like the aforementioned carnivores, European rabbits can reach comparatively high population densities in cities (Ziege et al. 2013, 2015; Arnold et al. 2016).

The spread of the viral diseases myxomatosis in 1952 and rabbit hemorrhagic disease (RHD) in the early 1980s, in combination with the continued loss of structural diversity in rural landscapes, led to starkly declining population dynamics or even local extinctions of European rabbits in rural areas of Europe, including Germany (Lees and Bell 2008; Arnold et al. 2016). Nevertheless, until today, no study has quantified home range dimensions of urban European rabbit populations. Our study fills this gap of knowledge and contributes to our understanding of how European rabbits—once common and widespread in Germany but now for many regions restricted to urban environments (Arnold et al. 2016)—make use of urban landscapes.

Based on the abovedescribed anthropogenic impacts within our study sites, we addressed two hypotheses. (1) We predicted home range dimensions of urban and suburban European rabbits in Frankfurt to be considerably smaller compared with previously reported values for European rabbits living in rural areas. More specifically, we expected 95% MCP values to be even smaller than 0.7 ha—the smallest value reported for European rabbits ($n = 16$) inhabiting favorable rural landscapes in France (i.e., cultivated open land characterized by mixed farming and hedgerows) during the reproduction season (Devillard et al. 2008). (2) We further hypothesized that if habitat fragmentation is a major determinant of home range dimensions, then rabbits from the urban study site should have even smaller home ranges than those from our suburban study site. At the urban study site, habitat available to European rabbits is even more fragmented by streets and pathways that potentially restrict their natural ranging behavior.

Materials and methods

Study populations and sampling sites

Based on records from the city archive, rabbit populations have been established in Frankfurt am Main at least since the 1930s (Stadtarchiv Frankfurt). Frankfurt is the largest city in the state of Hesse and the fifth-largest city in Germany (Brinkhoff 2016), about 736,000 people live in the city's administrative boundaries and about 2.4 million in its functional urban area, with an average density of 3000 inhabitants per square kilometer (Brinkhoff 2016). Nonetheless, Frankfurt is considered a "green city" since more than 58% of the area within the city limits are protected green areas (e.g., forest, parks, and gardens; Berliner Morgenpost, October 5,2016). We originally radio-collared 8 rabbits (4 males and 4 females) in a green area (*Friedberger Anlage*) in the city center (N 50°7.04 E 8° 41.5; 4.9 ha; Figs. 1 and 2) and 9 rabbits (5 males and 4 females) in a suburban park (*Rebstockpark*) located in the periphery of Frankfurt (N 50°6.674 E 8°36.773; 11 ha; Figs. 1 and 2; Table 1). At both sites, short-cut meadows were the dominant landscape element, with a grass cutting regime of up to once a week during summer. As mentioned above, both study sites differed in the overall "degree of urbanization" (Ziege et al. 2013).

We tracked radio-collared individuals from urban and suburban sites in the city of Frankfurt am Main to determine their home range dimensions. In previous studies, we assessed various parameters of different study sites in and around Frankfurt that were related to anthropogenic influence and summarized them by means of a factor reduction (i.e., principal component analysis), resulting in principal components that characterized the "degree of urbanization" (for more details see Ziege et al. 2013). Specifically, we assessed the proportion of artificial ground cover (e.g., streets and playgrounds) and numbers of anthropogenic objects per hectare (e.g., benches and street lamps). Our study sites clearly

Fig. 1 Suburban study site (*Rebstockpark*, left circle) and urban study site (*Friedberger Anlage,* right circle) in Frankfurt Main, Germany. Source: Google Earth

differed in the availability of continuous living space, with mean percentages of anthropogenic cover making up 17.1% in the urban area but only 10.6% in the suburban area. Numbers of anthropogenic objects per hectare were determined as 20 in our urban study area and 12 in the suburban area. We further obtained information on the direct intensity of disturbance by humans (pedestrians and bikers) and leashed or unleashed dogs (per minute and hectare) that rabbits were exposed to during their main activity periods at dusk and dawn through transect counts (for more details see Ziege et al. 2013, 2015). Mean values for our measure of disturbance per minute and hectare were as high as 0.64 in the urban, but only 0.09 in the suburban study area. Additionally, we obtained data on numbers of human residents located within a radius of 500 m from the borders of the study sites from the registration office of Frankfurt (*Einwohnermeldeamt*, updated: October 31,2010) to provide an estimate of overall and peak numbers of visitors in the park areas, as residents tend to walk in nearby city parks. The number of residents within 500 m was 4713 at the urban compared with 418 at the suburban study site.

