Do subterranean mammals use the Earth's magnetic field as a heading indicator to dig straight tunnels?

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Subterranean rodents are able to dig long straight tunnels. Keeping the course of such 'runways' is important in the context of optimal foraging strategies and natal or mating dispersal. These tunnels are built in the course of a long time, and in social species, by several animals. Although the ability to keep the course of digging has already been described in the 1950s, its proximate mechanism could still not be satisfactorily explained. Here, we analyzed the directional orientation of 68 burrow systems in five subterranean rodent species (*Fukomys anselli, F. mechowii, Heliophobius argenteocinereus, Spalax galili*, and *Ctenomys talarum*) on the base of detailed maps of burrow systems charted within the framework of other studies and provided to us. The directional orientation of the vast majority of all evaluated burrow systems on the individual level (94 %) showed a significant deviation from a random distribution. The second order statistics (averaging mean vectors of all the studied burrow systems of a respective species) revealed significant deviations from random distribution with a prevalence of north-south (*Heliophobius argenteocinereus*), NNW-SSE (*Ctenomys talarum*), and NE-SW (*Fukomys* mole-rats) oriented tunnels. Burrow systems of *Spalax galili* were randomly oriented. We suggest that the Earth's magnetic field acts as a common heading indicator, facilitating to keep the course of digging. This study provides a field test and further evidence for magnetoreception and its biological meaning in subterranean mammals. Furthermore, it lays the foundation for future field experiments.

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2 **indicator to dig straight tunnels?**

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Abstract

Subterranean rodents are able to dig long straight tunnels. Keeping the course of such 'runways' is important in the context of optimal foraging strategies and natal or mating dispersal. These tunnels are built in the course of several weeks to years, and, in social species, by several animals. Although the ability to keep the course of digging was described in the 1950s, its proximate mechanism could still not be satisfactorily explained. Here, we analyzed the directional orientation of 68 burrow systems in five subterranean rodent species (*Fukomys anselli, F. mechowii, Heliophobius argenteocinereus, Spalax galili,* and *Ctenomys talarum*) on the base of detailed maps of burrow systems charted within the framework of other studies and provided to us. The directional orientation of the vast majority (94 %) of all evaluated burrow systems on the individual level showed a significant deviation from a random distribution. The second order statistics (averaging mean vectors of all the studied burrow systems of a respective genus or species) revealed significant deviations from random distribution with a prevalence of north-south (*Heliophobius argenteocinereus*), NNW-SSE (*Ctenomys talarum*), and NE-SW (*Fukomys* mole-rats) oriented tunnels. Burrow systems of *Spalax galili* were randomly oriented. We suggest that the Earth's magnetic field acts as a common heading indicator, facilitating to keep the course of digging. This study provides a field test and further evidence for magnetoreception and its biological meaning in subterranean mammals. Furthermore, it lays the foundation for future field experiments.

45

Introduction

47 Across the globe, about 250 rodent species, belonging to different unrelated taxa (six families, 38

48 genera), have convergently adapted to permanent life in self-excavated extensive underground

49 burrow systems (for review see Begall et al., 2007, Lacey, 2000, Nevo, 1999). Burrow systems

50 inhabited by single individuals (solitary species) or families (social species) can reach lengths of

51 several hundred meters or, in social species, even kilometers (Brett, 1991, Šklíba et al., 2012,

52 Šumbera et al., 2003, Šumbera et al., 2012, Šumbera et al., 2008). Here, the animals live,

53 communicate, orientate in space and time in a dark, monotonous sensory environment free of

54 most orientation cues which are available aboveground. Especially light propagation is highly

55 limited in subterranean burrow systems, so that vision is of little use for subterranean rodents

56 there (Kott et al., 2014). Since environmental cues are mostly lacking in the subterranean

57 ecotope, rodents are forced to rely on idiothetic cues to orientate which are, however, prone to

58 accumulations of errors. Consequently, an external reference that could be used for orientation

59 and navigation would be of high value (Moritz et al., 2007). While the question, how these

60 animals can orientate in their complex underground maze, has been repeatedly addressed (Burda,

61 1987, Eloff, 1951, Kimchi et al., 2004, Kimchi and Terkel, 2001), one interesting sensory

