

1

2

3 Competition in the savanna: models of species assemblages in Kruger National Park, South

4 Africa

5

6

7 Sadie J. Ryan^{1*} and Joshua Ladau²

8

9 ^{1*}Corresponding Author: Sadie J. Ryan, Department of Geography, University of Florida,

10 Gainesville, FL 32601, USA, sjryan@ufl.edu

11

12 ²Gladstone Institutes GICD, 1650 Owens Street San Francisco, CA 94158, USA

13

14

15

16 **Abstract**

17 We examined hypotheses of spatial association arising from direct or indirect competitive
18 interactions, using thirteen years of gridded mammal census data from Kruger National Park,
19 South Africa. As interactions occur at different scales, we explored the data at 1, 5, 10, and 15
20 km². We proposed four hypotheses structuring the mammal community: H1. direct competition
21 between carnivores and herbivores; H2-4: indirect competition produced by each of three types
22 of herbivore diet specialization: H2. ruminants and non-ruminants, H3. grazers and browsers,
23 and H4. a four-way division of small and large grazers and browsers. We used the software
24 CoOccur to implement a robust test for evidence of our hypotheses against null models of
25 community assemblage. At 5, 10, and 15km² scales, the results supported a competition
26 mechanism in the majority of years for hypotheses H1, H3, and H4, and facilitation in H2. At the
27 finest spatial scale (1km²), we saw evidence for a mixture of competitive, neutral and facilitative
28 process. These results suggest strong, large-scale effects of interspecific interactions on
29 distributions of African megafauna, which may not operate at a more local (1km²) scale,
30 underscoring the importance of scale and mechanism in the guild structure of communities.

31
32 **Keywords:** competition; co-occurrence; savanna; carnivores; herbivores; guilds; South Africa;
33 scale

34

35 **Introduction**

36 Understanding and describing how species interactions structure communities remains a
37 fundamental goal of ecology (Diamond 1975, Connor and Simberloff 1979, Schoener 1983,
38 Schluter 1984, Stone and Roberts 1990, Manly 1995, Durant 1998, Roxburgh and Matsuki 1999,
39 Linnell and Strand 2000, Gotelli 2000, Gotelli and McCabe 2002, Gotelli and Ellison 2002,
40 Sfenthourakis et al. 2006, Ulrich et al. 2017). Understanding community structure requires both a
41 spatial and temporal perspective (Linnell and Strand 2000), but few datasets are available that
42 are expansive in both of these scales, in part due to declining sizes and numbers of remnant intact
43 wild populations. We present an analysis of long-term, multi-scale, spatially explicit census data
44 of savanna mammals (Table 1) in Kruger National Park, South Africa, testing hypotheses of
45 competition that shape the mammalian assemblage on the landscape. Using census data from a
46 large landscape (approximately 20,000 km²) over multiple years gives us the opportunity to
47 respond to the call by Linnell and Strand (2000) for more research into temporal and spatial
48 aspects of species co-existence, when discussing diverse guilds and communities. Using thirteen
49 years of data, we could assess whether patterns were consistent through time, and these data also
50 allowed us to examine patterns at multiple scales, to quantify the potential extent of behavioral
51 and ecological processes structuring communities.

52

53 ***Savanna community structure***

54 Carnivores are likely to shape savanna communities by acting as top predators (Radloff and Toit
55 2004, Pringle et al. 2007), excluding their prey through direct competition from predation, or via
56 prey avoidance and vigilance behavior (Schmitz 2007). This is expected to generate patterns of
57 competitive exclusion in presence-absence data. We analyzed data collected on larger carnivores

58 in the Felidae (lion, cheetah, leopard) and Canidae (Black-Backed Jackal, Wild dog), plus the
59 hyena and the honey badger. As the predator trophic level, they are more sparsely represented in
60 the data than their prey, but are nevertheless expected to exert detectable effects on the structure
61 of the community.

62 For large herbivores, the two dominant processes structuring assemblages in African
63 savannas are facilitation and competition (Arsenault and Owen-Smith 2002). Interspecific
64 competition predominates during the dry season, while plants are dormant and high quality
65 forage becomes depleted. Therefore, it has been suggested that in the dry season, this will lead to
66 competition among species with similar requirements, subject to habitat heterogeneity at
67 different scales (Redfern et al. 2006). As these census data were collected during the dry season,
68 we expect a dominance of interspecific competition to be occurring. At large scales, abiotic
69 characteristics of the landscape, such as underlying geology, will affect herbivore distribution
70 (Bailey et al. 1996). At smaller scales, biotic factors such as forage quality and quantity will
71 determine foraging decisions. The selection of feeding ranges, patches, plant species, and even
72 plant parts, will occur at multiple scales (Senft et al. 1987, Senft 1989). Arsenault and Owen-
73 Smith (2002) suggested that facilitation occurs primarily during the plant growing season, as
74 foraging by larger species can create a temporary improvement of forage conditions for smaller
75 species.

76 However, the spatial co-occurrence of herbivores may also result from habitat selection –
77 species feeding in the same area – rather than causal facilitation. Landscape configuration may
78 thus generate patterns of apparent facilitation, depending on the scale of selection. Distinguishing
79 behavioral differences between these two processes, which would produce identical patterns in
80 the data, requires direct observation and different methods than those we use here.

81 Based on existing theories of competition and community structure, we developed four
82 hypotheses (H1-4) of mechanisms generating patterns of competition for the vertebrate
83 community of Kruger National Park.

84 H1. We hypothesize that carnivores exclude their herbivore prey, either through direct
85 predation, or prey avoidance strategies (trait-mediated indirect effects), showing competitive (a
86 lack of co-occurrence) patterns at multiple scales.

87 H2-4: Within the herbivore suite, we hypothesize that interference competition structures
88 the assemblage via the ability to process food, leading to indirect competition through resource
89 manipulation or interspecific competition for similar diet or habitat (de Boer and Prins 1990).

90 H2: There is a guild division between ruminants and non-ruminants, based on the premise
91 that gut morphology and digestive ability determine the ability to exploit certain habitats. We
92 thus expect that each guild can exploit different habitats, leading to less co-occurrence of guilds,
93 and a pattern consistent with competition.

94 H3: A smaller suite of herbivores with a higher degree of habitat overlap represent a
95 guild division between grazers (Buffalo, Zebra, Wildebeest) and browsers (Elephant, Giraffe,
96 Kudu, Impala). Grazers and browsers can putatively exploit different food types, leading to less
97 spatial co-occurrence. While elephants are capable of grazing and browsing, since these data are
98 primarily dry season occurrences, we expect to see elephant occurrence reflecting a browsing
99 strategy. These herbivores will compete within feeding type (guild), although not necessarily
100 between feeding types, leading to indirect competition and generating a pattern consistent with
101 competition.

102 H4: Competitive structure within the assemblage can arise through a combination of
103 feeding type and body size. This generates indirect competition through highly specialized

104 feeding strategies. Four guild divisions are designated: 1. Large grazers (Buffalo) 2. Small
105 grazers (Zebra and Wildebeest) 3. Large browsers (Elephant) 4. Small browsers (Giraffe, Kudu,
106 Impala) (7 species), following Redfern et al. (2006) (and see Table 2). Feeding type and body
107 size will affect competitive ability for resources, and this will likely occur between different
108 species at different spatial scales, and generate a pattern consistent with competition.

