

J. V. Redfern · S. J. Ryan · W. M. Getz

## Defining herbivore assemblages in the Kruger National Park: a correlative coherence approach

Received: 29 November 2004 / Accepted: 10 August 2005 / Published online: 11 October 2005  
© Springer-Verlag 2005

**Abstract** Spatial associations of seven herbivore species in the Kruger National Park, South Africa, are analyzed using a new technique, Correlative Coherence Analysis (CoCA). CoCA is a generalization of the concept of correlation to more than two sequences of numbers. Prior information on the feeding ecology and metabolic requirements of these species is used to contrast spatial scales at which hypothesized guild aggregation or competition occurs. These hypotheses are tested using 13 years of aerial census data collected during the dry season. Our results are consistent with the hypothesis that distributions of large and small species of the same feeding type (i.e., grazers and browsers) overlap in potentially resource-rich areas, but have lower similarity values across all areas because the higher tolerance of large species for low quality foods results in a more even spatial distribution of large species compared to small species.

**Key words** Correlative coherence analysis · Herbivore communities · Interspecific competition · Guild aggregation · South Africa

### Introduction

Studies of community structure and species interactions frequently involve quantifying and identifying patterns of species co-occurrence or spatial association (inter alia Diamond 1975; Connor and Simberloff 1979; Schoener 1983; Schluter 1984; Stone and Roberts 1990; Manly 1995; Durant 1998; Roxburgh and Matsuki 1999; Gotelli 2000; Linnell and Strand 2000; Gotelli and Ellison 2002; Gotelli and McCabe 2002). Demonstration of a pattern or lack thereof has been the subject of heated debate in the ecological literature for almost 30 years (see the review in Gotelli and McCabe 2002). In 1975, Jared Diamond posited that species assemblages are determined by competitive interactions, citing a system in which co-occurrence of species diads was readily and frequently apparent. Diamond's conclusions were rebutted by Connor and Simberloff in 1979, when they demonstrated that random colonization events could result in similar patterns of co-occurrence. More recent studies of species co-occurrence or spatial association have focused on demonstrating outcomes of posited local competitive interactions, such as predation and resource partitioning (Durant 1998; Linnell and Strand 2000; Gotelli and Ellison 2002), or improving techniques for modeling random distributions on a landscape (Manly 1995; Roxburgh and Matsuki 1999; Gotelli 2000).

We quantify patterns of co-occurrence for seven herbivore species in 13 years of aerial census data collected during the dry season in the Kruger National Park (KNP), South Africa, using a new technique, Correlative Coherence Analysis (CoCA, Getz 2003). CoCA generalizes the concept of correlation between two species to the correlative coherence (CoC) of  $n$  species ( $n \geq 2$ ). In particular, CoCA summarizes the similarity of pairwise

---

Communicated by Thomas Miller

---

J. V. Redfern · S. J. Ryan · W. M. Getz  
Department of Environmental Science, Policy and Management,  
University of California, Berkeley, CA 94720, USA

S. J. Ryan  
Museum of Vertebrate Zoology,  
University of California, Berkeley, CA 94720, USA  
E-mail: sjryan@nature.berkeley.edu

W. M. Getz  
Mammal Research Institute,  
Department of Zoology and Entomology,  
University of Pretoria, 0002 Pretoria, South Africa  
E-mail: getz@nature.berkeley.edu

*Present address:* J. V. Redfern (✉)  
Southwest Fisheries Science Center,  
8604 La Jolla Shores Dr, La Jolla, CA 92037, USA  
E-mail: Jessica.Redfern@noaa.gov  
Tel.: +1-858-5467117  
Fax: +1-858-5465657

correlations between  $n$  species using a Shannon–Wiener type measure of the diversity of the normalized eigenvalues of an  $n$ -dimensional correlation matrix (Getz 2003). An assemblage of species with highly correlated distributions will have a CoC close to one while an assemblage of largely uncorrelated species will have a CoC close to zero.

We used CoCA because it is a relatively simple technique that simultaneously evaluates the similarity of the spatial distributions of multiple species, whereas other spatial statistics primarily assess distribution patterns of a single species or pairwise associations between species distributions. Additionally, CoCA is not subject to the “edge effects” that confound other spatial statistics (e.g., Ripley’s  $K$ , Geary’s  $C$ , Moran’s  $I$ —cf. Dale et al. 2002; Perry et al. 2002) because the spatial aspect of the data is considered implicitly. Thus CoCA is well suited to analyzing species distributions in irregularly shaped areas, such as the KNP, which is approximately five times longer than it is wide with a crenellated western boundary (Fig. 1). CoCA also simplifies examination of temporal patterns by providing a single association value (CoC) for each time period. We use CoCA to examine the consistency of species associations in the 13-year KNP data set, which is a novelty in species co-occurrence studies given the paucity of suitable long-term data sets. Hence, our study contributes to the need for more research into the temporal and spatial aspects of species co-existence (Linnell and Strand 2000).

