CHAPTER 3A

SPATIAL STATISTICS TO QUANTIFY PATTERNS OF HERD DISPERSION IN A SAVANNA HERBIVORE COMMUNITY

ALFRED STEIN[#] AND NICHOLAS GEORGIADIS[##]

[#] International Institute for Geo-Information Science and Earth Observation (ITC),
P.O. Box 6, 7500 AA Enschede, The Netherlands
[##] Mpala Research Centre, P.O. Box 555, Nanyuki, Kenya
E-mail: stein@itc.nl

Abstract. Understanding the spatial distribution of species is a fundamental issue in ecology, yet quantitative descriptions of animal species' distributions are rare. In this chapter, we use a spatial-statistics approach to describe the spatial distribution of herds of large herbivores in Laikipia, central Kenya. We used Global Positioning System technology and spatial point pattern analysis (*F*-, *G*- and *J*-functions) to characterise herd distributions of the 9 most abundant species comprising large herbivore communities in African savannas. *F*-function analysis is based on estimating the probability of a herd occurring within radius *r* of randomly selected focal points. *G*-function analysis is similar, but based on randomly selected focal herds. The *J*-function is derived from the ratio of *G*- and *F*-functions. Comparing results from the different functions was instructive about possible causes of spatial patterning at the landscape level. All species displayed consistently aggregated distributions under *F*- and *J*-function analyses, partly because wildlife has been displaced by humans and livestock from sections of the study area. By contrast, the *G*-function provides a description of dispersion under more natural conditions because areas lacking herds are excluded from the analysis. *G*-function results showed 5 species to display random or nearly random dispersion patterns (zebra, impala, Grant's gazelle, eland and hartebeest), while the remainder were aggregated (African elephant, giraffe, African buffalo and Thomson's gazelle). When data for all species were pooled, *G*-function results revealed an emergent property of this community: wild herbivore herds were arrayed across the landscape in a significantly regular fashion. Two possible causes of this pattern, invoking interspecific complementarity in habitat preference, or disaggregation by prey herds to counter predators, could not be distinguished. Both mechanisms may have been operating in savannas over such long evolutionary time that their effects cannot be separated without experimentation.

Keywords. nearest-neighbour distances; savanna; spatial point pattern; herbivores; Laikipia

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INTRODUCTION

Animals often aggregate in groups or herds, and usually do not randomly distribute. These herds, in turn, display spatial distribution patterns. Variation in animal grouping and distribution (Krause and Ruxton 2002) has been explained on physiological grounds, invoking metabolic requirements, on ecological grounds, invoking habitat preference (Lamprey 1963), feeding style, competition, facilitation (Prins and Olff 1998; Arsenault and Owen-Smith 2002) and food distribution (Voeten 1999), and on climatic grounds (Walker 1990). A key difference exists between habitat preference and prey preference. Habitat preference largely determines where animals have a good hiding, living and mating place, whereas prey preference determines the areas where prey animals tend to live. These two concepts are to some degree complementary, as prey animals may have another habitat preference than the predators.

Spatial statistics can quantify patterns in animals to explain wildlife diversity

Buckland and Elston (1993) modelled wildlife distributions in space, Augustin et al. (1996) applied an autologistic approach to modelling spatial distributions, and Li et al. (1997) used regression to model the spatial distribution of the red crowned crane. None of these studies, however, employs a point pattern spatial-statistics approach. Such an approach may be beneficial to discover and quantify patterns in herds, which in turn may lead to an ecological explanation and hence to a better understanding of wildlife diversity. Since spatial heterogeneity influences resource use and, thus, competitive interactions between herbivore species, analysing the distribution of animal groups may be helpful to understand these underlying mechanisms. It is important in that sense to test whether the distribution of the groups deviates from random. For a random distribution, the distribution of the groups is assumed to have no underlying mechanism. Resource ecology may benefit from such explanations since they may help to explain consumer distribution and resource use.