109

110 *Models of community assemblage*

111 The underlying ecological mechanisms and rules of community assemblage have been the
112 subject of studies in multiple systems (Diamond 1975, Connor and Simberloff 1979, Schoener
113 1983, Schluter 1984, Stone and Roberts 1990, Manly 1995, Durant 1998, Roxburgh and Matsuki
114 1999, Linnell and Strand 2000, Gotelli 2000, Gotelli and McCabe 2002, Gotelli and Ellison
115 2002, Sfenthourakis et al. 2006). Quantifying these patterns, or lack thereof, has led to a long
116 debate in the literature (reviewed by Gotelli and McCabe 2002), sparked by an initial study by
117 Diamond (1975) positing that species assemblages occur through competitive interactions and
118 rebutted by Connor and Simberloff four years later (1979), who demonstrated that random events
119 of colonization could produce similar co-occurrence patterns.

120 Connor and Simberloff's (1979) initial introduction of null models of community
121 structure was motivated by an interest to understand which mechanisms (e.g., competition) were
122 responsible for co-occurrence patterns. We follow this approach, developing null model tests
123 based on our specific hypotheses of the ecological mechanism of competition shaping the
124 community structure in question. We use a null model, developed by Ladau and Schwager
125 (2008), that yields a prediction assuming only an absence of competitive interactions (i.e., that

126 species occur independently of each other). Hence, finding data that are inconsistent with this
127 model allows a strong inference about whether competition shapes community assembly.

128

129 **Methods**

130 *Study site*

131 The Kruger National Park is located in the lowveld of South Africa, with a core area of nearly
132 20,000km², at the time of data collection. It has a north-south rainfall gradient of around 440mm-
133 750mm and is dominated by four major landscapes, essentially dividing the park into quadrants
134 due to a basalt/granite geological split the length of the park (Gertenbach 1980, 1983, Redfern et
135 al. 2006) (Figure 1).

136

137 *Data*

138 We analyzed the annual fixed-wing census from Kruger National Park collected during 1981-
139 1993. The Ecological Aerial Survey (EAS) was conducted annually, during the dry season
140 between May and August, using a total area count on 800m-wide strip transects (Viljoen 1996a,
141 1996b). Point counts of herds or groups of animals (listed in Table 1) were conducted by four
142 observers in the plane, and recorded to spatial location by GPS, using four corners and a center
143 point on a quadrat system approximately 2km on a side (Viljoen 1996a). The observation
144 recording patterns changed between 1984 and 1985, in which the number of positions in a
145 sample grid space recorded was increased from four corners to an additional centroid position
146 (Viljoen 1996a, 1996b). This affects the 1km data structure by increasing the number of grid
147 cells 4-fold between the two years. Although the method suffers population level bias from

148 undercounts (Redfern and Getz 2002), it is a systematic bias, allowing us to make appropriate
149 hypothesis comparisons.

150

151 *Data sampling method*

152 We created grids of the park boundary at 1km, 5km, 10km, and 15km resolutions, and
153 aggregated the EAS data species counts to grid cells, removing partial boundary grid cells from
154 the analyses. The resulting data sets comprise 17,813, 621, 130 and 43 grid cells, or sites,
155 respectively. GIS data manipulations were conducted in ArcGIS 10.2. These data were then
156 converted to binary species presence-absence data in R.

157

158 *Statistical tests of species associations*

159 The EAS data we analyzed for each hypothesis comprise four subsets, sequentially reducing the
160 number of species (Table 2).

161 The competition model from which the null model is developed is based on two premises:

- 162 I. Regardless of how competition acts – evolutionarily or ecologically, and extrinsically or
163 intrinsically – it will reduce the co-occurrence of ecologically similar organisms, which we
164 refer to as guilds.
- 165 II. Ecological similarity can be specified using a hierarchical classification system. Species can
166 be classified into “units,” with species in the same unit being more ecologically similar to each
167 other than those in different units. The quality of “units” can be interpreted, for example, as
168 guilds or trophic levels, depending on the hypothesized structure of competition or interactions.

169 Defining the $\langle ij \rangle$ as the event that the i th and j th species to arrive at a community belong
170 to the same unit, competitive structuring predicts

171
$$P(\langle 13 \rangle | \langle 12 \rangle) < P(\langle 13 \rangle | \langle 12 \rangle^c), P(\langle 23 \rangle | \langle 12 \rangle) < P(\langle 23 \rangle | \langle 12 \rangle^c),$$

172 or

173
$$P(\langle 34 \rangle | \langle 23 \rangle \cap \langle 12 \rangle^c) < P(\langle 34 \rangle | \langle 23 \rangle^c \cap \langle 12 \rangle^c),$$

174 (where c denotes complement). Thus, an appropriate null hypothesis for testing for the absence

175 of interspecific interactions is to set all relevant pairs of conditional probabilities equal. This

176 alone is sufficient to specify a distribution on the set of partitions of species into units, with

177 minimal additional assumptions: there is no autocorrelation, and $P(\langle ij \rangle) > 0$ for all i and j .

178 Hence, to test robustly for interspecific interactions, it is sufficient to assess the agreement

179 between observed and predicted distributions of partitions.

180 The hypothesis test that we used was as follows:

- 181 1. At each site, in this case, a grid cell, the partition of species into units was computed. For
182 example, if three species were observed, two in the same unit (guild) and the other in a
183 different one, then the partition would be “2-1.” If four species were observed, all in different
184 units (guilds), the partition would be “1-1-1-1.”
- 185 2. We computed the total sum of squares of the block sizes across all partitions. In the above
186 example, the sum would be $2^2 + 1^2 + 1^2 + 1^2 + 1^2 = 9$. We used this sum as our test
187 statistic (V).
- 188 3. Conditional on the observed number of species (c) and units (u), the probability of a given
189 partition I is $\psi(I)/S(c, u)$, where $\psi(I)$ gives the number of set partitions corresponding to
190 the given species-unit partition, and S is a Stirling number of the second kind - the number of
191 possible ways to partition n elements into k non-empty subsets. Conditional on the number of

192 species observed at each site, we used this result to compute the expectation value and
193 variance of the sum of squares at each site.

194 4. With the computed expectation values and variances for each site, we used a 2-tailed test for
195 patterns of both competition and facilitation ($\alpha=0.05$, Lyapunov CLT). We also used a one-
196 tailed version (Ladau and Schwager 2008), which has power to reject the null hypothesis
197 only if the deviation from it is consistent with effects of competition. This test is uniformly
198 most powerful (UMP) against a broad range of alternatives consistent with competition. We
199 also numerically confirmed that tests had adequate power (>0.80).

200 We implemented this test using software “CoOccur” written in Visual Basic 6.0,
201 developed by the authors, and available online (<http://www.sadieryan.net/cooccur.html>). We
202 summarized the results for each hypothesis in Table 3, and report the significance, size and
203 power of the one- and two-tailed tests in full in Supplemental Table 1.

204

205 **Results**

206 The results varied by both scale and hypothesis in question. Results for potential predation
207 effects (H1), at both 5km and 10km, suggested competition in all years ($p<0.05$) and 8 of 13
208 years at 15km resolution ($p<0.05$). At 1km resolution, 2 years suggested competition ($p<0.05$);
209 six years suggested facilitation ($p=1.00$) and the other years were not indicative of a mechanism.

210 At 1km, the one-sided test only had sufficient size and power (minimum and maximum) for the
211 first 4 years; the two-tailed test had sufficient size for these four years and for two additional
212 years, but had insufficient power after the first four years. We thus cannot make robust
213 conclusions after the first four years at the 1km scale.