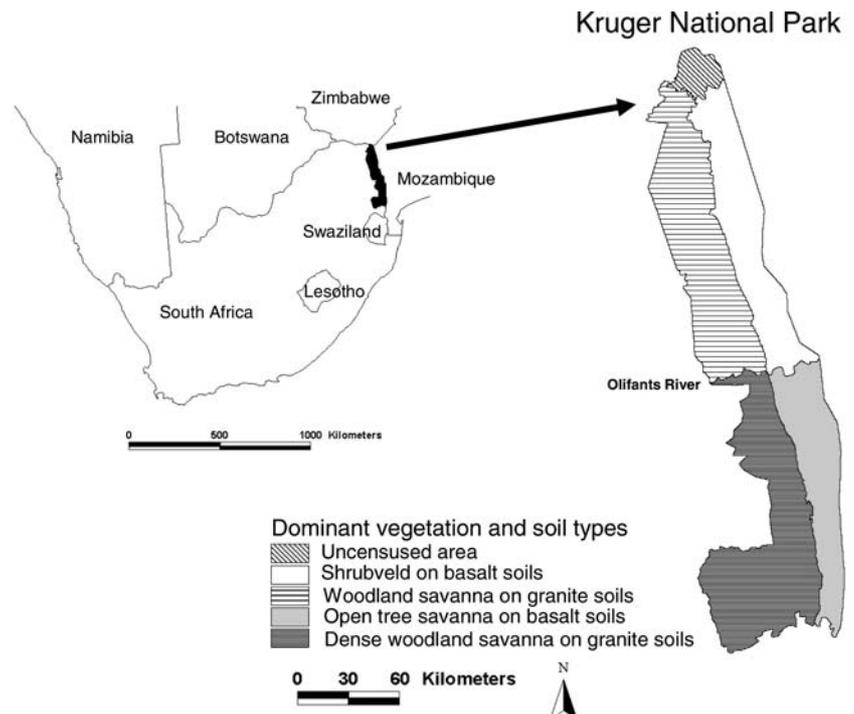
Processes determining co-occurrence or lack thereof in assemblages of African savanna herbivores may de-

pend on the spatial scale at which species associations are analyzed. At relatively large scales, guild aggregation may result from abiotic constraints on herbivore distributions, such as slope and distance to water sources (Bailey et al. 1996; Redfern et al. 2003). Within these constraints, herbivore foraging decisions occur at multiple scales, including selection of a home range, feeding patch, plant species, and plant parts (Senft et al. 1987; Senft 1989). At the scale of home ranges and feeding patches, competition may result in non-overlapping distributions of species requiring the same limited resources. In African savanna ecosystems, Arsenault and Owen-Smith (2002) suggest that interspecific competition predominates during the dry season when plants are dormant and forage of adequate quality becomes depleted.

Detection of competition in species association data is complicated by the fact that competition does not always produce negative associations (Hastings 1987). Competition in herbivores is not manifested by removal and replacement of opponents, but by indirect interactions such as the depletion of resources or dominance. Consequently, the effects of this scramble or indirect competition are hard to determine in the presence/absence data sets traditionally used to assess species co-occurrence. We use the number of animals counted, rather than presence/absence, to facilitate detection of competition.

The influence of resource patches on species distributions can also confound detection of competition. Specifically, resources with a patchy distribution may be associated with spatial autocorrelation in species distri-

**Fig. 1** The Kruger National Park (KNP) is located in the northeastern corner of South Africa. The KNP can be divided into four landscapes, based on dominant vegetation and soil types (adapted from Venter and Gertenbach 1986). This broad landscape definition subsumes smaller patches of differing vegetation and soil types that increase heterogeneity at finer scales. Herbivore censuses do not occur regularly in the northernmost section of the KNP and hence this region is not included in our analyses



butions. If the scale of autocorrelation does not match the scale chosen for analyses of co-occurrence, interpretation of the resulting association patterns may be spurious. Although scales of analyses may be suggested by mechanisms of competition, such as territorial exclusion, it is important to conduct analyses at multiple scales to account for the effects of autocorrelation. Roxburgh and Matsuki (1999), for example, examined the effect of autocorrelation using a series of random models of association. They found that type I error increased, even at low autocorrelation values (Moran's I), invalidating statistical tests. We mitigate these potential statistical artifacts by comparing sets of correlations at three different scales and using Monte Carlo methods to obtain confidence intervals for the CoC of species associations.