Analysing the distribution of animals provides understanding how spatial heterogeneity influences competitive interactions

Distribution patterns have an important effect on sampling and analysis (Borchers et al. 2002). For example, preferential sampling can be carried out if herds are known to disperse according to preferential habitats, or adaptive sampling may be useful if herds tend to cluster, both leading to estimates with a lower variance. Detailed distributional data, however, are rare for large vertebrate species comprising a community or guild. After more than 50 years of research on wild herbivores in Africa, for example, we could find no statistically supported descriptions of herd distribution at the ecosystem or landscape level. Systematic sample surveys (Norton-Griffiths 1978; Grunblatt et al. 1995; Khaemba and Stein 2000) have been routinely used to monitor wildlife distribution and dynamics because this method is efficient in terms of effort and repeatability (Caughley 1977; Krebs 1989). They provide impressions of spatial variation in density (e.g., Sinclair and Arcese 1995a), but the data do not allow formal descriptions of dispersion, rather, the method itself is based on the generally untested assumption that focal species are randomly dispersed.

Advances in Global Positioning System technology (GPS; see Wint 1998) and spatial point pattern analysis (Ripley 1981; Diggle 2003), permitted us to characterise spatial distributions of the 9 most abundant large herbivore species in the Laikipia ecosystem of central Kenya (in order of decreasing abundance: plains zebra, *Equus burchelli*; impala, *Aepyceros melampus*; Grant's gazelle, *Gazella granti*; Thomson's gazelle, *Gazella thomsoni*; eland, *Taurotragus oryx*; African buffalo, *Syncerus caffer*; African elephant, *Loxodonta africana*; hartebeest, *Alcelaphus buselaphus*; and giraffe, *Giraffa camelopardalis*).

The data, representing point measurements of herds, were collected during a total count of wildlife in an area of 7,100 km^2, using 10 aircraft equipped with GPS receivers (Georgiadis 1997). Three methods of spatial point pattern analysis were used to characterise the distributions of wild herbivore herds for each species separately, and for all species combined. Possible causes of observed patterns of dispersion within and among species are discussed.

GEOSTATISTICAL METHODS

Distribution data

Data in this study were collected during a total count within Laikipia District over three days in September 1996 (Georgiadis 1997; the region is also described in Heath 2000 and Georgiadis et al. 2003). The area was divided into three sections, each sub-divided into daily counting blocks of approximately 200 to 300 km^2, and each block was allocated to one aircraft per day. Ten high-winged aircraft were used simultaneously to search each block systematically. Each aircraft flew at heights between 70 and 130 m above ground level, following transects spaced 1 km apart. Each aircraft carried a crew of pilot, front-seat observer and two rear-seat observers. Whenever an animal or a group of animals was spotted, the aircraft deviated from its flight line to circle the observed animals until their number was counted. Observers in the aircraft estimated group size. This may be different from ordinary harem sizes, as these aggregate and disaggregate on a daily basis. Geographical coordinates of their positions were recorded using a Trimble GPS receiver. Overlaps and double counts at the boundaries of the blocks were identified and subtracted from the total wildlife numbers as a correction for count overlaps. This resulted in a data set of 1828 locations where at least one animal was observed (Figure 3.1).

For these purposes the observation of one or more animals at a given location is termed a herd. We make the basic assumption that each location is equally likely to host a herd. Deviations from randomness are then of interest, both for individual herds, and in their mutual relationships. Also of interest in this study is the data