62 ecological aspect remained understudied. How do subterranean mammals manage to keep the

63 course of digging? This question was first raised approximately 70 years ago in 1951 when Eloff

64 mentioned the 'remarkable ability [of the South-African *Cryptomys* mole-rat] to follow a

65 direction or find a spot where it previously bored a tunnel' (Eloff, 1951, p. 145). The African

66 mole-rat's ability to maintain its course while digging long, straight tunnels (Eloff, 1951) gave

67 rise to speculations on possible orientation cues: air currents (de Graaff, 1972, Eloff, 1958,

68 Poduschka, 1978) and acoustic cues (Eloff, 1951, Müller and Burda, 1989, Rosevear, 1969) have

69 been discussed, as well as internal mechanisms based on kinesthetic and/or vestibular cues

70   (Teroni et al., 1988). However, none of these mechanisms provide a satisfactory explanation for

71   the highly efficient directional orientation observed in *Cryptomys hottentotus* (Eloff, 1951).

72   Inspired by the mentioned enigmatic ability, about 40 years after Eloff, Burda (Burda,

73   1987) postulated that the mole-rats might use magnetic cues to orientate and navigate, an ability

74   which was then explicitly proven in the laboratory repeatedly, specifically for the Zambian

75   Ansell's mole-rat (*Fukomys anselli*, formerly assumed to represent the same species as the South

76   African *Cryptomys hottentotus* and in papers published before 2006 named so) (Burda, 1987,

77   Burda et al., 1990, Malewski et al., 2018, Marhold, 1997, Thalau et al., 2006, Wegner et al.,

78   2006). The phenomenon of magnetoreception, meaning an animal's sensory ability to extract

79   information from the Earth's magnetic field, has been investigated since the 1960s (for review

80   see Begall et al., 2014, Wiltschko and Wiltschko, 1995). However, studies with the purpose to

81   unravel the function of the mammalian magnetic sense are still rare (Holland et al., 2006, Kimchi

82   et al., 2004). Following the finding that African mole-rats are magnetosensitive (Burda et al.

83   1990), Lovegrove et al. (1992) investigated directional orientation of burrow systems of

84   Damaraland mole-rats (*Fukomys damarensis*) in the field, inferring that the 'orientation of the

85   burrow system with respect to a specific compass orientation may represent an intrinsic

86   requirement of successful geomagnetic orientation and direction finding' (Lovegrove et al.,

87   1992, p. 631). However, no correlation between the Earth's magnetic field and the burrow

88   system's orientation was found. Years later, Schleich and Antinuchi (2004) performed a

89   comparable study on burrow systems of Talas tuco-tucos (*Ctenomys talarum*), and achieved also

90   negative results. However, in both studies, the data were analyzed by means of a Chi²-test, which

91   does not take the specific characteristics of circular data into account (e.g. 10° is close to 350°),

92   and which is therefore less powerful than circular statistics. Furthermore, the previously used

93   'polygon method' expressed directional alignment of the burrow system through a line

94   connecting the most distant points of a polygon surrounding the burrow system. Since this

95   method ignores all the shorter side branches of a burrow system within the circumferential

96   polygon, a new, more detailed and accurate method would be of avail.

97   In our study, we revive the question raised by Eloff (1951), and test if subterranean

98   rodents use the Earth's magnetic field as a heading indicator to keep a straight course of digging.

99   Keeping a digging direction, for example during foraging (Burda, 1987) or during natal or

100   mating dispersal (Hickman, 1990, Nevo, 1999, Rado et al., 1992) would be advantageous, as

101   digging curvy tunnels would imply increased or even devastating energetic costs; note that costs

102   for digging are between 360 and up to 3,400 times higher than if the animal moves the same

103   distance above ground (Vleck, 1979). We may assume that straight tunnels longer than e.g. one

104   meter are not the product of a single digging bout, and in the case of social species, not even of a

105   single individual (Jarvis et al., 1994). This fact points out the necessity of a heading indicator to

106   keep the course of digging. While diverse heading indicators (visual or olfactory landmarks, sun

107   position, wind direction) can be used to keep the course of locomotion aboveground, availability

108   of such cues is restricted underground.