Species considered in our analyses include three grazers (buffalo, *Syncerus caffer*; zebra, *Equus burchelli*; and wildebeest, *Connochaetes taurinus*) and four species whose diets contain a high proportion of browse during the dry season (elephant, *Loxodonta africana*; giraffe, *Giraffa camelopardalis*; kudu, *Tragelaphus strepsiceros*; and impala, *Aepyceros melampus*). We use CoCA to test hypotheses (Table 1) about the processes structuring herbivore assemblages. We hypothesize that all herbivore distributions will be similar at large scales because of the influence of abiotic factors. At smaller scales, we expect the relative importance of guild aggregation versus competition in structuring assemblages to become apparent. Specifically, if guild aggregation exerts a dominant influence on species assemblages, high CoC values will be obtained for the grazer and browser assemblages (Table 1). Alternatively, competition may exist between larger and smaller species of the same feeding type, producing low CoC values for the grazer and browser assemblages. Competition may also occur between species of similar size and feeding type, producing low CoC values for the assemblage of smaller

grazers (zebra, wildebeest) and/or the assemblage of smaller browsers (giraffe, kudu, impala).

## Methods

### Data sources

The KNP is located in the Transvaal Lowveld (Fig. 1) and can be broadly characterized as a deciduous savanna (Venter and Gertenbach 1986). The size and location of herbivore herds in the KNP was recorded from 1981 to 1993 during an annual, dry-season aerial census (Viljoen 1996). The northernmost section of the park was not surveyed regularly; hence, this section of the park is not included in our analyses. The spatial accuracy of the data varies throughout the study period. A coarse data recording procedure was used from 1981 to 1984, resulting in a range of spatial accuracy with an upper bound of approximately 1.5 km (P. C. Viljoen, personal communication). Improved recording procedures, implemented from 1985 to 1993, increased spatial accuracy to within approximately 800 m (P. C. Viljoen, personal communication).

No estimates of bias or precision error were obtained for the herbivore counts (Viljoen 1996). A model of the potential bias contained in the census data suggests that visibility bias may represent a major source of error in the data and that this bias may vary among species (Redfern et al. 2002). In our analyses, visibility bias may confound interpretation of correlations observed among species that occur in more open versus dense vegetation communities or correlations between large and small species (e.g., giraffe may be easier to detect than impala implying greater visibility bias in the impala census data). A visual inspection, however, of the spatial distributions of the species considered in our analyses suggests that a number of areas throughout the KNP

**Table 1** The species assemblages considered in our analyses and the hypotheses relating the correlative coherence (CoC) value to the processes influencing the spatial distributions of the species in the assemblages (see Methods for details on calculating the CoC va-

lue). The significance of the difference (at the family level of  $\alpha = 0.5$ ) between CoC values was calculated using a *t*-test with a Bonferroni correction for multiple comparisons

Assemblage	Species	CoC value	Hypotheses/explanations	Significantly different		
				5 km	10 km	15 km
All species	Buffalo, zebra, wildebeest, elephant, giraffe, kudu, impala	$r^a$	$r^a$ is a baseline for comparison against the other assemblages.			
Grazers	Buffalo, zebra, wildebeest	$r^g$	$r^g > r^a$ suggests that species are associated with grassland patches.	Yes	No	No
Browsers	Elephant, giraffe, kudu, impala	$r^b$	$r^b > r^a$ suggests that species are associated with woodland patches.	Yes	Yes	Yes
Smaller grazers	Zebra, wildebeest	$r^{sg}$	$r^{sg} > r^g$ suggests that smaller grazers avoid areas with larger grazers.	Yes	Yes	Yes
Smaller browsers	Giraffe, kudu, impala	$r^{sb}$	$r^{sb} > r^b$ suggests that smaller browsers avoid areas with larger browsers.	Yes	Yes	Yes

contain high densities of all three grazers and high densities of the two smaller grazers and the three smaller browsers. It seems unlikely, therefore, that visibility bias substantially confounds the CoCA.

## Analyses

We used the geographic information systems software ARC/INFO (version 8.0.2, Environmental Systems Research Institute, Inc.) to discretize a map of the KNP into a grid of 846 5×5 km<sup>2</sup> cells, 233 10×10 km<sup>2</sup> cells, and 113 15×15 km<sup>2</sup> cells. Using gridded data, the co-occurrence of two species can be scored either by a presence/absence association index (i.e., divide the number of cells in which both species occur by the number of cells in which at least one species occurs to obtain a value between zero and one) or a correlation coefficient based on the number of individuals of each species in each cell. Sizes of all herbivore herds are estimated in the KNP aerial census data, allowing us to calculate pairwise correlation coefficients for the seven species at each spatial scale. All cells on the boundary of the KNP were included in our analyses, regardless of the fraction of the cell occurring within the KNP (CoCA does not require cells to be of the same size). Thus, a 7×7 correlation matrix *C* was obtained for each of the 13 years under consideration at all three spatial scales. For purposes of illustration, the 13 year average-value correlation matrix at each spatial scale is given in