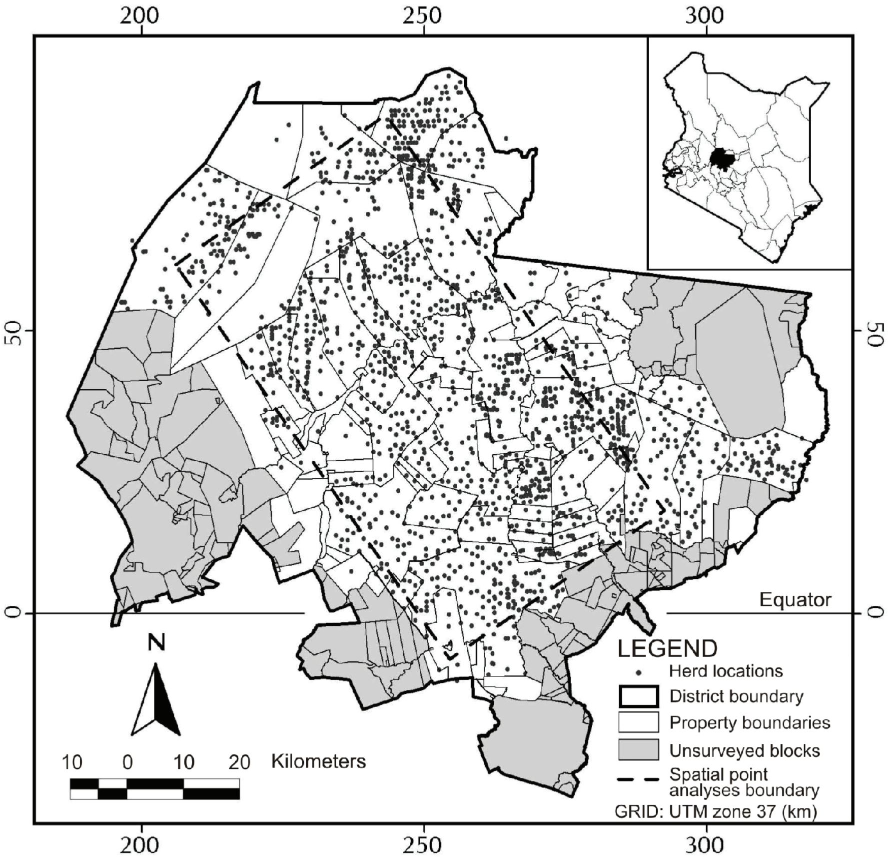

Figure 3.1. *Map of the study region in Kenya showing the set of all locations where a herd (at least one animal) was observed, i.e., the process X•. The rectangular box delineates the area used for point pattern analysis*

quality issue ‘positional accuracy’ (Goodchild and Jeansoulin 1998). Estimates of dispersion used here were affected (but to the same degree) by subjective variation among observers in their assignment of individuals to a herd. The scale at which these decisions were manifested as errors should be limited to distances no greater than the counting-strip width (0.5 km). Similarly, errors in the position of herds, due to the aircraft not passing directly overhead when the GPS location was recorded, should also amount to less than 0.5 km. Visibility for all species declines with distance from the aircraft, affecting dispersion patterns at distances up to the interval between transects (approximately 1 km; see also Ottichilo et al. 2000a; 2001). As is shown in this study, departures from complete spatial randomness generally occurred at values of $r > 1$ km; we assume conclusions drawn from these results will not be qualitatively affected by these errors.

Measures of dispersion

Spatial aggregation is the most frequent dispersion pattern encountered in nature, due to the prevalence of potent aggregating forces such as habitat specificity, social structure and organisation, philopatry, predator avoidance, and limited dispersal. Analysis of spatial patterns as spatial processes has now found a wide acceptance (see Lawson et al. (1999) for a recent overview in disease mapping, Manly (1999) for applications in biology, and Dale (1999) for applications in plant ecology). Spatial processes yielding observed animal counts are characterised by a simple stochastic model applied to a region A. Herds are represented by the coordinates of their centre of gravity marked by observed animal species. As a result, A is summarised by a mapped point pattern, consisting of the presence of at least one animal out of the nine species. The density of the processes is denoted by λ. Density in this study is similar to the number of herds per unit area. It is estimated by the ratio of the number of herds, divided by the size of the area.

To describe the spatial point pattern generated by the distribution of the nine ungulates, we let $Y = (X_1,\ldots,X_9)$ be a nine-variate point process in A with jointly stationary components. On the one hand we have the total pattern Y, on the other hand the 9 different patterns of the herds of individual species. Stationarity means that the position of the herds is independent of the location, although differences in densities may emerge due to stochastic influences. The process consisting of all points regardless of type is denoted by

$$X_{\bullet} = \bigcup_{i=1}^{9} X_i \ .$$

In this paper, statistical inference for Y is based on distances, either those between a fixed reference point $a \in A$ and the points of the process $X_{\bullet}$, or those between the points of $X_{\bullet}$ themselves. We take stationary processes as the starting point for our research; for non-homogeneous populations we refer to Diggle and Chetwynd (1991).

Thus, for each $a \in A$, let $\rho(a, X_{\bullet})$ denote the distance from a to the nearest herd. Then the empty-space function of $X_{\bullet}$ for $r \geq 0$ equals

$$F_{\bullet}(r) = \Pr\left(\rho(a, X_{\bullet}) \leq r\right),$$

the probability of observing at least one herd closer than r to the arbitrary point a in the area. Under the assumption of stationarity, $F_{\bullet}(r)$ does not depend upon a. The heuristic explanation of $1 - F_{\bullet}(r)$ is the probability that a circle with radius r placed at random in the area does not contain a herd, thus explaining the terminology. The empty-space function of X_i, $i \in \{1,\ldots,9\}$, is denoted by $F_i(r)$. By the stationarity assumption, neither $F_{\bullet}(r)$, $F_i(r)$, $i = 1,\ldots,9$ depend on the choice of the reference point a. A completely spatially random (CSR) pattern of herds with density λ shows an F-function equal to $F(r) = 1 - \exp(-\pi\lambda r^2)$. A clumped distribution has an F-function below this function, as on short distances fewer herds are encountered than for a random pattern, whereas a regular pattern has an F-function above it.