Capture of animals and radio tracking

During the hunting period from October to March, rabbits are hunted by certified hunters employed by the city of Frankfurt with an exclusive hunting license for selected parks inside the city. We took advantage of a hunting method called "ferreting" to catch rabbits in March 2012. We used domestic ferrets (*Mustela putorius furo*) to drive rabbits out of their burrows into wire cages placed into the burrow entrances (cages were self-build by the responsible hunter). We noted the sex of captured individuals and weighed them inside a linen sack. Body weight served as a rough estimate of age, and only adult individuals were collared (> 1220 g; see Kolb 1991). We equipped hand held rabbits with PD-2C radio collars (Holohil Systems, Carp, Canada; 4 g total weight) and afterwards released them at the capture site. We started data collection 1 week after this procedure to allow freshly collared specimens to recover from capture stress (Zollner et al. 2000). Individual location fixes were collected during five randomly selected days per week by several research assistants at both sites simultaneously. Data collection took place either between 06:00 a.m. and 02:00 p.m. or between 02:00 p.m. and 09:00 p.m., based on the flip of a coin (Zollner et al. 2000), from March to September 2012. Two times a week, we also collected location fixes between 09:00 p.m. and 06:00 a.m. The location of each focal individual was recorded at least once between 06:00 a.m. and 09:00 p.m. and at least twice during 09:00 p.m. and 06:00 a.m. until death of the collared individuals or transmitter failure (Zollner et al. 2000). We used antennae and receivers from Biotrack Ltd. (Wareham Dorset, UK) and Telonics Inc. (Mesa, AZ, USA) to locate focal individuals using a combination of triangulation and "homing in" (Garrott and White 1990). This included cases in which individuals were located underground (in burrows). We noted the time at which location fixes were taken (noted first into a high-resolution physical map and later transferred into GPS coordinates). Moreover, we noted the overall weather conditions for the day, i.e., temperature and precipitation gained from the daily weather forecast as well as the current weather situations at the time we took the location fixes, i.e., using a digital outside thermometer and noting the following variables: cloudy (yes/no), rain (yes/no), and sunshine (yes/no). All experimental procedures described here were in accordance with the current laws on animal experimentation in Germany and the European Union (hunting license 1000250221; ID: V54-19c 20/15 – F 104/59).

Statistical analyses

After visual inspection of asymptotic area-observation plots using the incremental area function in Ranges v. 8 (Kenward 1990; Nilsen et al. 2008), we decided to include only individuals with a minimum number of 95 fixes per individual. We obtained a sufficient number of location fixes for 4 females