Table 2. Our analysis, however, depends on obtaining a single CoC value that can be used to compare the 39 correlation matrices (3 spatial scales by 13 years) obtained for each of the following assemblages: all-species (buffalo, zebra, wildebeest, elephant, giraffe, kudu, impala), grazers (buffalo, zebra, wildebeest), browsers (elephant, giraffe, kudu, impala), small grazers (zebra, wildebeest), and small browsers (kudu, impala).

In behavioral studies, pairwise associations among a group of *n* identified individuals have been summarized by averaging the  $n(n-1)/2$  pairwise association values (Whitehead 1997). This technique is not statistically robust because the  $n(n-1)/2$  pairwise associations are not independent; hence, the degrees of freedom for the average are less than the expected  $n-1$ . For example, consider the case where species A is perfectly correlated with species B (i.e., a correlation value of one) and both are entirely unrelated to species C (i.e., correlation values of zero). Averaging the pairwise correlations produces an estimated association value of one-third. However, two of three species are perfectly correlated, so it is reasonable to expect the association value to be close to two-thirds.

Correlative coherence analysis provides a method for “averaging” that has the appropriate  $n-1$  degrees of freedom (Getz 2003) and yields CoC values (e.g., average association values) that are more in line with our intuition (in the example presented above the CoC value is 0.702). The CoC of an *n*-dimensional correlation matrix, *C*, is calculated using the *n* eigenvalues  $\lambda_i$

**Table 2** For each pair of species, a correlation coefficient was calculated between species spatial distributions, described at three spatial scales, for each year of the study period (1981–1993). We summarize the yearly correlations by averaging the 13 correlation coefficients at each spatial scale

	Buffalo	Zebra	Wildebeest	Giraffe	Kudu	Elephant	Impala
<i>5×5 km<sup>2</sup> spatial scale</i>							
Buffalo	1	0.072	0.025	0.020	0.020	0.042	0.021
Zebra		1	0.452	0.179	0.193	0.004	0.076
Wildebeest			1	0.249	0.158	−0.036	0.154
Giraffe				1	0.280	0.047	0.413
Kudu					1	0.067	0.308
Elephant						1	0.094
Impala							1
<i>10×10 km<sup>2</sup> spatial scale</i>							
Buffalo	1	0.182	0.048	0.048	0.089	0.156	0.065
Zebra		1	0.535	0.250	0.334	0.073	0.102
Wildebeest			1	0.382	0.303	−0.045	0.190
Giraffe				1	0.439	0.116	0.542
Kudu					1	0.144	0.434
Elephant						1	0.184
Impala							1
<i>15×15 km<sup>2</sup> spatial scale</i>							
Buffalo	1	0.293	0.126	0.121	0.159	0.244	0.148
Zebra		1	0.612	0.371	0.437	0.158	0.177
Wildebeest			1	0.521	0.416	0.005	0.250
Giraffe				1	0.567	0.151	0.633
Kudu					1	0.212	0.562
Elephant						1	0.264
Impala							1

( $i = 1, \dots, n$ ) of  $C$  (Getz 2003). Specifically, the CoC of  $C$  is the solution,  $r$ , to the equation

$$(1 + (n - 1)r) \ln(1 + (n - 1)r) + (n - 1)(1 - r) \ln(1 - r) = n \ln n + \sum_{i=1}^n \lambda_i \ln \left( \frac{\lambda_i}{n} \right)$$

which can be solved numerically using an appropriate package such as S-Plus, Mathematica (we use Version 4.2 Wolfram Research, Inc. 2002, in our calculations), or Maple. This equation is based on a Shannon-Wiener type measure of the diversity of the eigenvalues of  $C$ , which is minimized when all pairwise correlations are zero (in this case all eigenvalues are one) and is maximized when all pairwise correlations are one (in this case the largest eigenvalue is  $n$  and all other eigenvalues are zero). This eigenvalue diversity could also be obtained from a correlation matrix in which all off-diagonal elements are  $r$  (in this case the largest eigenvalue is  $(n - 1)r + 1$  and all other eigenvalues are  $1 - r$ ). Therefore, we identify the CoC value,  $r$ , as the “average” of a correlation matrix. This “average” does not depend on the dimension of the correlation matrix when all off-diagonal elements are  $r$ . When the off-diagonal elements differ from one another, however, the variance of the elements may affect the CoC value. In our analyses, the elements in the correlation matrices differ but the CoC values are influenced by the strength of the correlations among species rather than the dimensions of the matrices (Fig. 2 and Table 1).