Turning to inter-herd distances, the nearest-neighbour distance function $G_\bullet(r)$ is the distribution function of the distance from a typical herd to its nearest neighbour,

$$G_\bullet(r) = \Pr{}^{!a}\left(\rho(a, X_\bullet) \le r\right)$$

for $r \geq 0$. Here, $\Pr^{!a}$ denotes the distribution of $X_\bullet$ at $a \in A$, *i.e.*, the conditional probability distribution that the distance from the point a to an arbitrary herd is less than or equal to r, given the location a (Stoyan et al. 1995). The function $G_\bullet(r)$ can be interpreted as the conditional distribution that a herd occurs within a distance r from a herd located at location a. Formally, it equals $\Pr\left(\rho(a, X_\bullet \setminus a) \le r \mid y \in X_\bullet\right)$, where $a, X_\bullet \setminus a$ denotes the full process $X_\bullet$ from which the herd at location a is excluded. A heuristic description of 1 - $G_\bullet(r)$ is the probability that within a circle with radius r centred on a randomly selected herd no further herd occurs. Again, $G_\bullet(r)$ does not depend on a because of stationarity. The univariate nearest-neighbour distance functions are denoted by $G_i(r)$, $i \in \{1,\ldots,9\}$. The empirical distribution function (EDF) for the G-function is obtained for each distance r by counting the number of herds at distances less than or equal to r from each of the herds. For example, for the ith species with n_i occurrences in A, it

$$\hat{G}_i(r) = \frac{1}{n_i}\sum_{r_i \le r} 1 .$$

A random pattern of herds with density λ shows a G-function equal to $G(r) = 1 - \exp(-\pi\lambda r^2)$. A clumped distribution has a G-function higher than this function, as on short distances more herds are encountered than for a random pattern, whereas a regular pattern has a G-function below it.

Comparison of inter-herd distances to distances with respect to a reference point, say $a = 0$, yields the $J_\bullet(r)$ -function, defined by

$$J_\bullet(r) = \frac{1 - G_\bullet(r)}{1 - F_\bullet(r)}$$

for all $r \geq 0$ satisfying $F_\bullet(r) < 1$. For Poisson processes (*i.e.*, fully random processes without any aggregation or regularity), $J_\bullet(r) = 1$; $J_\bullet(r) > 1$ indicates inhibition between the points, aggregated patterns generally result in $J_\bullet(r)$-function values smaller than one. Moreover, the $J_\bullet(r)$ function is constant beyond the effective range of interaction (Van Lieshout and Baddeley 1999). The $J_\bullet(r)$ function is a useful index for the type and strength of spatial interaction (Stein et al. 2001).

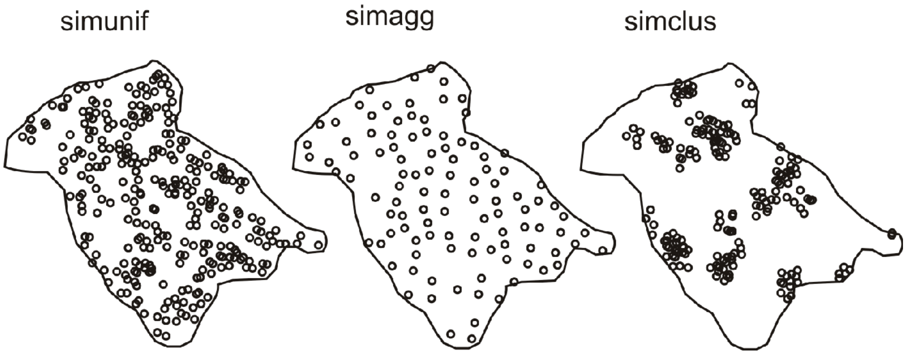

Figure 3.2. Simulated random (simunif), aggegated (simagg) and clustered (simclus) process in the Laikipia area. The patterns have 300, 100 and 191 herds, respectively. See Box 3.1 for further explanation