109   To test the hypothesis of a magnetic heading indicator, we analyzed the directional

110   orientation of complete burrow systems excavated in the field of five subterranean rodent

111   species, three of which are already known to be magnetosensitive (Oliveriusová et al., 2012):

112   two *Fukomys* mole-rat species (*Fukomys anselli* and *Fukomys mechowii*), the silvery mole-rat

113   (*Heliophobius argenteocinereus*), the blind mole rat (*Spalax galili*), and the Talas tuco-tuco

114   (*Ctenomys talarum*) by means of two different methods.

115

116 **Material and Methods**

117 Our dataset consisted of 68 burrow systems of five subterranean rodent species (*Fukomys anselli*,

118 *Fukomys mechowii*, *Heliophobius argenteocinereus*, *Ctenomys talarum*, *Spalax galili*),

119 belonging to three non-related families with different geographic distribution, and representing

120 both solitary or social lifestyles (Table 1). All burrow systems were mapped within the

121 framework of previous field ecological studies (Lövy et al., 2015, Schleich and Antinuchi, 2004,

122 Šklíba et al., 2012, Šklíba et al., 2010, Šklíba et al., 2009, Šumbera et al., 2003, Šumbera et al.,

123 2012, Šumbera et al., 2008), and the maps were provided to us for this study. They were

124 digitized true to scale by means of Guantum GIS (QGIS Geographic Information System,

125 www.qgis.osgeo.org) for burrow systems of silvery mole-rats, *Fukomys* mole-rats, and *Spalax*,

126 and by means of ImageJ (Schneider et al., 2012) for burrow systems of Talas tuco-tucos. We

127 pooled the data of both species of *Fukomys* mole-rats in order to increase the sample size. It

128 should be noted that both species are phylogenetically related, live in the same habitat in the

129 same geographic region and have the same lifestyle. The direction of magnetic North was noted

130 as accompanying information as usual in geographical mapping. The data has been collected

131 blindly with respect to the analysis of compass directionality, since the original purpose of the

132 excavation was not to study burrow orientation, but to obtain data about other aspects of

133 subterranean life (e.g. burrow architecture). In our study, the systems were digitally analyzed

134 twice, by applying two different methods: the 'polygon method', which was applied already in

135 previous studies (Lovegrove et al., 1992, Schleich and Antinuchi, 2004), and the 'long tunnel

136 method', introduced by us here (Figure S1). Since the animals' original digging direction

137 (unidirectional) cannot be deduced from the excavations or drawings, bidirectional analysis was

138 the method of choice, i.e., data are doubled (modulo 360) before being analyzed, and the

139   resulting mean vector is then back-converted, thus ranging in the interval (0°; 180°). All axial

140   values are reported as XX°/XX° (N/S).

141

142   Table 1: Tested rodent species (sorted alphabetically by their common names). Additionally,

143   number of mapped burrow systems, locality and year of excavation, rodent family, lifestyle, and

144   references to the studies describing burrow architecture of the respective species are listed.

145

146   The 'polygon method' (Figure S1 (A), (C)) is based on drawing a convex polygon

147   connecting the outermost points of a burrow system. A diagonal, marking the longest distance

148   within the polygon, was drawn, representing the main axis of the burrow system. The direction

149   of the longest distance within the polygon was measured blindly (i.e. without knowing the

150   direction of magnetic North) by means of a digital compass rose. Subsequently, all measured

151   values were unblinded by normalizing the data relative to the direction of true magnetic North.

152   The 'long tunnel method' (Figure S1 (B), (E)) weights the magnetic axial direction of the

153   branches within a burrow system depending on their length. The underlying hypothesis

154   concerning this approach was the following: The longer the distance, which was dug in a specific

155   magnetic direction, the stronger is the animal's preference for that particular direction. To apply

156   this method, first, we determined the directions of all straight tunnels of a burrow system blindly

157   (i. e. the evaluator did not know the direction of magnetic North). We defined a 'straight tunnel'

158   as straight segment including small turns/curves which ended at a clear change in direction of

159   more than 30° (see Figure S1 (E)). Only straight tunnels that were at least as long as 5 % of the

160   polygon's length surrounding the whole system were included in our data set. The tunnels' axial

161   directions were measured by means of a digital compass rose. After unblinding the data, vector

162 analysis of each straight tunnel direction weighted by the tunnels' lengths was performed to

163 calculate the mean direction for each burrow system separately. Therefore, the vector's direction

164 was treated as value and its length as frequency (see frequency editor of Oriana 4.0, Kovach

165 computing systems).