We used Monte Carlo simulations to determine whether the observed CoC value for the assemblage of all seven species was significantly different from a CoC value for a random data set. We tested the significance of the seven species assemblage because it is the most arbitrary assemblage containing species of different feeding types, gut morphologies, and sizes. The Monte Carlo simulations were conducted by randomly permuting the order of the data set for each species (i.e., randomly assigning the spatial position of the total number of individuals in each of the original grid cells) 500 times for each year. The observed CoC value was assumed to differ significantly from the simulated CoC value if the observed value was not contained within the interval defined by the 2.5 and 97.5% quantiles of the simulated value. We used a  $t$ -test with a Bonferroni correction (Neter et al. 1996) to determine whether the average CoC value, calculated over the 13-year study period, was significantly different at the family level of  $\alpha = 0.5$  for the four comparisons of herbivore assemblages described in Table 1.

## Results

The average pair-wise correlations between species spatial distributions (Table 2) indicate that the high CoC values obtained for particular species assemblages represent positive associations among species distributions.

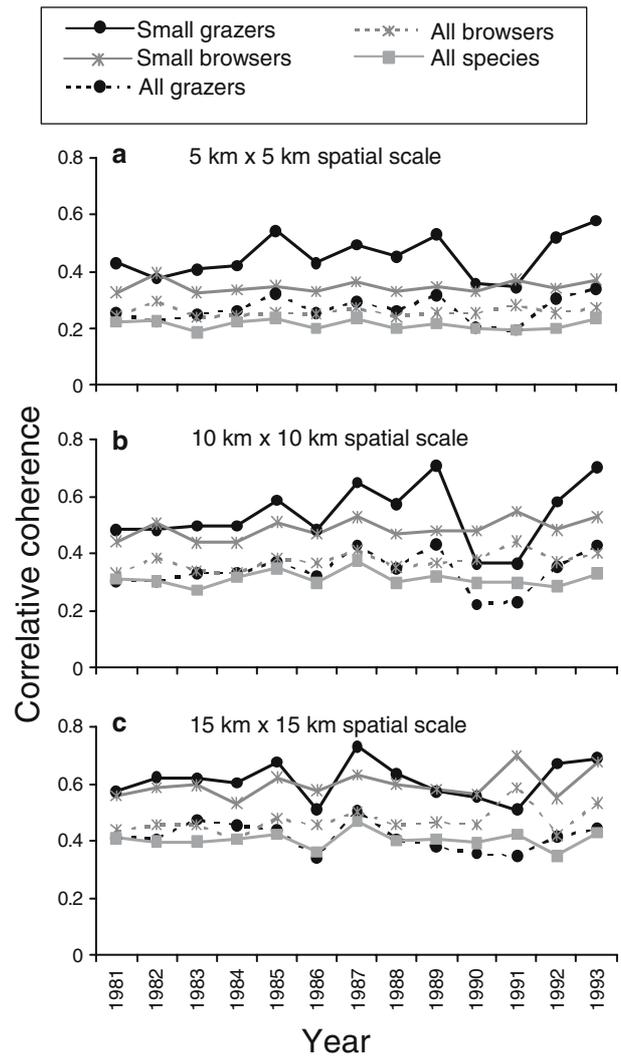


Fig. 2 The correlative coherence values, calculated yearly from 1981 to 1993, are plotted at three spatial scales for the species assemblages considered in our analyses (see Table 1)

At all spatial scales, the CoC value for the assemblage containing all seven species was significantly different from the simulated CoC value for the randomly permuted data sets. A majority of the comparisons between herbivore assemblages described in Table 1 were significant; the only insignificant comparisons occurred between the assemblage of grazers and the assemblage of all seven species at the 10 and 15 km scales. In general, the relative differences among the CoC values for each assemblage were similar at all spatial scales (Fig. 2) but the absolute CoC values differed among the spatial scales. Overall, CoC values increased with increasing spatial scale (Fig. 2).