Box 3.1. *F-, G-, and J-functions to describe spatial point patterns*

To show the functioning of the different functions, three processes were simulated: a uniform pattern (denoted as simunif), an aggregated pattern (denoted as simagg) and a clustered pattern (simclus) (Figure 3.2). For the aggregated pattern, a simple sequential inhibition process was used with an inhibition parameter equal to 5 km, and a Matèrn Cluster process was applied for the clustered process. Parameters were set such that the area corresponded with Laikipia area, yielding 300, 100 and 191 herds, respectively. The F-function for simagg was well inside the confidence bounds, the simagg was above the confidence bounds, the simclus was below the confidence bounds for randomness (Figure 3.3). Deviations from randomness were much clearer when a G-function was estimated (Figure 3.4). First, the simagg pattern is below the confidence envelope for randomness. It further showed very nicely the inhibition in the simagg data, i.e., a 0-valued G-function for distances up to 5 km. The simclus pattern is now above the simulation envelope for randomness. Finally, the J-function estimates (Figure 3.5) show that up to distances of 2 to 2.5 km simunif yields a horizontal function, which then drops, whereas the simagg pattern yields a J-function above the simulation envelope, and the simclus yields a J-function that falls well below the confidence envelope.

From the above it follows that the *F*- and the *G*-function show an opposite behaviour. A pattern with a *G*-function above that for CSR means aggregation, because as measured from a herd there are more short distances to other herds than expected on the assumption of spatial randomness. A *G*-function below that for CSR means regularity, because small distances to herds occur less often than expected under the assumption of spatial randomness. For the *F*-function the opposite applies. In case of uniformity the expected distance from an arbitrary point in the area to the nearest herd is smaller than what would be expected on the basis of CSR. Therefore, in this case the *F*-function is above that of CSR. In case of aggregation, however, small distances are under-represented and the expected distance to the closest herd would be larger. Therefore, the estimated *F*-function falls below that for CSR. Opposite behaviour of the *F*- and *G*-functions therefore leads to the same conclusion when considering deviation from CSR. The *J*-function leads to similar conclusions as both the *F*- and the *G*-function, but it does not rely in any sense on the Poisson model. In Box 3.1, the *F*-, *G*-, and *J*-functions are demonstrated using simulated point patterns.

To facilitate calculation of nearest-neighbour distances during spatial point pattern analysis using the S-Plus software package (Kaluzny et al. 1998), we rotated the pattern by an angle of 55°, so that the area is close to a rectangle of size 60 by 110 km (Figure 3.1).

SPATIAL DISTRIBUTION OF HERDS OF LARGE HERBIVORES

Population size and density

In total, 57,928 animals of the nine species were observed in this study, distributed over 3,034 herds. The maximum herd size equals 473 animals, whereas 322 solitary animals were observed, i.e., herds of size 1.

Abundance varied among the nine species 23-fold, the largest herds occurring for plains zebra and the smallest for giraffe (Table 3.1). Mean herd size varied 4.5-fold, with plains zebra having the highest mean herd size (30.5 individuals per herd) and giraffe the lowest mean herd size. The impala, although less abundant than the Thomson's gazelle, aggregates in smaller herds and hence has a higher number of herds. The buffalo forms relatively large herds (22.7 individuals per herd), whereas all other species form much smaller herds (8.0 - 14.1 individuals per herd) (Table 3.1; compare Voeten 1999). Densities, i.e., number of herds km^{-2}, vary 11-fold in the area, the highest density occurring for plains zebra, the lowest density for buffalo (Table 3.1).

Table 3.1. *The nine animal species under study, including their mean and median herd size, standard deviation and total count*

Process	Species	No. of herds	Total count	Group size			Area (km^2)	Density (n km^{-2})
				mean	median	sd		
X_1	plains zebra	1,034	31,517	30.5	18	39.7	7,103	0.1456
X_2	impala	431	5,707	13.2	10	13.5	6,567	0.0656
X_3	Thomson's gazelle	211	4,255	20.2	12	31.0	5,487	0.0385
X_4	Grant's gazelle	436	3,507	8.0	6	8.0	5,735	0.0760
X_5	eland	258	3,164	12.3	6	20.9	5,681	0.0454
X_6	elephant	162	2,287	14.1	9	22.2	5,319	0.0305
X_7	hartebeest	206	1,681	8.2	7	9.5	6,048	0.0341
X_8	buffalo	69	1,563	22.7	15	25.7	5,370	0.0128
X_9	giraffe	218	1,340	6.2	4	8.0	5,292	0.0412