166   All drawings of polygons and diagonals as well as their evaluations were performed with Fiji

167 (Schindelin et al., 2012). Circular statistics (Batschelet, 1981) and vector analyses were

168 calculated by using Oriana 4.0 (Kovach computing systems). Axial mean values were calculated

169 for each species and each method (for the 'long tunnel method', the mean vector (grand mean)

170 was calculated over the mean axial directions of the respective tunnels). The Rayleigh-test of

171 uniformity was used to test for significant deviations from a random distribution. Watson-

172 Williams F-test (pairwise comparison) was applied to compare the burrow systems' directions

173 achieved by both methods for each species, respectively.

174

175 **Results**

176 By applying the 'long tunnel method', the axial orientation of the vast majority of all evaluated

177 burrow systems (94 %) showed a significant deviation from a random distribution, i. e. in 64 out

178 of the 68 analyzed tunnel systems the straight tunnel segments were oriented significantly in a

179 certain axial compass direction (*Fukomys*: 100 %; *H. argenteocinereus*: 90 %; *C. talarum*: 95 %;

180 *S. galili*: 100 %). Considering the second order statistics (averaging the mean vectors of all

181 analyzed burrow systems of a respective genus or species), a significant deviation from random

182 orientation was found for the *Fukomys* mole-rats, the silvery mole-rat, and the Talas tuco-tuco

183 (Figure 1). An axial directional preference for the North-South axis was observed for the silvery

184 mole-rat, while it was slightly shifted to NNW/SSE in the Talas tuco-tuco. The *Fukomys* mole-

185   rats showed a preference for the NE/SW. No prevailing magnetic direction of the studied

186   burrows was found in the blind mole rat (*S. galili*) (Figure 1).

187   Since most burrow systems (N=31) were available for the silvery mole-rats, we analyzed

188   whether the tunnel systems' lengths and locality of excavation (Blantyre, Mpalaganga, Mulanje;

189   Table 1) had an effect on the orientation of the mean axial direction. A significant deviation from

190   random orientation was found for systems which were shorter than 100 m (N=15, μ=1/181°,

191   SD=31°, P=0.007; mean length = 57 m, SD = 26 m), in contrast to systems which were longer

192   than 100 m (N=16, μ=15/195°, SD=48°, P=0.406; mean length = 192 m, SD = 68 m). With

193   respect to the locality of excavation, a significant deviation from random orientation was only

194   observable in one out of three localities (Blantyre: N=17, μ=5/185°, SD=34°, P=0.015;

195   Mpalaganga: N=10, μ=169/349°, SD = 52°, P = 0.702; Mulanje: N=4, μ=20/200°, SD=30°,

196   P=0.272). Furthermore, we did not find statistical sex-dependent differences in mean orientation

197   for any of the solitary species (statistics not shown). The 'polygon method' revealed that the

198   alignment of the burrow systems of the Talas tuco-tuco deviated significantly from random

199   orientation (Figure 1 B, F). A similar strong tendency was observable for the silvery mole-rat's

200   systems (Figure 1 A, E). The burrow systems of the *Fukomys* mole-rats (Figure 1 C, G) and the

201   blind mole rat (Figure 1 D, H) showed random directional orientation.

202   The axial directional orientation of the burrow systems as assessed by the 'polygon

203   method' (Figure 1 A-D) and the prevailing direction of the burrows estimated by the 'long tunnel

204   method' (Figure 1 E-H) did not differ significantly except for the *Fukomys* mole-rats (Watson-

205   Williams F-test (pairwise comparisons for each species): *Fukomys* mole-rats: p=0.042, silvery

206   mole-rat: p=0.423, tuco-tuco: p=0.455, blind mole rat: p=0.636), however, a greater scatter was

207   observable by applying the 'polygon method'.