The largest CoC values were consistently obtained for the assemblage composed of the two smaller grazers and the assemblage composed of the three smaller browsers (Fig. 2). The smallest CoC values were typically obtained for the assemblage composed of all seven species, particularly at the smaller spatial scales. The CoC value

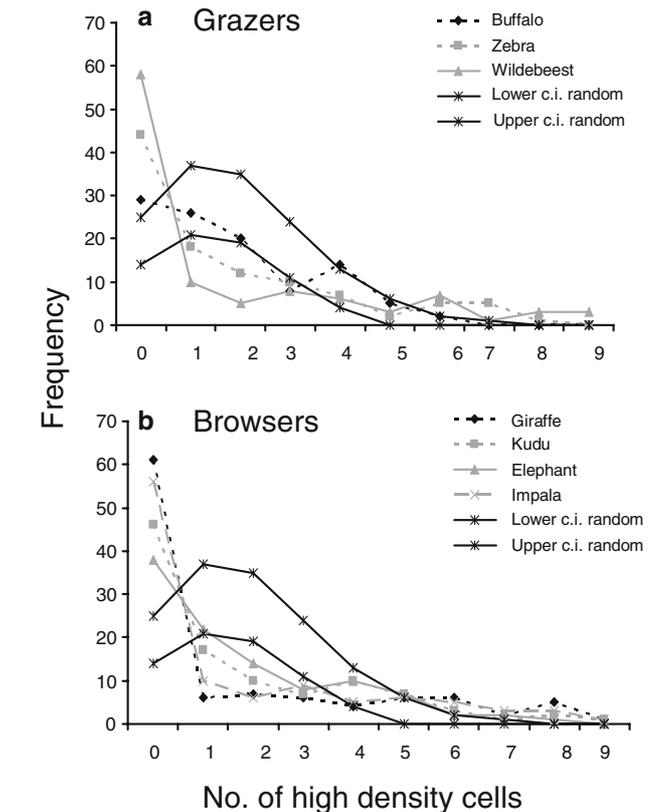
for the assemblage composed of the small grazers was significantly higher than the CoC value for the assemblage composed of all grazers at all spatial scales (Fig. 2); the same pattern was observed for browsers (Fig. 2). Although we did not calculate the CoC value for assemblages containing other permutations of the seven herbivore species, the generality of our results can be clearly seen in the average of the pairwise correlations between species calculated over our 13-year study period (Table 2).

To explore why the CoC values for the assemblages composed of all grazers and all browsers were lower than the CoC values for the assemblages composed of small grazers and small browsers, respectively, we conducted a simple, post-hoc analysis to assess whether species were characterized by a relatively even spatial distribution throughout the KNP. Specifically, we summed the number of individuals for each species over the entire study period in the  $5 \times 5 \text{ km}^2$  grid cells and defined high-density cells as those in the top quartile. We considered only those grid cells in which 50% or more of the cell's area occurred within the KNP boundary, yielding 183 high-density grid cells for each species. The evenness of the spatial distribution of the high-density grid cells was summarized by calculating the number of cells contained in each of the 104  $15 \times 15 \text{ km}^2$  grid cells (nine  $15 \times 15 \text{ km}^2$  cells occurring on the boundary of the KNP were excluded because they did not overlap with the truncated  $5 \times 5 \text{ km}^2$  grid). For each species, the observed distribution of the  $q=0, \dots, 9$  high-density grid cells in the  $15 \times 15 \text{ km}^2$  grid cells was compared to a simulated random distribution produced by randomly assigning the 183 high-density grid cells among the total possible  $5 \times 5 \text{ km}^2$  grid cells 500 times. The observed distribution of high-density cells was considered significantly different from random if it did not occur within the 95% confidence interval of the simulated random distribution.

The distribution of high-density cells was non-random for all species (Fig. 3). For both grazers and browsers, the largest species (buffalo and elephant, respectively) were the most evenly distributed throughout the KNP (Figs. 3, 4). Among the smaller grazers, cells containing high zebra densities were more evenly distributed throughout the KNP than cells containing high densities of wildebeest (Figs. 3, 4). The three smaller browsers occurred predominantly in the southern KNP landscapes (Fig. 4).

## Discussion

For all assemblages, the decrease in CoC values at smaller spatial scales (Fig. 2) suggests that the spatial distributions of KNP herbivores show greater similarity at large scales but are increasingly disjoint at smaller scales. Hence, large-scale constraints imposed by abiotic factors may partition the KNP into regions supporting either high or low herbivore densities. At smaller scales, however, species assemblages may reflect selection for



**Fig. 3** The evenness of the spatial distribution of **a** grazers and **b** browsers is summarized by plotting the frequency of the 104  $15 \times 15 \text{ km}^2$  grid cells containing  $5 \times 5 \text{ km}^2$  grid cells in the top density quartile (mapped in Fig. 4). The 95% confidence interval for a random distribution of the high-density grid cells within the  $15 \times 15 \text{ km}^2$  grid cells is also plotted

differing resource characteristics. Access to surface water sources, forage quality, and forage quantity may be particularly important habitat characteristics in the KNP during the dry season. A significant relationship exists between distance to water and the distributions of the herbivore species considered in our analyses (Redfern et al. 2003). However, Redfern et al. (2003) found that larger grazers, such as buffalo, occurred farther from water under conditions correlated with lower forage quantity while smaller grazers, such as zebra and wildebeest, occurred farther from water under conditions correlated with lower forage quality. Hence, at the smaller spatial scales considered in our analyses, forage quality and quantity may influence the composition of species assemblages.