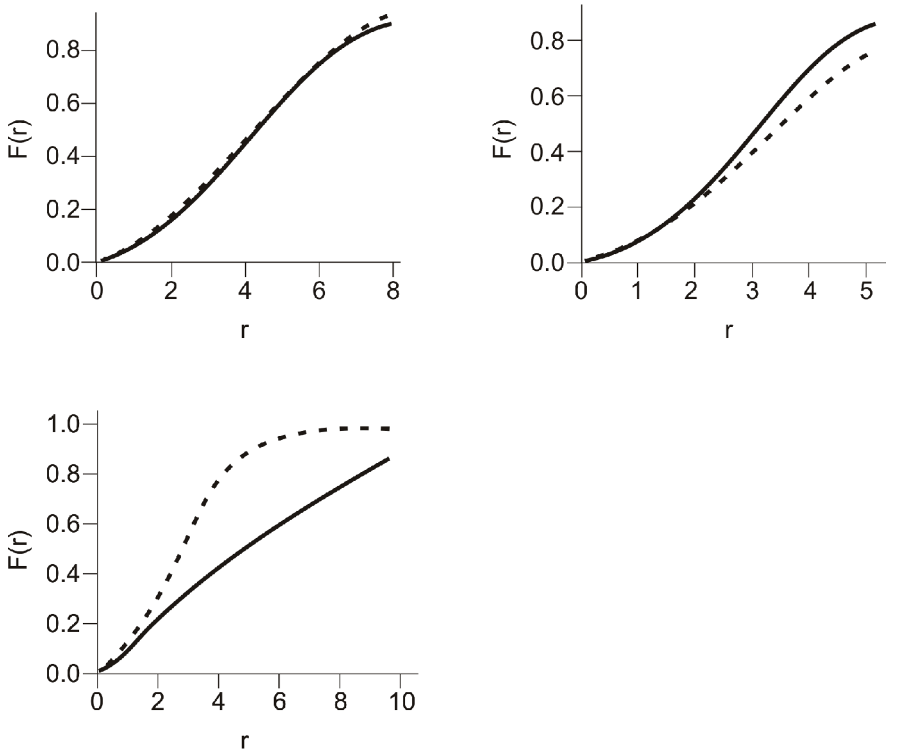

Figure 3.3. *F-Functions for the random, aggregated and clustered processes. See Figure 3.2 for the corresponding patterns*

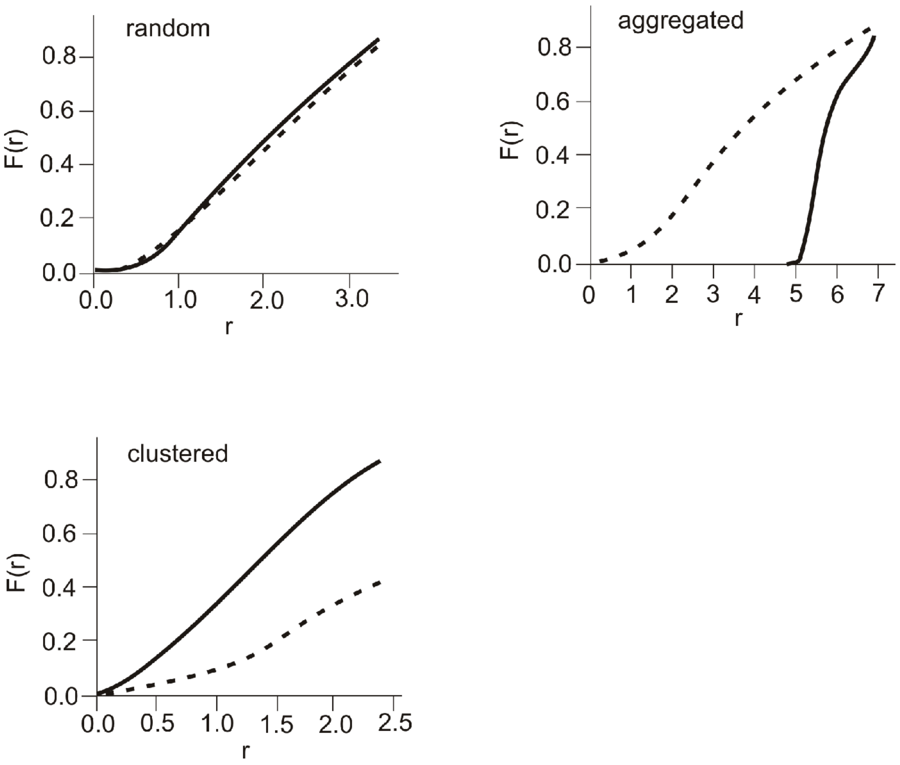

Figure 3.4. *G-functions for the random, aggregated and clustered processes. See Figure 3.2 for the corresponding patterns*