208

Discussion

210 Figure 1 illustrates that the 'polygon method' provides less consistent results than the 'long

211 tunnel method'. Since the 'polygon method' has been employed in previous studies (Lovegrove

212 et al., 1992, Schleich and Antinuchi, 2004), we decided to use this method and present its results

213 for the sake of comparability, too. However, the 'polygon method' is generally suitable only for

214 rather linear instead of circular burrow systems, where the long diagonal within a polygon

215 represents the directional alignment of the whole burrow system. In a more circular system,

216 several diagonals of similar lengths can be drawn (Figure S1 (D)). Various ecological factors

217 influence the geometry of a burrow system. Radiality (high branching) of a burrow system is

218 expected to increase with uniformity and predictability of food resources, age of the burrow

219 system, and with the number of inhabitants (Romañach et al., 2005, Sichilima et al., 2008,

220 Thomas et al., 2016). Moreover, the architecture of burrow systems can vary seasonally and in

221 dependence on the inhabitant's sex (e.g. dispersing and mate-seeking individuals might build

222 more linear tunnels) (Antinuchi and Busch, 1992, Nevo, 1999, Šklíba et al., 2012, Šumbera et al.,

223 2003, Šumbera et al., 2012, Šumbera et al., 2008). Indeed, the index of circularity (formula: 4π

224 (area) / perimeter^2, 0 = linear, 1 = circular; Romañach et al., 2005) identifies 60% of the studied

225 burrow systems of the solitary silvery mole-rats (Figure 2A) and 70% of the systems of the

226 solitary tuco-tucos as being rather linear (with an index < 0.7 as exemplarily defined threshold

227 separating the upper third as being circular), while all systems of the social *Fukomys* mole-rats

228 exhibited values > 0.7 (Figure 2B).

229 In contrast to the 'polygon method', the 'long tunnel method' revealed constant results

230 for different species independent from the respective indices of circularity. Having applied this

231   method, we found a significant deviation from random axial orientation for burrowing longer

232   straight tunnels along a certain axis, which was specific for each burrow system. Moreover, the

233   second order statistics (averaging mean vectors of all burrow systems of a respective genus or

234   species) revealed significant deviation from random orientation in all the tested species but

235   *Spalax galili* (Figure 1), including a prevalence of NNW/SSE in case of Talas tuco-tucos and

236   NE-SW in case of *Fukomys* mole-rats. The fact that the studied burrow systems have been

237   uncovered in different regions (even continents) and areas (e.g. grassland, woodland,

238   mountainous areas), and thus accompanying different habitats, as well as in different years

239   (1998-2012; Table 1), support the assumption that the Earth's magnetic field seems to be a

240   globally common and stable potential heading indicator. Accordingly, we suggest that the

241   studied species use magnetic cues as heading indicator to keep the course of digging. This

242   hypothesis does not exclude that the animals use also further, locally available heading

243   indicators, for this purpose.   Indeed, magnetoreception has been proved in the laboratory for *F.*

244   *anselli* (Burda et al., 1990, Marhold et al., 1997), *F. mechowii* (Oliveriusová et al., 2012), and *H.*

245   *argenteocinereus* (Oliveriusová et al., 2012). Interestingly, magnetoreception was not proved in

246   laboratory maze experiments in *C. talarum* (Schleich and Antinuchi, 2004), which, however,

247   could have been due to an inappropriate experimental design as discussed by the authors

248   themselves (Schleich and Antinuchi, 2004). On the other hand, magnetoreception has been

249   proven in *Spalax judaei* (Kimchi and Terkel, 2001, Marhold et al., 2000), a close relative of *S.*

250   *galili* for which no directional preference for digging was found here. The reasons, why no

251   directional digging preference was found in *S. galili*, can be manifold. All analyzed burrow

252   systems originate from a single small area in the Upper Galilee Mountains, and six of nine

253   examined burrow systems were located in basaltic soils. Basaltic soils are generally

254 characterized by rather strong magnetic signatures and the studied region is known for magnetic

255 anomalies (Eppelbaum et al., 2004) that might compromise magnetic orientation. Furthermore,

256 the population density in basaltic soil is five times higher than in rendzina soil (Lövy et al.,

257 2015). The avoidance of crossing a neighboring burrow system might influence the burrow

258 systems orientation and thus possibly override orientation via magnetic cues. Therefore, it is of

259 great interest to analyze comparative data on directionality of burrow systems of *Spalax* from

260 other geographic regions and other habitats (cf., Nevo et al., 1995, Reyes et al., 2003, Savić,

261 1973, Yağci et al., 2010).