214 Perhaps due to sparse observations of carnivores due to their low abundance, or due to
215 the change in recording methods for observations, we found that the minimum criterion of (n
216 genera + 2)* species) at a site was not always met, drastically reducing the power of the test for
217 H1. This meant that tests at 1km, after 1984, had no power, and therefore did not produce
218 reliable answers, including the 6 years' results suggesting facilitation. For the remaining 44 tests
219 for H1, all the one-tailed tests had sufficient size and power, as did 43 of the two-tailed tests
220 (Table 3, Table S1).

221 The ruminant and non-ruminant hypothesis (H2) for structure arising from competition,
222 generated results indicating facilitation $p=1.00$ at all scales in all years. The size and power of all
223 tests for this mechanism was sufficient. For feeding competition between grazers and browsers
224 (H3), all years and scales indicated competition ($p<0.05$), except 1991 at 1km where $p=0.05$. All
225 tests for this mechanism, both one and two-tailed, had sufficient size and power (see Table 3,
226 Table S1).

227 H4 considered the contributions of grazing and browsing and also body size to
228 competition; the test indicated competition in 9 of the years at a 1km resolution. At a 5km
229 resolution, the test suggested competition in 8 of the years, and facilitation in 2 of the years. At
230 both 10km and 15km resolution, competition was suggested by the test in all 13 years. The size
231 and minimum and maximum power criteria were satisfied for both the one and two-tailed tests in
232 all cases (Table 3, Table S1).

233 In all cases (4 mechanisms, 13 years, 4 resolutions; total: 208 cases), the Type I error rate
234 of both the one and two-tailed tests were acceptably low. In addition, the power was sufficiently
235 high for all cases, both one and two-tailed tests, with the exception of years 1985-1993 at 1km
236 resolution for H1 (Table 3, Table S1).

237

238 **Discussion**

239 We sought to test hypotheses describing the mechanisms that may structure the community of
240 savanna mammals on the Kruger National Park landscape, using tests for species assemblage that
241 allow strong conclusions about mechanisms. We found support for competitive structure
242 patterning for three of our four hypotheses, while the other suggested facilitation in all years.

243 Testing suites of species involved in specific guild structuring mechanisms meant we
244 could explicitly formulate hypotheses. In addition, creating a software interface (CoOccur), in
245 which the size and power of the test is explicitly evaluated, allowed us to explore potential
246 pitfalls in attaining results, but thereby gave us confidence in our conclusions. For the one-tailed
247 test, rejecting the null hypothesis indicates effects of competition (negative non-independence),
248 while rejecting the null hypothesis in the two-tailed test can indicate competition or facilitation
249 (positive non-independence).

250 We found evidence of competition at the 5km and 10km scales when carnivores were
251 hypothesized to generate direct competition. We only found evidence for competitive structure
252 for roughly 60% of the years in question at the largest scale (15km). A close examination of the
253 years in question (Table 4) reveals no apparent temporal pattern, suggesting that this may be a
254 sufficiently large spatial scale that direct competition may not always exert a strong effect. At the
255 other extreme, at 1km resolution, for the four years with sufficient power, we found evidence for
256 both competition and a lack of interactions. Evidence of direct competition effects via carnivore
257 presence could indicate direct exclusion by predation, but more likely, behavioral avoidance of
258 carnivores by prey species. Predator vigilance and avoidance has been cited as likely shaping

259 herbivore distributions for savanna mammals, even resulting in unpredictable apparent
260 facilitation of herbivores, wherein mixed grazer herds group together (de Boer and Prins 1990).

261 In contrast to our expectation that the suite of herbivores might show evidence of
262 resource competition based on the division of ruminants and non-ruminants (H2), we found
263 evidence for facilitation at all scales, including the finer 1km scale. It is plausible that the test
264 was instead detecting habitat selection, at least at large scales, consistent with apparent
265 facilitation due to habitat selection. The ability to monopolize feeding patches at a scale relevant
266 to these herbivores, in terms of home range or daily traveling distance (Estes 1991) (1km or
267 5km), appears not to be conferred by ruminant ability. However, the more specialized herbivore
268 suites, with guilds of grazers and browsers and even small and large body size (H3 and H4)
269 showed patterns consistent with competitive structure (except one at 1km resolution). The
270 grazer/browser guild showed competition at 5km, 10km, and 15km, and inclusion of body size as
271 a factor also showed patterns consistent with competition at 10km and 15km resolutions, but was
272 less consistent at 5km and 10km. As pointed out by Farnsworth et al. (2002), in theory,
273 organisms sharing the same niche should competitively exclude each other to the point of one
274 species going extinct. However, a model of specialization by plant parts suggests that grazers can
275 co-exist on a landscape, if they can exploit different parts of plant structure. We found that if we
276 partition the guilds along the lines of niche specialization, i.e. grazers and browsers, we start to
277 find evidence of competitive structure. It is plausible that the very broad guilds of ruminants and
278 non-ruminants show apparent facilitation due to clumping of herbivores on the landscape into
279 preferred habitats.

280 Fritz (1997) conducted a comprehensive study on ungulate biomass at multiple sites in
281 Africa to assess whether the patterns in these communities could be attributable to missing

282 predator guilds, or missing megaherbivores. These guilds both exert pressure on other sympatric
283 guilds, but in slightly different ways, leading to interesting feedbacks on the relative abundance
284 and biomass of medium-sized ungulates. In the study, he attributed the missing guild structure in
285 part to high hunting pressures in certain areas. This is a major consideration for reserve design
286 and conservation of these savanna suites of mammals, and the effects of assemblage disruption
287 and community shifts are evident. Feeley (2003), in a study of avian assemblages on islands
288 resulting from establishment of a large reservoir, pointed out that community structure is an
289 important consideration in reserve design. More recently, studies in savanna systems have shown
290 that the removal of large herbivores can cause unexpected trophic cascades, down to the level of
291 complex feedbacks on ant-plant interactions (Pringle et al. 2007, Palmer et al. 2008, Estes et al.
292 2011).

293 Current distribution patterns of herbivores on landscapes may result from currently
294 absent or extinct competitors that once shaped the context for current species. This concept, the
295 “ghost of competition” (Connell 1980), is complicated to address, even with the luxury of this
296 type of long term data. In this study, we assume that patterns reflect interactions within the
297 complement of species over a period of thirteen years. Codron et al. (2008) asked whether large-
298 scale climatic factors or niche specialization may have shaped the assemblage of savanna species
299 over much longer timescales (the Quaternary Land Mammal Ages), and found that adaptation
300 through diet specialization (grazing and browsing) appears to continue through recent evolution,
301 and may be plastic throughout evolutionary history.

302 These census data do not represent a complete inventory of Kruger National Park. In
303 particular, the carnivore suite suffers not only from detection issues, but also omission of several
304 smaller carnivores. With more detailed carnivore behavioral data, we would be able to explore

305 potential facilitative mechanisms which have been suggested for other systems, such as smaller
306 carnivores (hyenas, jackals, etc.) benefiting from behaving as scavengers at larger carnivore
307 (lion, leopard, e.g.) kills (Grange and Duncan 2006). In addition, there were population declines
308 in several of the herbivore species during this time span, attributed in part to high rates of lion
309 predation (Ogutu and Owen-Smith 2003, Owen-Smith et al. 2005). How this might have affected
310 the data is unclear; we found no changes in potential structuring mechanisms within the
311 herbivores.