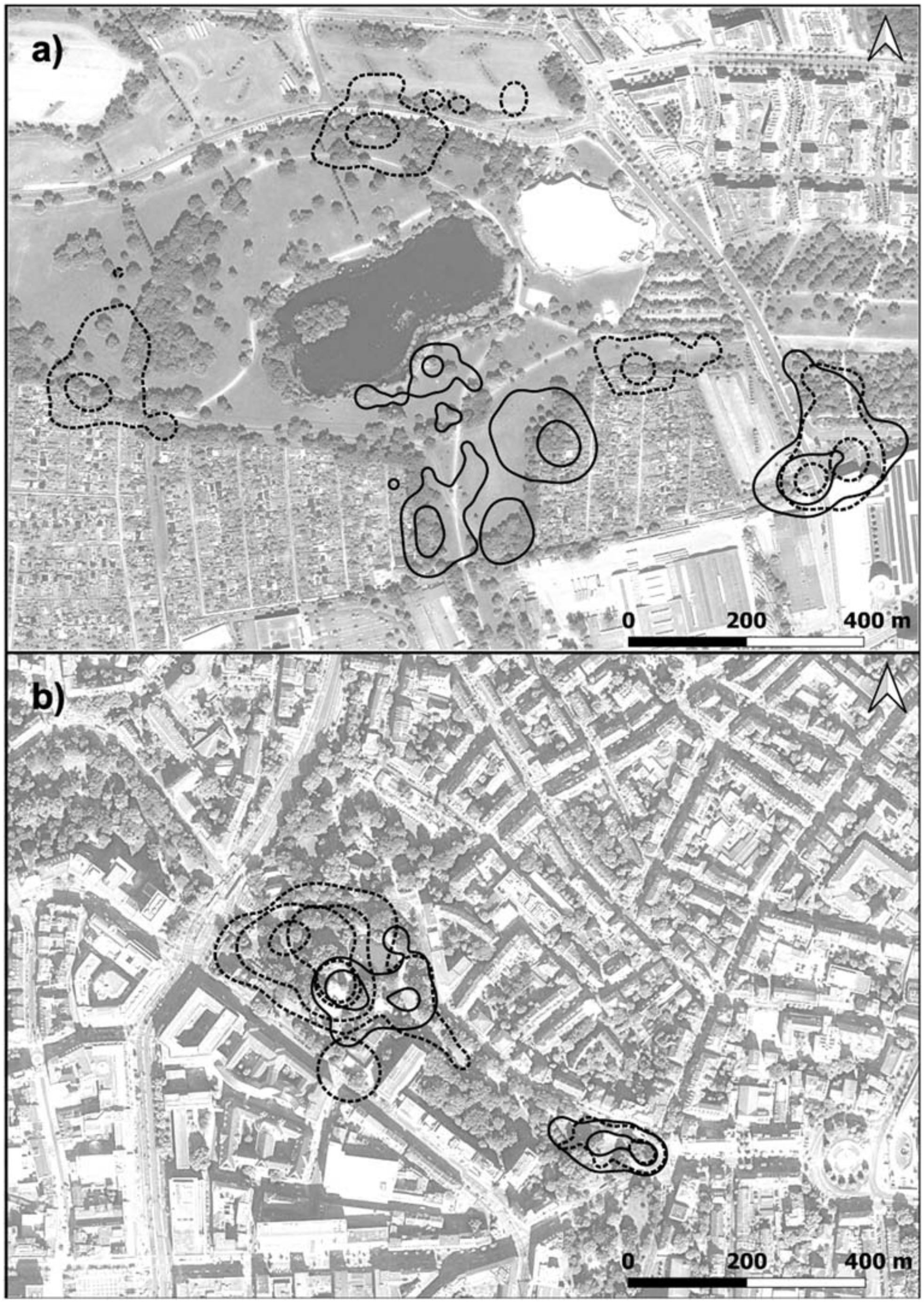

Fig. 2 Kernel density estimates (95% and 50% KDEs) of 8 animals in the suburban study site (*Rebstockpark*) (**a**) and 5 animals in the urban study site (*Friedberger Anlage*) (**b**). Full-line circles indicate male individuals; dashed-line circles, female individuals

(95–98 sampling points per individual) and 4 males (95–97 sampling points) at our suburban study site, and 3 females (113–117 sampling points) and 2 males in the city center (114 and 115 sampling points; see Table 1). From the remaining collared individuals, we could not collect sufficient location fixes for meaningful statistical analyses. This was due either to the death of the tracked individual (1 case) or the premature loss of the radio collar (3 cases). Prior to data analysis, we tested for site fidelity in conjunction with home range asymptote exploration, which was apparent for 12 out of 13 animals, while one individual (ID number 3; Table 1) did not show a clear pattern of site fidelity. We analyzed the data with and without this particular individual, but the results were qualitatively similar, demonstrating the robustness of our analyses. We therefore decided to base our subsequent calculations on home range sizes on all 13 animals.