262   The burrow systems of *Heliophobius* analyzed here (N=31) were excavated at three

263 different localities, characterized by different landscapes (Blantyre, N=17: grassland;

264 Mpalaganga, N=10: woodland; Mulanje, N=4: mountainous) and thus habitats. A significant

265 deviation from random axial orientation was only observable for the systems from Blantyre. The

266 larger scatter of mean vectors at Mulanje might be partially explained by the lower sample size.

267 Secondly, at Mpalaganga and Mulanje, several systems were excavated in cultivated areas,

268 where higher density and uniformity of food resources might have had influenced foraging

269 strategies and thus also the burrow architecture. Another factor, which seems to affect the burrow

270 system's orientation of silvery mole-rats is the system's length – while shorter systems (< 100 m)

271 were oriented significantly in North-South direction (every other direction would have been

272 equally plausible), longer systems (> 100 m) were not. This is, however, not surprising,

273 considering that the larger a system becomes, the stronger an original alignment might be

274 overridden or masked. Trying to explain these findings, we have to consider that a system's size

275 presumably grows with its age. Consequently, a system's axial orientation may rather be

276 observable when it is shorter (*in statu nascendi*) compared to when it is longer and older.

277   While using a magnetic compass as a heading indicator, in general, the animals could

278   follow every direction, and indeed, species-specific differences in chosen nest-building

279   directions were already reported repeatedly (for review see Oliveriusová et al., 2012). However,

280   the North-South axis might be the direction of choice. A preference for this axis, as observed in

281   our study for silvery mole-rats and Talas tuco-tucos, is common in studies on magnetic

282   orientation (e.g. Malkemper et al., 2015, Oliveriusová et al., 2014, Phillips, 1986) and magnetic

283   alignment (for review see Begall et al., 2013, Malkemper et al., 2016), and is observable in

284   diverse contexts: landing in waterfowl (Hart et al., 2013), escape in roe deer (Obleser et al.,

285   2016), activity in cattle and deer (Begall et al., 2008), flamingos (Nováková et al., 2017), corvids

286   (Pleskač et al., 2017), wild boars and warthogs (Červený et al., 2017), carps (Hart et al., 2012).

287   Considering that species-specific burrowing behavior in North American *Peromyscus* rodents

288   was reported to have a genetic basis (Dawson et al., 1988, Hu and Hoekstra, 2017, Metz et al.,

289   2017, Weber et al., 2013), we would like to point to the possibility that 'magnetic digging' might

290   be genetically determined, too, representing a highly interesting research question.

291   Since magnetic and further orientation cues are not exclusive, apart from the Earth's

292   magnetic field, several other cues might influence the alignment of the burrow systems. The

293   most crucial external cues might be food resources (e.g. Heth et al., 2002, Romañach et al.,

294   2005), soil condition (implying the presence of stones and other obstacles) (e.g. Ebensperger and

295   Bozinovic, 2000, Kimchi et al., 2005, Luna et al., 2002, Zuri and Terkel, 1997), and landscape

296   characteristics (e.g. dunes, vegetation, slopes, water currents), and even subsurface geological

297   fractures might function as orientation cues (Olson and Pollard, 1989). Presence of food

298   resources influences goal-directed burrowing at shorter distances (Eloff, 1951, Voigt, 2014).

299   Since geophytes are usually clumped, and can be located at a limited distance by smelling plant

300   kairomones diffused in the soil (Heth et al., 2002, Lange et al., 2005), an optimal foraging

301   strategy is expected to involve digging straight scouting tunnels with perpendicular shorter

302   branches in fertile areas (following kairomone cues). Although season is expected to affect the

303   digging activity (Sichilima et al., 2008) and general architecture of the burrow system (Šumbera

304   et al., 2003), it is highly unlikely that its main orientation, if present, changes seasonally,

305   wherefore we do not assume significant seasonal influences.