312

313

314 **Acknowledgments**

315 This work was supported by a Santa Fe Institute Postdoctoral Fellowship and Gordon and Betty
316 Moore Foundation Grant (J.L.), and in part by an NSF Biological Informatics Fellowship (S.J.R.)
317 and funding from the National Center for Ecological Analysis and Synthesis, a Center funded by
318 NSF (Grant EF-0553768), the University of California, Santa Barbara, and the State of
319 California. The authors thank Scientific Services at Kruger National Park for all their support
320 and data access, and we thank AW and EW for comments and edits.

321

322 **References**

- 323 Arsenault, R., and N. Owen-Smith. 2002. Facilitation versus competition in grazing herbivore
324 assemblages. *Oikos* 97:313–318.
- 325 Bailey, D. W., J. E. Gross, E. A. Laca, L. R. Rittenhouse, M. B. Coughenour, D. M. Swift, and P.
326 L. Sims. 1996. Mechanisms that result in large herbivore grazing distribution patterns.
327 *Journal of Range Management* 49:386–400.
- 328 de Boer, W. F., and H. H. T. Prins. 1990. Large herbivores that strive mightily but eat and drink
329 as friends. *Oecologia* 82:264–274.
- 330 Codron, D., J. S. Brink, L. Rossouw, and M. Clauss. 2008. The evolution of ecological
331 specialization in southern African ungulates: competition- or physical environmental
332 turnover? *Oikos* 117:344–353.
- 333 Connell, J. H. 1980. Diversity and the co-evolution of competitors, or the ghost of competition
334 past. *Oikos* 35:131–138.
- 335 Connor, E. F., and D. Simberloff. 1979. The Assembly of Species Communities - Chance or
336 Competition. *Ecology* 60:1132–1140.
- 337 Diamond, J. M. 1975. Assembly of Species Communities. Pages 342–444 in J. . Diamond and
338 M. . Cody, editors. *Ecology and Evolution of Communities*. Harvard University Press,
339 Cambridge, MA.
- 340 Durant, S. M. 1998. Competition refuges and coexistence: an example from Serengeti
341 carnivores. *Journal of Animal Ecology* 67:370–386.
- 342 Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T.
343 E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T.
344 Paine, E. K. Pickett, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B.

- 345 Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, and D. A. Wardle. 2011. Trophic
346 Downgrading of Planet Earth. *Science* 333:301–306.
- 347 Estes, R. D. 1991. The behavior guide to Africa mammals: including hoofed mammals,
348 carnivores, primates. University of California Press, London.
- 349 Farnsworth, K. D., S. Focardi, and J. A. Beecham. 2002. Grassland and herbivore interactions:
350 how do grazers coexist? *The American Naturalist* 159:24–39.
- 351 Feeley, K. 2003. Analysis of avian communities in Lake Guri, Venezuela, using multiple
352 assembly rule models. *Oecologia* 137:113.
- 353 Fritz, H. 1997. Low Ungulate Biomass in West African Savannas: Primary Production or
354 Missing Megaherbivores or Large Predator Species? *Ecography* 20:421.
- 355 Gertenbach, W. P. 1980. Rainfall Patterns in the Kruger National Park. *Koedoe* 23:35–43.
- 356 Gertenbach, W. P. 1983. Landscapes of Kruger National Park. *Koedoe* 26:9–121.
- 357 Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* 81:2606–
358 2621.
- 359 Gotelli, N. J., and A. M. Ellison. 2002. Assembly rules for new England ant assemblages. *Oikos*
360 99:591–599.
- 361 Gotelli, N. J., and D. J. McCabe. 2002. Species co-occurrence: A meta-analysis of J. M.
362 Diamond’s assembly rules model. *Ecology* 83:2091–2096.
- 363 Grange, S., and P. Duncan. 2006. Bottom-up and top-down processes in African ungulate
364 communities: resources and predation acting on the relative abundance of zebra and
365 grazing bovids. *Ecography* 29:899–907.
- 366 Ladau, J., and S. Schwager. 2008. Robust hypothesis tests for independence in community
367 assembly. *Journal of Mathematical Biology* 57:555.

- 368 Linnell, J. D. ., and O. Strand. 2000. Interference interactions, co-existence and conservation of
369 mammalian carnivores. *Diversity and Distributions* 6:169–176.
- 370 Manly, B. F. J. 1995. A Note on the Analysis of Species Cooccurrences. *Ecology* 76:1109–1115.
- 371 Ogutu, J. O., and N. Owen-Smith. 2003. ENSO, rainfall and temperature influences on extreme
372 population declines among African savanna ungulates. *Ecology Letters* 6:412–419.
- 373 Owen-Smith, N., D. R. Mason, and J. O. Ogutu. 2005. Correlates of survival rates for 10 African
374 ungulate populations: density, rainfall and predation. *Journal of Animal Ecology* 74:788.
- 375 Palmer, T. M., M. L. Stanton, T. P. Young, J. R. Goheen, R. M. Pringle, and R. Karban. 2008.
376 Breakdown of an Ant-Plant Mutualism Follows the Loss of Large Herbivores from an
377 African Savanna. *Science* 319:192–195.
- 378 Pringle, R. M., T. P. Young, D. I. Rubenstein, and D. J. McCauley. 2007. Herbivore-initiated
379 interaction cascades and their modulation by productivity in an African savanna.
380 *Proceedings of the National Academy of Sciences* 104:193–197.
- 381 Radloff, F. G. T., and J. T. D. Toit. 2004. Large predators and their prey in a southern African
382 savanna: a predator’s size determines its prey size range. *Journal of Animal Ecology*
383 73:410–423.
- 384 Redfern, J. V., and W. M. Getz. 2002. Limiting factor mitigation: evaluating determinants of
385 herbivore distribution in an African savanna. Not published:1–23.
- 386 Redfern, J. V., S. J. Ryan, and W. M. Getz. 2006. Defining herbivore assemblages in the Kruger
387 National Park: a correlative coherence approach. *Oecologia* 146:632–640.
- 388 Roxburgh, S. H., and M. Matsuki. 1999. The statistical validation of null models used in spatial
389 association analyses. *Oikos* 85:68–78.

- 390 Schluter, D. 1984. A Variance Test for Detecting Species Associations, with Some Example
391 Applications. *Ecology* 65:998–1005.
- 392 Schmitz, O. J. 2007. Predator diversity and trophic interactions. *Ecology* 88:2415–2426.
- 393 Schoener, T. W. 1983. Field Experiments on Interspecific Competition. *American Naturalist*
394 122:240–285.
- 395 Senft, R. L. 1989. Hierarchical Foraging Models - Effects of Stocking and Landscape
396 Composition on Simulated Resource Use by Cattle. *Ecological Modelling* 46:283–303.
- 397 Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift.
398 1987. Large Herbivore Foraging and Ecological Hierarchies. *Bioscience* 37:789-.
- 399 Sfenthourakis, S., E. Tzanatos, and S. Giokas. 2006. Species co-occurrence: the case of
400 congeneric species and a causal approach to patterns of species association. *Global*
401 *Ecology and Biogeography* 15:39–49.
- 402 Stone, L., and A. Roberts. 1990. The Checkerboard Score and Species Distributions. *Oecologia*
403 85:74–79.
- 404 Ulrich, W., F. Jabot, and N. J. Gotelli. 2017. Competitive interactions change the pattern of
405 species co-occurrences under neutral dispersal. *Oikos* 126:91–100.
- 406 Viljoen, P. 1996a. Ecological aerial survey monitoring programme in the Kruger National Park;
407 Data Catalogue. National Parks Board, Republic of South Africa, Skukuza.
- 408 Viljoen, P. C. 1996b. Ecological aerial surveys (EAS) in the Kruger National Park. Summary of
409 current methodology - 1996 update. Unpublished, National Parks Board, Republic of
410 South Africa, Skukuza.