As most studies on the ranging behavior of European rabbits provided minimum convex polygon estimates (MCPs),

Table 1 Individual home range sizes (ha) of all focal individuals included in this study. We used 95% and 50% minimum convex polygons (MCPs) as well as 95%, 75%, and 50% kernel density estimators (KDEs) as proxies for home range dimensions

Focal individual's ID	Sex	MCPs (ha)		KDEs (ha)			Number of location fixes
		95%	50%	95%	75%	50%	
(**a**) Suburban study site (*Rebstockpark*)							
1	Male	0.75	0.02	1.27	0.48	0.18	97
2	Male	0.53	0.21	1.22	0.55	0.24	95
3	Female	0.65	0.02	1.21	0.45	0.15	97
4	Female	0.95	0.11	1.63	0.73	0.28	91
5	Female	0.65	0.07	1.22	0.39	0.17	97
6	Male	0.43	0.07	0.80	0.29	0.14	96
7	Male	0.34	0.01	0.45	0.09	0.04	95
8	Female	0.35	0.03	0..62	0.24	0.09	98
(**b**) Urban study site (*Friedberger Anlage*)							
9	Female	0.52	0.09	0.99	0.44	0.21	117
10	Male	0.20	0.10	0.57	0.28	0.14	115
11	Male	1.96	0.27	3.10	1.14	0.52	114
12	Female	0.13	0.04	0.40	0.13	0.05	113
13	Female	0.64	0.31	1.35	0.66	0.30	117

we decided to calculate the same proxy of individuals' home range dimensions using the R package *adehabitatHR* (Kenward 1990; Nilsen et al. 2008; Calenge 2006). However, to ensure comparability of our data to future studies, we also calculated kernel-based home range estimators (KDEs) using the reference bandwidth (Worton 1989; Signer and Balkenhol 2015), applying point KDEs and fixed kernels. As the home range sizes were not normally distributed, we used non-parametric Mann-Whitney *U* tests in R (version 3.4.4) to test whether home range dimensions might differ between both study sites or between sexes.

Results

We found mean 95% minimum convex polygons (MCPs)—based on data of both study sites combined—to be smaller than ever reported before for our study species, covering 0.50 ± 0.13 ha (mean ± SE; $n = 13$). Mann-Whitney *U* tests detected no significant differences in 95% and 50% MCPs as well as 95% and 50% KDEs between our two study sites (Table 2; Fig. 2). Also, both MCP and KDE estimates did not differ significantly between male and female focal individuals (Table 2).

At both study sites, we were able to track individuals underground. At the suburban study site, we twice followed one male individual while it was crossing a street underground to switch between interconnected burrow systems during daytime. Using Google maps, we estimated the distance (above ground) between the two nearest burrow entrances of those two burrows to be approximately 30 m.

Discussion

The results of our present study confirm our first prediction that European rabbits in urban and suburban areas used exceedingly small home ranges compared with those reported for rural populations in other study areas. Devillard et al. (2008) reported the smallest 95% MCP home range dimensions observed in rural populations, with mean values ranging between 7333 m^2 (0.733 ha, $n = 24$ individuals) and 6878 m^2 (0.688 ha, $n = 20$) in two rural areas in France with heterogeneous land-use forms. Mean 95% MCPs in our present study were even smaller but did not differ statistically between sites.

We argue that this pattern can be explained, for the most part, by the high level of structural heterogeneity in suburban and urban areas (Ditchkoff et al. 2006; Kowarik 2011) which allows rabbits to find the required resources within a relatively small area (Gibb 1993; Moreno and Villafuerte 1995;

Table 2 Results of Mann-Whitney *U* tests using 95% and 50% MCPs as well as 95%, 75%, and 50% KDEs as dependent variables. "Study site" (urban vs. suburban) and "sex" were explanatory variables

Home range estimates	Study site		Sex	
	z	*P*	*z*	*P*
95% MCPs	0.732	0.46	0.142	0.886
50% MCPs	− 1.763	0.08	0	1
95% KDEs	0.146	0.88	0.143	0.886
75% KDEs	− 0.293	0.77	0	1
50% KDEs	− 0.878	0.38	0.143	0.886

Devillard et al. 2008). For example, dense park vegetation and anthropogenic structures within urban and suburban areas provide sufficient shelter for rabbits to establish their burrows, while nearby meadows or urban gardens provide ample food. Rabbits in Frankfurt are even fed by humans in front of their burrow entrances (pers. observation).