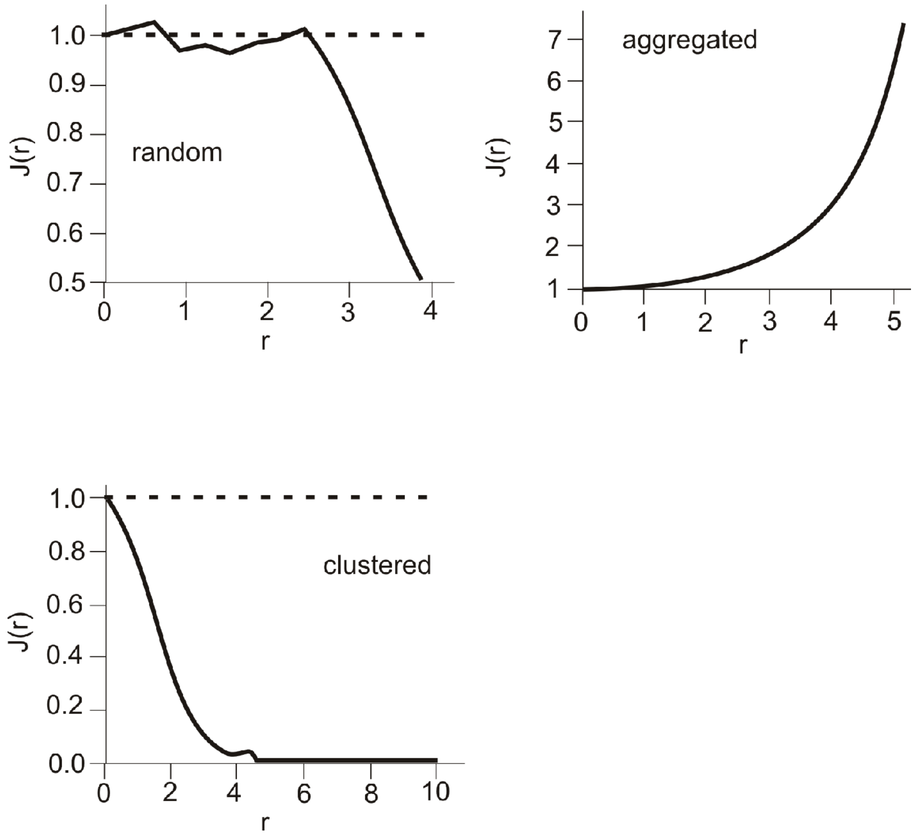

Figure 3.5. *J-functions for the random, aggregated and clustered processes. See Figure 3.2 for the corresponding patterns*