The highest CoC values were consistently obtained, throughout the study period and at all spatial scales, for the assemblage composed of the two smaller grazers and the assemblage composed of the three smaller browsers. These results suggest that processes resulting in guild aggregation, such as patch resources (e.g., the percentage of woodland compared to grassland) or other benefits (e.g., mutual predator avoidance through complimentary sensory acuities, de Boer and Prins 1990), exert a strong influence on species assemblages.

**Fig. 4** Locations of the highest densities of **a** buffalo, **b** zebra, **c** wildebeest, **d** elephant, **e** giraffe, **f** kudu, and **g** impala in the Kruger National Park from 1981 to 1993. For each species, we summed the number of individuals occurring in the 5×5 km<sup>2</sup> grid cells throughout the study period and mapped the 183 cells falling within the top quartile. Cells in which more than 50% of the area occurred outside the KNP boundary were excluded, resulting in a total of 732 cells (out of 846) considered in this analysis



However, our analyses also suggest that size-based metabolic factors influence species assemblages. In particular, lower CoC values were obtained for the all grazer assemblage compared to the small grazer assemblage and for the all browser assemblage compared to the small browser assemblage, demonstrating that the similarity of species spatial distributions decreases when larger and smaller species of the same feeding type are considered together.

Larger species, such as buffalo and elephant, use a disproportionately larger share of resources than smaller species because population metabolism scales positively with body mass (du Toit and Owen-Smith 1989). Large species are also able to feed in a wider range of habitats, and hence may be characterized by a more even distribution than smaller species, because of their higher tolerance for low quality foods (du Toit and Owen-Smith 1989). Consequently, a decrease in similarity among

distributions of species of the same feeding type when larger and smaller species are included in the same assemblage may result from two alternative processes. The disproportionate use of resources by large species may lead to increased scramble competition during the dry season as access to forage of adequate quality progressively declines (Arsenault and Owen-Smith 2002). As a result of this competition, smaller species may avoid foraging in areas containing high densities of large species, producing disjoint distributions of small and large species. Alternatively, decreased similarity among species distributions when large and small species are considered in the same assemblage may arise because large species are characterized by relatively even spatial distributions (du Toit and Owen-Smith 1989). In this case, although distributions of small and large species may overlap in relatively resource rich areas, global similarity among distributions will be low because of the

even distribution of large species and the patchy distribution of small species.

Among the KNP grazers, a relationship appears to exist between the evenness of a species' spatial distribution and the species' size and gut morphology. In particular, the largest ruminant grazer (buffalo) was distributed the most evenly throughout the KNP (Figs. 3a, 4a), whereas the smallest ruminant grazer (wildebeest) occurred primarily in the southeastern landscape (Figs. 3a, 4c). The distribution of zebra, a non-ruminant of similar size to wildebeest, occurs somewhere between these two extremes (Figs. 3a, 4a–c). The strong similarity between zebra and wildebeest distributions (hence the high CoC values for this assemblage) is apparent in the open tree savanna occurring on basalt soils in the southeastern KNP landscape (Figs. 1, 4b, c). Overall, the results for the KNP grazers appear consistent with the hypothesis that the higher tolerance of large species for low quality foods results in spatial distributions that are more even for large compared to small species.

The relationship between the evenness of a species' spatial distribution and the species' size and gut morphology is not as apparent among the KNP browsers. The largest browser, elephant, did have the most even distribution (Figs. 3b, 4d). However, it is apparent that high elephant densities are closely related to the location of the main rivers in the KNP (Fig. 4d). The three smaller browsers (giraffe, kudu, impala) occur predominantly in the southern KNP landscapes (Fig. 4e–g). Within these landscapes, areas occupied primarily by high densities of a single species produce disjoint distribution patterns. Hence, the high CoC values for these species may indicate regional distribution patterns (i.e., the increase in densities from north to south).

Results of our CoCA analyses provide insight into the processes influencing assemblages of African savanna herbivores at different spatial scales. In particular, results for grazers and browsers do not appear to agree with the hypothesis that smaller species avoid foraging in areas containing high densities of large species as a result of scramble competition. Rather, the results for grazers and browsers agree more closely with the hypothesis that distributions of large and small species overlap in relatively resource-rich areas, but have lower global similarity values because the higher tolerance of large species for low quality foods results in a more even spatial distribution of large species compared to small species. To further explore the relationship between species assemblages and foraging decisions at multiple scales, the collection of detailed forage quality and quantity data throughout the KNP is necessary.