411

412

413 **Figures and Tables**

414 Figure 1: Location of Kruger National Park in Africa, with inset showing the four quadrants (NE,
415 NW, SE, SW) created by the East-West granitic-basaltic landscape split, and the North-South
416 division as a proxy for rain gradient, and a far northern, uncensused (U) region of the park.

417

418 Table 1: Mammal species observed in the EAS census data and used in the study

419

420 Table 2: Species divisions into guilds as specified in hypotheses H1-H4.

421

422 Table 3: Summary results of the robust test, by mechanism (H1-H4) and resolution; number of
423 years are given in their p -value ranges

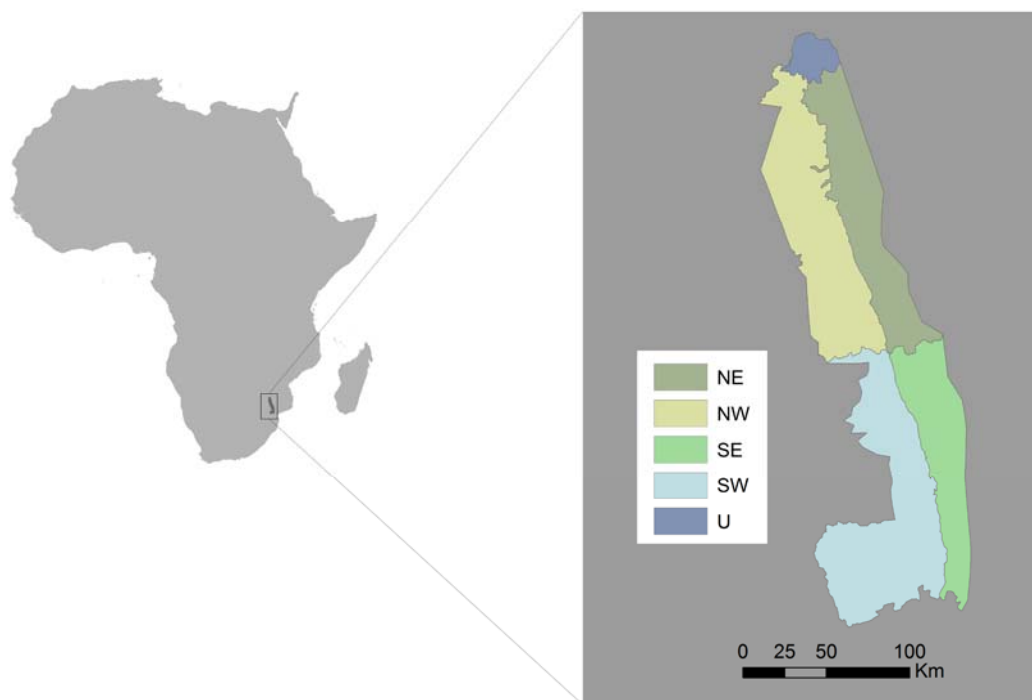
424

425 Supplemental Table 1: Full results for the statistical tests, by hypothesis H1-H4

426

427

428 **Figure 1**



429

430

431 **Table 1**

<i>Order</i>	<i>Family</i>	<i>Species</i>	<i>Common Name</i>		
Artiodactyla	Bovidae	<i>Aepyceris melampus</i>	Impala		
		<i>Connochaetes taurinus</i>	Blue Wildebeest		
		<i>Damaliscus lunatus</i>	Tsessebe		
		<i>Hippotragus equinus</i>	Roan Antelope		
		<i>Hippotragus niger</i>	Sable Antelope		
		<i>Kobus ellipsiprymnus</i>	Waterbuck		
		<i>Oreotragus oreotragus</i>	Klipspringer		
		<i>Ourebia ourebi</i>	Oribi		
		<i>Raphicerus campestris</i>	Steenbuck		
		<i>Redunca arundinum</i>	Reedbuck		
		<i>Sigmoceros lichtensteinii</i>	Lichtenstein's Hartebeest		
		<i>Syncerus caffer</i>	Buffalo		
		<i>Sylvicapra grimmia</i>	Duiker		
		<i>Taurotragus oryx</i>	Eland		
		<i>Tragelaphus angasii</i>	Nyala		
		<i>Tragelaphus scriptus</i>	Bushbuck		
		<i>Tragelaphus strepsiceros</i>	Kudu		
			Giraffidae	<i>Giraffa camelopardalis</i>	Giraffe
			Hippopotamidae	<i>Hippopotamus amphibius</i>	Hippo
	Suidae	<i>Phacochoerus africanus</i>	Warthog		
		<i>Potamochoerus larvatus</i>	Bushpig		
Perissodactyla	Equidae	<i>Equus quagga</i>	Zebra		
	Rhinocerotidae	<i>Ceratotherium simium</i>	White Rhino		
<i>Diceros bicornis</i>		Black Rhino			
Proboscidea	Elephantidae	<i>Loxodonta africana</i>	Elephant		
Carnivora	Canidae	<i>Canis mesomelas</i>	Black-Backed Jackal		
		<i>Lycaon pictus</i>	Wild Dog		
	Felidae	<i>Acinonyx jubatus</i>	Cheetah		
		<i>Panthera leo</i>	Lion		
		<i>Panthera pardus</i>	Leopard		
	Hyaenidae	<i>Crocuta crocuta</i>	Hyaena		
	Mustelidae	<i>Mellivora capensis</i>	Honey Badger		

432

433

434 **Table 2**

<i>Hypothesis</i>	<i>Guild divisions and species (common names)</i>	
H1	Carnivores: Black-Backed Jackal, Wild dog, Cheetah, Lion, Leopard, Hyaena, Honey Badger	Herbivores: Impala, Blue Wildebeest, Tsessebe, Roan Antelope, Sable Antelope, Waterbuck, Klipspringer, Oribi, Steenbuck, Reedbuck, Lichtenstein's Hartebeest, Buffalo, Duiker, Eland, Nyala, Bushbuck, Kudu, Giraffe, Hippo, Warthog, Bushpig, Zebra, White Rhino, Black Rhino, Elephant
H2	Ruminants: Roan Antelope Bull, Buffalo, Bushbuck, Duiker, Eland, Kudu, Giraffe, Klipspringer, Lichtenstein's Hartebeest, Nyala, Oribi, Impala, Roan Antelope, Reedbuck, Sable Antelope, Steenbuck, Tsessebe, Blue Wildebeest, Waterbuck	Non-Ruminants: Bushpig, Hippo, Zebra, Elephant, Black Rhino, Warthog, White Rhino
H3	Grazers: Buffalo, Zebra, Wildebeest	Browsers: Elephant, Giraffe, Kudu, Impala
H4	Grazers: <i>Small</i> Zebra, Wildebeest <i>Large</i> Buffalo	Browsers: <i>Small</i> Giraffe, Kudu, Impala <i>Large</i> Elephant