306

307   Conclusion and outlook

308   To conclude, the *Fukomys* mole-rats, the silvery mole-rat, as well as the Talas tuco-tuco were

309   shown to dig their burrow systems with respect to a certain axis, and are assumed to use the

310   Earth's magnetic field as a possible heading indicator. In future studies, animals might be

311   released at a new site so that the genesis of the new burrow system might be monitored *in situ* as

312   for example done by Voigt et al. (2014). Furthermore, digging experiments should be performed

313   under controlled laboratory conditions to unequivocally experimentally demonstrate that

314   subterranean rodents use magnetic cues to keep a heading direction during digging.

315

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322

323 **Data accessibility**

324 The dataset supporting this article will be made accessible via university homepage upon

325 acceptance of the manuscript.

326

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Tested rodent species (sorted alphabetically by their common names)

Additionally, number of mapped burrow systems, locality and year of excavation, as well as references to the studies describing burrow architecture of the respective species are listed.

Species	Family	Social/solitary	Number of burrow systems	Locality	Year of excavation	Reference, burrow systems were originally used for
Ansell's mole-rat (*Fukomys anselli*)	**Bathyergidae**	**Social**	7	Lusaka East Forest Reserve (Zambia)	2010	(Šklíba et al., 2012)
Giant mole-rat (*Fukomys mechowii*)	**Bathyergidae**	**Social**	2	Ndola Hill Forest Reserve (Zambia)	2009	(Šumbera et al., 2012)
Silvery mole-rat (*Heliophobius argenteocinereus*)	**Bathyergidae**	**Solitary**	31	Blantyre, Mulanje, Mpalaganga (Malawi)	2000, 2005	(Šklíba et al., 2010, Šklíba et al., 2009, Šumbera et al., 2003, Šumbera et al., 2008), and additional previously unpublished burrow systems (cf. raw data)
Talas tuco-tuco (*Ctenomys talarum*)	**Ctenomyidae**	**Solitary**	19	Mar de Cobo, Buenos Aires (Argentina)	1998, 1999	(Schleich and Antinuchi, 2004)
Upper Galilee Mountains blind mole rat (*Spalax galili*)	**Spalacidae**	**Solitary**	9	Upper Galilee Mountains (Israel)	2012	(Lövy et al., 2015)

Figure 1

Burrow system's orientation

Directional orientation of the burrow systems (estimated by the 'long tunnel method', A-D) and the prevailing direction of burrows (estimated by the 'polygon method', E-H) of the tested rodent species – the silvery mole-rat *H. argenteocinereus* (A, E), Talas tuco-tuco *C. talarum* (B, F), *Fukomys* mole-rats (Ansell's mole-rat *F. anselli* and the giant mole-rat *F. mechowii*) ((C, G), and the Upper Galilee Mountains blind mole rat *S. galili* (D, H) (sorted by sample size) – relative to magnetic North (0°). Two mirrored dots represent the axial direction of one burrow system, which is in case of the long tunnel method an axial mean vector calculated over all directions of straight tunnel segments weight by the segments' lengths. The double-headed arrow indicates the (grand) mean vector, and the inner circle marks the significance level of 0.05 (Rayleigh test). Sample size (N), mean axial direction (μ), circular standard deviation (SD) and P-value are given for each tested species.