**Acknowledgements** Code for calculating CoC values can be obtained directly from WMG (getz@nature.berkeley.edu). We wish to thank Chris Redfern, Allison Bidlack, Tom Miller, and anonymous reviewers for valuable comments on this manuscript. We thank the South African National Parks and the Scientific Services Division of Kruger National Park for permission to work in the KNP and use census data collected primarily under the direction of

Salomon Joubert and Petri Viljoen. This research was supported by NSF Grants INT-9731202 and DEB-0090323 to WMG.

## References

- Arsenault R, Owen-Smith N (2002) Facilitation and competition in grazing herbivore assemblages. *Oikos* 97:313–318
- Bailey DW, Gross JE, Laca EA, Rittenhouse LR, Coughenour MB, Swift DM, Sims PL (1996) Mechanisms that result in large herbivore grazing distribution patterns. *J Range Manage* 49:386–400
- Connor EF, Simberloff D (1979) The assembly of species communities: chance or competition? *Ecology* 60(6):1132–1140
- Dale MRT, Dixon P, Fortin MJ, Legendre P, Myers DE, Rosenberg MS (2002) Conceptual and mathematical relationships among methods for spatial analysis. *Ecography* 25:558–577
- de Boer WF, Prins HHT (1990) Large herbivores that strive mightily but eat and drink as friends. *Oecologia* 82:264–274
- Diamond JM (1975) Assembly of species communities. In: Diamond JM, Cody ML (eds) *Ecology and evolution of communities*. Harvard University Press, Cambridge, pp 342–444
- du Toit JT, Owen-Smith N (1989) Body size, population metabolism, and habitat specialization among large African herbivores. *Am. Nat* 113:736–740
- Durant SM (1998) Competition refuge and coexistence: an example from Serengeti carnivores. *J Anim Ecol* 67(3):370–386
- Getz WM (2003) Correlative coherence analysis: variation from intrinsic and extrinsic sources in competing populations. *Theor Popul Biol* 64 (1):89–99
- Gotelli NJ (2000) Null model analysis of species co-occurrence patterns. *Ecology* 81(9):2606–2621
- Gotelli NJ, Ellison AM (2002) Assembly rules for New England ant assemblages. *Oikos* 99(3):591–599
- Gotelli NJ, McCabe DJ (2002) Species co-occurrence: a meta-analysis of JM Diamond's assembly rules model. *Ecology* 83(8):2091–2096
- Hastings A (1987) Can competition be detected using species co-occurrence data? *Ecology* 68(1):117–123
- Linnell JDC, Strand O (2000) Interference interactions, co-existence and conservation mammalian carnivores. *Divers Distrib* 6:169–176
- Manly BF (1995) A note on the analysis of species co-occurrences. *Ecology* 76(4):1109–1115
- Neter J, Kutner MH, Nachtsheim CJ, Wasserman W (1996) *Applied linear statistical models*. Irwin, Chicago
- Perry JN, Liebhold AM, Rosenberg MS, Dungan J, Miriti M, Jakomulska A, Citron-Pousty S (2002) Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data. *Ecography* 25(5):578–600
- Redfern JV, Viljoen PC, Kruger JM, Getz WM (2002) Biases in estimating population size from an aerial census: a case study in the Kruger National Park, South Africa. *S Afr J Sci* 98:455–461
- Redfern JV, Grant CC, Biggs HC, Getz WM (2003) Surface water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology* 84(8):2092–2107
- Roxburgh SH, Matsuki M (1999) The statistical validation of null models used in spatial association analyses. *Oikos* 85:68–78
- Schoner TW (1983) Field experiments on interspecific competition. *Am Nat* 122:240–285
- Schluter D (1984) A variance test for detecting species associations, with some example applications. *Ecology* 65(3):998–1005
- Senft RL (1989) Hierarchical foraging models: effects of stocking and landscape composition on simulated resource use by cattle. *Ecol Model* 46:283–303
- Senft RL, Coughenour MB, Bailey DW, Rittenhouse LR, Sala OE, Swift DM (1987) Large herbivore foraging and ecological hierarchies. *Bioscience* 37:789–799
- Stone L, Roberts A (1990) The checkerboard score and species distributions. *Oecologia* 85:74–79

- Venter FJ, Gertenbach WPD (1986) A cursory review of the climate and vegetation of the Kruger National Park. *Koedoe* 29:139–148
- Viljoen PC (1996) Ecological aerial surveys (EAS) in the Kruger National Park. Summary of current methodology—1996 update. Unpublished report, South African National Parks, Skukuza
- Whitehead H (1997) Analyzing animal social structure. *Anim Behav* 53:1053–1067