435

436

437 **Table 3**

438

<i>Mechanism</i>	<i>Spatial Resolution</i>	<i>p < 0.05</i>	<i>0.05 ≤ p ≤ 0.95</i>	<i>p > 0.95</i>
H1	1km	2	5	6
	5 km	13	--	--
	10 km	13	--	--
	15 km	8	5	--
H2	1km	--	--	13
	5 km	--	--	13
	10 km	--	--	13
	15 km	--	--	13
H3	1km	12	1	--
	5 km	13	--	--
	10 km	13	--	--
	15 km	13	--	--
H4	1km	9	4	--
	5 km	8	3	2
	10 km	13	--	--
	15 km	13	--	--

439 **Supp 1.**

H1		One-tailed test				Two-tailed test					
Scale	Year	P-value	Size	Minimum Power	Maximum Power	P-value	Size	Minimum Power	Maximum Power	Rows	Cols
1km	1981	0.08	0.04	0.07	0.22	0.15	0.05	0.04	1.00	32	3377
	1982	0.00	0.04	0.07	0.31	0.00	0.05	0.05	1.00	32	3347
	1983	0.06	0.05	0.06	0.22	0.12	0.04	0.04	1.00	34	3366
	1984	0.00	0.04	0.07	0.26	0.00	0.05	0.05	1.00	33	3390
	1985	0.12	0.01	0.00	0.00	0.23	0.05	0.00	0.29	35	12402
	1986	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	36	12234
	1987	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	36	12493
	1988	0.16	0.00	0.00	0.00	0.32	0.05	0.00	0.30	35	12351
	1989	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	35	11718
	1990	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	34	11905
	1991	0.12	0.00	0.00	0.00	0.25	0.00	0.00	0.00	36	11330
	1992	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	36	11811
	1993	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	36	10772
5km	1981	0.00	0.04	0.12	0.61	0.00	0.05	0.05	1.00	31	604
	1982	0.00	0.04	0.14	0.78	0.00	0.05	0.05	1.00	32	605
	1983	0.00	0.04	0.13	0.77	0.00	0.05	0.05	1.00	34	605
	1984	0.00	0.05	0.16	0.83	0.00	0.05	0.05	1.00	32	604
	1985	0.00	0.04	0.16	0.85	0.00	0.05	0.05	1.00	34	617
	1986	0.00	0.04	0.13	0.73	0.00	0.05	0.05	1.00	36	607
	1987	0.00	0.04	0.13	0.75	0.00	0.06	0.06	1.00	35	617
	1988	0.00	0.05	0.12	0.66	0.00	0.05	0.05	1.00	35	619
	1989	0.00	0.04	0.11	0.53	0.00	0.05	0.05	1.00	35	620
	1990	0.00	0.04	0.13	0.71	0.00	0.05	0.05	1.00	34	611
	1991	0.01	0.04	0.09	0.46	0.02	0.05	0.05	1.00	36	620
	1992	0.00	0.04	0.09	0.37	0.00	0.05	0.05	1.00	35	621
	1993	0.01	0.03	0.06	0.18	0.02	0.05	0.01	1.00	36	620

440

441

442

H1		One-tailed test				Two-tailed test					
Scale	Year	P-value	Size	Minimum Power	Maximum Power	P-value	Size	Minimum Power	Maximum Power	Rows	Cols
10km	1981	0.00	0.04	0.13	0.68	0.00	0.04	0.04	1.00	31	130
	1982	0.00	0.04	0.15	0.81	0.00	0.05	0.05	1.00	32	129
	1983	0.00	0.04	0.15	0.87	0.00	0.05	0.05	1.00	33	130
	1984	0.00	0.05	0.17	0.88	0.00	0.05	0.05	1.00	32	130
	1985	0.00	0.05	0.16	0.88	0.01	0.05	0.05	1.00	34	130
	1986	0.00	0.04	0.14	0.81	0.00	0.05	0.05	1.00	36	130
	1987	0.00	0.04	0.15	0.81	0.00	0.05	0.05	1.00	35	130
	1988	0.00	0.05	0.14	0.74	0.00	0.05	0.05	1.00	35	130
	1989	0.00	0.04	0.13	0.66	0.00	0.06	0.06	1.00	34	130
	1990	0.00	0.04	0.14	0.75	0.00	0.05	0.05	1.00	34	130
	1991	0.02	0.04	0.12	0.58	0.03	0.05	0.05	1.00	36	130
	1992	0.00	0.05	0.12	0.60	0.00	0.05	0.05	1.00	35	130
	1993	0.00	0.03	0.08	0.40	0.00	0.04	0.04	1.00	36	130
15km	1981	0.03	0.04	0.10	0.45	0.07	0.05	0.05	1.00	31	43
	1982	0.00	0.04	0.11	0.56	0.00	0.05	0.05	1.00	32	43
	1983	0.07	0.04	0.13	0.71	0.13	0.06	0.06	1.00	33	43
	1984	0.01	0.04	0.13	0.63	0.01	0.05	0.05	1.00	31	43
	1985	0.11	0.04	0.12	0.62	0.21	0.05	0.05	1.00	34	43
	1986	0.14	0.04	0.12	0.61	0.28	0.04	0.04	1.00	36	43
	1987	0.05	0.04	0.12	0.57	0.10	0.04	0.04	1.00	35	43
	1988	0.01	0.03	0.11	0.53	0.01	0.05	0.05	1.00	34	43
	1989	0.00	0.04	0.10	0.47	0.01	0.05	0.05	1.00	34	43
	1990	0.00	0.04	0.11	0.48	0.00	0.05	0.05	1.00	34	43
	1991	0.12	0.04	0.09	0.43	0.24	0.04	0.04	1.00	36	43
	1992	0.00	0.04	0.10	0.45	0.00	0.05	0.05	1.00	35	43
	1993	0.00	0.04	0.08	0.29	0.00	0.05	0.05	1.00	35	43

443

444

445

446

H2		One-tailed test				Two-tailed test					
Scale	Year	P-value	Size	Minimum Power	Maximum Power	P-value	Size	Minimum Power	Maximum Power	Rows	Cols
1km	1981	1.00	0.05	0.00	1.00	0.00	0.05	0.04	1.00	26	3377
	1982	1.00	0.05	0.00	1.00	0.00	0.05	0.04	1.00	27	3347
	1983	1.00	0.05	0.01	1.00	0.00	0.05	0.05	1.00	28	3366
	1984	1.00	0.06	0.00	1.00	0.00	0.06	0.03	1.00	27	3390
	1985	1.00	0.06	0.08	1.00	0.00	0.06	0.06	1.00	29	12402
	1986	1.00	0.05	0.07	1.00	0.00	0.06	0.06	1.00	29	12234
	1987	1.00	0.07	0.08	1.00	0.00	0.05	0.05	1.00	29	12493
	1988	1.00	0.05	0.07	1.00	0.00	0.05	0.05	1.00	28	12351
	1989	1.00	0.05	0.06	1.00	0.00	0.05	0.05	1.00	28	11718
	1990	1.00	0.05	0.06	1.00	0.00	0.05	0.05	1.00	28	11905
	1991	1.00	0.06	0.07	1.00	0.00	0.06	0.06	1.00	29	11330
	1992	1.00	0.05	0.07	0.99	0.00	0.05	0.05	1.00	29	11811
	1993	1.00	0.05	0.07	0.97	0.00	0.05	0.05	1.00	30	10772
5km	1981	1.00	0.05	0.00	1.00	0.00	0.06	0.06	1.00	26	604
	1982	1.00	0.04	0.00	1.00	0.00	0.04	0.04	1.00	27	605
	1983	1.00	0.05	0.00	1.00	0.00	0.06	0.06	1.00	28	605
	1984	1.00	0.05	0.00	1.00	0.00	0.05	0.05	1.00	27	604
	1985	1.00	0.04	0.00	1.00	0.00	0.05	0.05	1.00	29	617
	1986	1.00	0.05	0.00	1.00	0.00	0.05	0.05	1.00	29	607
	1987	1.00	0.05	0.00	1.00	0.00	0.05	0.05	1.00	29	617
	1988	1.00	0.05	0.00	1.00	0.00	0.05	0.05	1.00	28	619
	1989	1.00	0.06	0.00	1.00	0.00	0.06	0.06	1.00	28	620
	1990	1.00	0.06	0.00	1.00	0.00	0.06	0.06	1.00	28	611
	1991	1.00	0.05	0.00	1.00	0.00	0.05	0.05	1.00	29	620
	1992	1.00	0.05	0.00	1.00	0.00	0.05	0.05	1.00	29	621
	1993	1.00	0.05	0.00	1.00	0.00	0.05	0.05	1.00	30	620