Gibb (1993) argued that the combination of food biomass per unit area and access to areas suitable for burrow construction primarily determines home range dimensions in *O. cuniculus* (but see Lombardi et al. 2003, 2007). Agriculturally transformed areas in Central Europe are becoming less structurally diverse, with only few remaining stretches of bushy vegetation remaining in which rabbits can construct burrows (Devillard et al. 2008). Daniels et al. (2003) compared the ranging behavior of rural rabbit populations in Scotland between two sites that differed in land use. If sufficient food is available, rabbits feed on herbs or agricultural crops, while during winter months, they tend to feed on grass and tree bark (Lombardi et al. 2007). At the study site where land-use forms were more suitable to meet those requirements and where sufficient shelter was available, Daniels et al. (2003) calculated a mean home range size of 2.1 ha (95% minimum convex polygon (MCP) dimensions) during spring time. In the second study area, where the preferred landscape elements were less available, mean 95% MCP dimensions (5.2 ha) were more than twice as big (see also Lombardi et al. 2007). Likewise, Ullmann et al. (2018) reported for another lagomorph—the European hare (*Lepus europaeus*)—that individuals in structurally impoverished landscapes had larger home ranges when resource variability was greater, while hares in structurally complex landscapes did not enlarge their home ranges as a function of resource variability.

Unlike Devillard et al. (2008), we detected no sex differences in home range sizes, which may indicate that sample sizes were not sufficient to detect such an effect, even though other studies also found no sex differences (Daniels et al. 2003; Moseby et al. 2005; Lombardi et al. 2007). Likewise, it remains unclear if conclusions can be drawn from our observation that home range dimensions did not differ statistically between suburban and urban sites. If this result can be trusted (i.e., if the pattern is not affected by small sample sizes), then it might indicate that habitat fragmentation plays a minor role in determining home range dimensions compared with the aforementioned factors.

Besides equipping more individuals with radio collars in order to compensate 23.5% failure of radio tags (the loss we experienced in our present study), future studies should also follow collared individuals over a longer period of time. This could provide deeper insights into the question of how often rabbits use underground passages to overcome anthropogenic barriers (such as streets) and how often traffic is a cause of death. We observed individuals to avoid daytime traffic by crossing streets during the night (see also Dowding et al. 2010 for hedgehogs, *Erinaceus europaeus*). While we did find rabbit carcasses along streets, in only few cases could we unequivocally identify traffic accidents as the cause of death, precluding a quantitative analysis of those incidences.

It remains unclear at present whether and how predation affects the ranging behavior of urban rabbit populations: although common natural predators of the European rabbit such as red foxes, *Vulpes vulpes* (Gloor 2001); mustelids like *Martes foina* and *Mustela erminea* (Duduś et al. 2014) or birds of prey like kestrels, *Falco tinnunculus* (Kübler et al. 2005); and northern goshawks, *Accipiter gentilis* (Rutz 2006) or sparrowhawks, *Accipiter nisus* (Risch et al. 1996) can reach high densities in cities, their mere presence does not necessarily mean that they exert strong predation on urban rabbit populations. For example, as reported for red foxes (Contesse et al. 2004) or Cooper's hawk (Estes and Mannan 2003), predators in cities sometimes start exploiting other (more abundant) food sources. Nevertheless, for some species, including European rabbits, hunting has been used to manage urban populations.

In conclusion, our study adds to the very limited information on home range dimensions of a medium-sized, herbivorous mammalian species living in an urban environment. Although our sample size was fairly low, we report the lowest home range dimension ever reported for the European rabbit during the reproduction season. In conjunction with our previous studies reporting on increased densities of European rabbits in urban areas in and around the city of Frankfurt am Main (Ziege et al. 2013), our present study highlights the importance of urban ecosystems not only for human recreation but also for the conservation of populations of otherwise declining wildlife species.

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Author's contributions MZ designed, led, and coordinated the project, with input from SM, MP, and SW. MZ, SK, and SW collected field data and undertook data analysis. MZ, BH, SK, SM, WU, SW, and MP undertook further data analysis and data interpretation. MZ, SM, BS, and MP drafted the manuscript. All authors contributed to and approved the final manuscript.

Compliance with ethical standards

Competing interests The authors declare that they have no competing interests.

Ethical approval All experimental procedures described here were in accordance with the current laws on animal experimentation in Germany and the European Union and approved by licensed hunters (hunting license 1000250221; ID for permission to radio collar rabbits: V54-19c 20/15 152 – F 104/59).

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