Long tunnel method

Polygon method

A — Silvery mole-rat

N=31
μ=5°/185°
SD=40°
P=0.009

E

N=31
μ=176°/356°
SD=44°
P=0.056

B — Tuco-tuco

N=19
μ=159°/339°
SD=35°
P=0.013

F

N=19
μ=167°/347°
SD=28°
P<0.001

C — *Fukomys* mole-rats

N=9
μ=47°/227°
SD=30°
P=0.04

G

N=9
μ=87°/267°
SD=37°
P=0.185

D — Blind mole rat

N=9
μ=32°/212°
SD=64°
P=0.941

H

N=9
μ=50°/230°
SD=57°
P=0.844
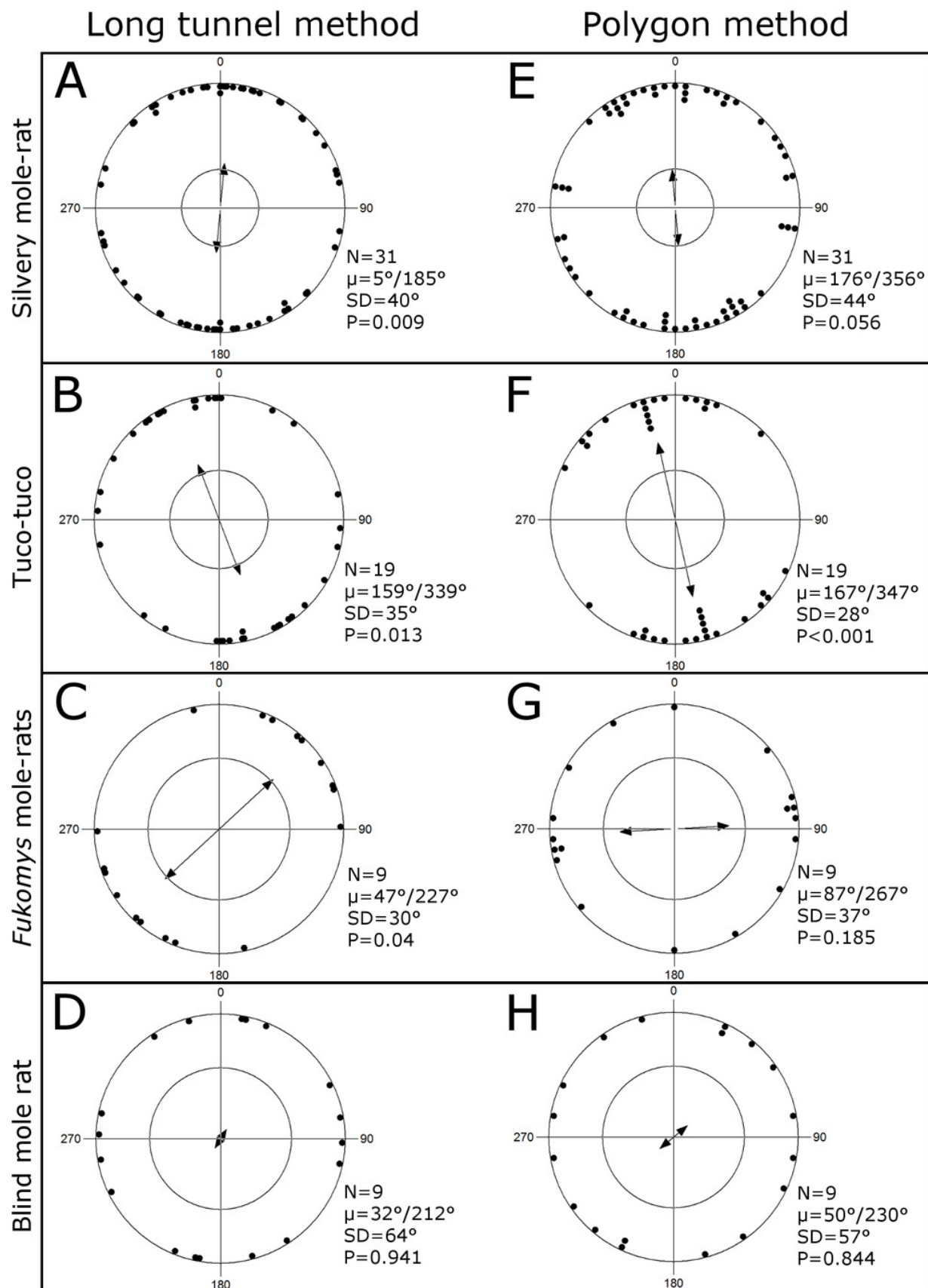
Figure 2

Examples of burrow systems of a (A) solitary (here *Heliophobius argenteocinereus*) and (B) social species (here *Fukomys anselli*).

Index of circularity (0 = linear, 1 = circular; Romañach et al., 2005) for (A)=0.42, and (B)=0.83.