447

448

449

H2		One-tailed test				Two-tailed test					
Scale	Year	P-value	Size	Minimum Power	Maximum Power	P-value	Size	Minimum Power	Maximum Power	Rows	Cols
	1982	1.00	0.04	0.00	1.00	0.00	0.05	0.04	1.00	27	129
	1983	1.00	0.04	0.00	1.00	0.00	0.05	0.02	1.00	28	130
	1984	1.00	0.04	0.00	1.00	0.00	0.05	0.05	1.00	27	130
	1985	1.00	0.04	0.00	1.00	0.00	0.05	0.04	1.00	29	130
	1986	1.00	0.05	0.00	1.00	0.00	0.05	0.03	1.00	29	130
	1987	1.00	0.05	0.00	1.00	0.00	0.05	0.02	1.00	29	130
	1988	1.00	0.05	0.00	1.00	0.00	0.06	0.02	1.00	28	130
	1989	1.00	0.04	0.00	1.00	0.00	0.04	0.02	1.00	28	130
	1990	1.00	0.04	0.00	1.00	0.00	0.05	0.03	1.00	28	130
	1991	1.00	0.05	0.00	1.00	0.00	0.05	0.01	1.00	29	130
	1992	1.00	0.05	0.00	1.00	0.00	0.05	0.01	1.00	29	130
	1993	1.00	0.05	0.00	1.00	0.00	0.06	0.02	1.00	30	130
15km	1981	1.00	0.04	0.00	1.00	0.00	0.05	0.02	1.00	26	43
	1982	1.00	0.03	0.00	1.00	0.00	0.05	0.02	1.00	27	43
	1983	1.00	0.03	0.00	1.00	0.00	0.05	0.03	1.00	28	43
	1984	1.00	0.03	0.00	1.00	0.00	0.04	0.02	1.00	27	43
	1985	1.00	0.04	0.00	1.00	0.00	0.05	0.03	1.00	29	43
	1986	1.00	0.04	0.00	1.00	0.00	0.05	0.02	1.00	29	43
	1987	1.00	0.04	0.00	1.00	0.00	0.05	0.02	1.00	29	43
	1988	1.00	0.04	0.00	1.00	0.00	0.05	0.02	1.00	28	43
	1989	1.00	0.04	0.00	1.00	0.00	0.04	0.02	1.00	28	43
	1990	1.00	0.04	0.00	1.00	0.00	0.05	0.02	1.00	28	43
	1991	1.00	0.04	0.00	1.00	0.00	0.05	0.02	1.00	29	43
	1992	1.00	0.04	0.00	1.00	0.00	0.05	0.02	1.00	29	43
	1993	1.00	0.04	0.00	1.00	0.00	0.04	0.02	1.00	29	43

450

451

H3		One-tailed test				Two-tailed test					
Scale	Year	P-value	Size	Minimum Power	Maximum Power	P-value	Size	Minimum Power	Maximum Power	Rows	Cols
1km	1981	0.00	0.05	0.04	1.00	0.00	0.05	0.05	1.00	11	3377
	1982	0.00	0.05	0.04	1.00	0.00	0.05	0.05	1.00	11	3347
	1983	0.00	0.04	0.05	1.00	0.00	0.04	0.04	1.00	11	3366
	1984	0.00	0.05	0.04	1.00	0.00	0.05	0.05	1.00	11	3390
	1985	0.00	0.05	0.07	0.98	0.01	0.05	0.05	1.00	11	12402
	1986	0.00	0.05	0.07	0.89	0.00	0.05	0.05	0.98	11	12234
	1987	0.00	0.05	0.07	0.90	0.00	0.05	0.05	0.99	11	12493
	1988	0.00	0.06	0.07	0.96	0.00	0.05	0.05	1.00	11	12351
	1989	0.01	0.05	0.06	0.87	0.02	0.05	0.04	0.97	11	11718
	1990	0.01	0.05	0.07	0.91	0.02	0.05	0.05	0.99	11	11905
	1991	0.05	0.05	0.07	0.86	0.10	0.06	0.05	0.97	11	11330
	1992	0.00	0.05	0.07	0.83	0.00	0.05	0.05	0.96	11	11811
	1993	0.00	0.05	0.07	0.75	0.00	0.05	0.05	0.91	11	10772
5km	1981	0.00	0.05	0.00	1.00	0.00	0.05	0.05	1.00	11	604
	1982	0.00	0.05	0.00	1.00	0.00	0.05	0.05	1.00	11	605
	1983	0.00	0.05	0.00	1.00	0.00	0.05	0.05	1.00	11	605
	1984	0.00	0.05	0.00	1.00	0.00	0.05	0.05	1.00	11	604
	1985	0.00	0.05	0.00	1.00	0.00	0.05	0.05	1.00	11	617
	1986	0.00	0.05	0.00	1.00	0.00	0.05	0.05	1.00	11	607
	1987	0.00	0.04	0.00	1.00	0.00	0.05	0.05	1.00	11	617
	1988	0.00	0.05	0.00	1.00	0.00	0.05	0.05	1.00	11	619
	1989	0.00	0.05	0.00	1.00	0.00	0.05	0.05	1.00	11	620
	1990	0.00	0.04	0.00	1.00	0.00	0.05	0.05	1.00	11	611
	1991	0.00	0.05	0.00	1.00	0.00	0.05	0.05	1.00	11	620
	1992	0.00	0.05	0.00	1.00	0.00	0.05	0.05	1.00	11	621
	1993	0.00	0.05	0.01	1.00	0.00	0.05	0.05	1.00	11	620

452

453

454

H3		One-tailed test				Two-tailed test					
Scale	Year	P-value	Size	Minimum Power	Maximum Power	P-value	Size	Minimum Power	Maximum Power	Rows	Cols
	1982	0.00	0.04	0.00	1.00	0.00	0.05	0.05	1.00	11	129
	1983	0.00	0.04	0.00	1.00	0.00	0.05	0.05	1.00	11	130
	1984	0.00	0.05	0.00	1.00	0.00	0.05	0.05	1.00	11	130
	1985	0.00	0.04	0.00	1.00	0.00	0.04	0.04	1.00	11	130
	1986	0.00	0.05	0.00	1.00	0.00	0.05	0.05	1.00	11	130
	1987	0.00	0.05	0.00	1.00	0.00	0.05	0.05	1.00	11	130
	1988	0.00	0.05	0.00	1.00	0.00	0.05	0.05	1.00	11	130
	1989	0.00	0.05	0.00	1.00	0.00	0.05	0.05	1.00	11	130
	1990	0.00	0.04	0.00	1.00	0.00	0.05	0.05	1.00	11	130
	1991	0.00	0.05	0.00	1.00	0.00	0.05	0.05	1.00	11	130
	1992	0.00	0.05	0.00	1.00	0.00	0.05	0.05	1.00	11	130
	1993	0.00	0.04	0.00	1.00	0.00	0.05	0.05	1.00	11	130
15km	1981	0.00	0.04	0.00	1.00	0.00	0.05	0.05	1.00	11	43
	1982	0.00	0.04	0.00	1.00	0.00	0.04	0.04	1.00	11	43
	1983	0.00	0.04	0.00	1.00	0.00	0.05	0.05	1.00	11	43
	1984	0.00	0.03	0.00	1.00	0.00	0.05	0.05	1.00	11	43
	1985	0.00	0.04	0.00	1.00	0.00	0.05	0.05	1.00	11	43
	1986	0.00	0.04	0.00	1.00	0.00	0.05	0.05	1.00	11	43
	1987	0.00	0.03	0.00	1.00	0.00	0.05	0.05	1.00	11	43
	1988	0.00	0.03	0.00	1.00	0.00	0.05	0.05	1.00	11	43
	1989	0.00	0.04	0.00	1.00	0.00	0.05	0.05	1.00	11	43
	1990	0.00	0.04	0.00	1.00	0.00	0.04	0.04	1.00	11	43
	1991	0.00	0.04	0.00	1.00	0.00	0.05	0.05	1.00	11	43
	1992	0.00	0.04	0.00	1.00	0.00	0.05	0.05	1.00	11	43
	1993	0.00	0.04	0.00	1.00	0.00	0.05	0.05	1.00	11	43

455

456

457

H4		One-tailed test				Two-tailed test					
Scale	Year	P-value	Size	Minimum Power	Maximum Power	P-value	Size	Minimum Power	Maximum Power	Rows	Cols
1km	1981	0.86	0.06	0.13	1.00	0.29	0.05	0.05	1.00	11	3377
	1982	0.29	0.05	0.12	1.00	0.58	0.04	0.04	1.00	11	3347
	1983	0.07	0.05	0.11	1.00	0.14	0.05	0.05	1.00	11	3366
	1984	0.00	0.05	0.12	1.00	0.01	0.05	0.05	1.00	11	3390
	1985	0.04	0.05	0.08	0.89	0.07	0.05	0.05	0.99	11	12402
	1986	0.00	0.05	0.07	0.79	0.00	0.05	0.05	0.94	11	12234
	1987	0.00	0.06	0.07	0.76	0.01	0.05	0.05	0.91	11	12493
	1988	0.01	0.05	0.06	0.91	0.02	0.05	0.05	0.98	11	12351
	1989	0.01	0.05	0.08	0.79	0.02	0.05	0.05	0.94	11	11718
	1990	0.01	0.05	0.08	0.80	0.03	0.05	0.05	0.96	11	11905
	1991	0.13	0.05	0.06	0.74	0.25	0.05	0.05	0.91	11	11330
	1992	0.01	0.05	0.06	0.69	0.02	0.04	0.04	0.86	11	11811
	1993	0.00	0.05	0.07	0.61	0.00	0.05	0.05	0.76	11	10772
5km	1981	0.98	0.05	0.17	1.00	0.04	0.04	0.04	1.00	11	604
	1982	1.00	0.05	0.21	1.00	0.00	0.04	0.04	1.00	11	605
	1983	0.13	0.05	0.18	1.00	0.26	0.05	0.05	1.00	11	605
	1984	0.04	0.05	0.20	1.00	0.07	0.04	0.04	1.00	11	604
	1985	0.42	0.05	0.21	1.00	0.84	0.05	0.05	1.00	11	617
	1986	0.07	0.05	0.19	1.00	0.13	0.05	0.05	1.00	11	607
	1987	0.02	0.04	0.17	1.00	0.03	0.05	0.05	1.00	11	617
	1988	0.00	0.05	0.20	1.00	0.00	0.05	0.05	1.00	11	619
	1989	0.03	0.04	0.19	1.00	0.06	0.05	0.05	1.00	11	620
	1990	0.00	0.06	0.17	1.00	0.00	0.05	0.05	1.00	11	611
	1991	0.00	0.04	0.16	1.00	0.00	0.05	0.05	1.00	11	620
	1992	0.00	0.04	0.17	1.00	0.01	0.04	0.04	1.00	11	621
	1993	0.00	0.04	0.15	1.00	0.00	0.05	0.05	1.00	11	620

458

459

460

H4		One-tailed test				Two-tailed test					
Scale	Year	P-value	Size	Minimum Power	Maximum Power	P-value	Size	Minimum Power	Maximum Power	Rows	Cols
	1982	0.02	0.05	0.17	1.00	0.03	0.06	0.06	1.00	11	129
	1983	0.00	0.04	0.16	1.00	0.00	0.05	0.05	1.00	11	130
	1984	0.00	0.04	0.17	1.00	0.00	0.05	0.05	1.00	11	130
	1985	0.01	0.05	0.15	1.00	0.02	0.06	0.06	1.00	11	130
	1986	0.00	0.05	0.15	1.00	0.00	0.05	0.05	1.00	11	130
	1987	0.00	0.05	0.16	1.00	0.00	0.05	0.05	1.00	11	130
	1988	0.00	0.04	0.15	1.00	0.00	0.05	0.05	1.00	11	130
	1989	0.00	0.05	0.15	1.00	0.00	0.06	0.06	1.00	11	130
	1990	0.00	0.05	0.16	1.00	0.00	0.05	0.05	1.00	11	130
	1991	0.00	0.04	0.14	1.00	0.00	0.05	0.05	1.00	11	130
	1992	0.00	0.05	0.15	1.00	0.00	0.06	0.06	1.00	11	130
	1993	0.00	0.05	0.13	1.00	0.00	0.05	0.05	1.00	11	130
15km	1981	0.00	0.04	0.09	0.99	0.00	0.05	0.05	1.00	11	43
	1982	0.00	0.04	0.09	1.00	0.00	0.05	0.05	1.00	11	43
	1983	0.00	0.03	0.10	1.00	0.00	0.05	0.05	1.00	11	43
	1984	0.00	0.04	0.09	0.99	0.00	0.04	0.04	1.00	11	43
	1985	0.00	0.04	0.09	0.99	0.00	0.04	0.04	1.00	11	43
	1986	0.00	0.04	0.10	0.99	0.00	0.05	0.05	1.00	11	43
	1987	0.00	0.05	0.09	0.99	0.00	0.05	0.05	1.00	11	43
	1988	0.00	0.05	0.10	0.99	0.00	0.05	0.05	1.00	11	43
	1989	0.00	0.05	0.09	0.99	0.00	0.05	0.05	1.00	11	43
	1990	0.00	0.04	0.10	1.00	0.00	0.05	0.05	1.00	11	43
	1991	0.00	0.04	0.09	0.98	0.00	0.04	0.04	1.00	11	43
	1992	0.00	0.04	0.09	0.99	0.00	0.05	0.05	1.00	11	43
	1993	0.00	0.04	0.09	0.98	0.00	0.05	0.04	1.00	11	43

461