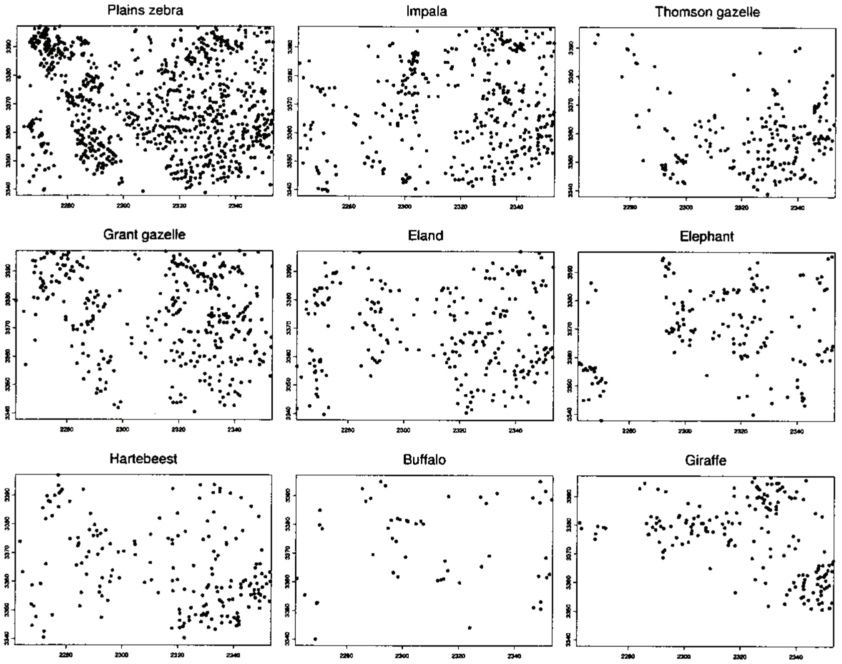

__Figure 3.6.__ Spatial point patterns for the nine animal species in the study area. Coordinates are in km along a 55 ° rotated image

Spatial point patterns

Spatial point patterns for individual species cover different areal extents, with convex hulls ranging from 7,103 km^2 for the plains zebra to 5,300 km^2 for the elephant and giraffe, suggesting a restricted use of the habitat for these two species (Table 3.1).

The plot of the combined spatial pattern is fairly dense with no apparent spatial pattern (Figure 3.1). A section with almost no herds occurs in the northern part of the area. Evidence of aggregation emerges from individual species point patterns (Figure 3.6). The plains zebra has both a high density and a highly aggregated spatial point pattern. The impala occurs more often in the southern part of the region, the Thomson's gazelle in the south-western part, the giraffe in the eastern part of the area. Buffalo is typically a somewhat rare species, at least its herds are found at a lower frequency than those of the other species. Each species appears to exhibit some aggregation. Such visual assessments are to be tested using distance measures for confirmation.

Evidence of aggregation emerges from individual species point patterns

The estimated $\hat{F}_i(r)$-function plots for individual species (i = 1,…,9) display significantly aggregated patterns at radii > 0.5 km (plains zebra) to 3 km (buffalo) (Figure 3.7). The $\hat{F}_i(r)$-function for plains zebra, which had by far the highest density, shows a value equal to 0.6 at distances of 3.5 km. Similar results were obtained for Grant's gazelle and impala. Despite their differing densities, therefore, herd spatial distributions for these species are comparable. For the remaining species, $\hat{F}_i(r)$-functions display lower steepness, but so too were expectations of functions observed under CSR conditions. Accordingly, the $\hat{F}_\bullet(r)$-function plot for all species combined (Figure 3.7) shows the observed $\hat{F}_\bullet(r)$-function to be more aggregated than random at all radii.

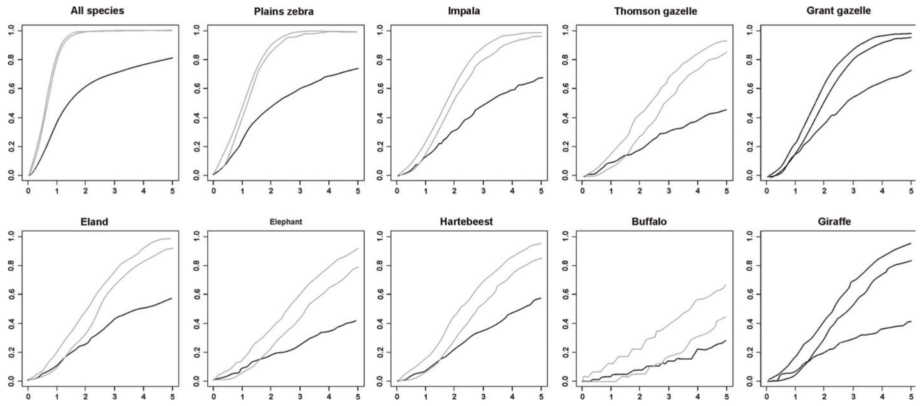

Figure 3.7. *The estimated* $\hat{F}_\bullet(r)$ *function for* $X_\bullet$, *the combined data, and the* $\hat{F}_i(r)$-*functions (solid lines) of the nine animal species with envelopes (dotted lines) for testing for spatial randomness. Coordinates along the horizontal axis are in km. The figure seems to imply regularity, as the estimated* $\hat{F}(r)$ *functions are below the confidence bounds, both for all species and for each individual species. This is hard to justify, as a probable cause may be the empty sub-area in the northern part of the study area*

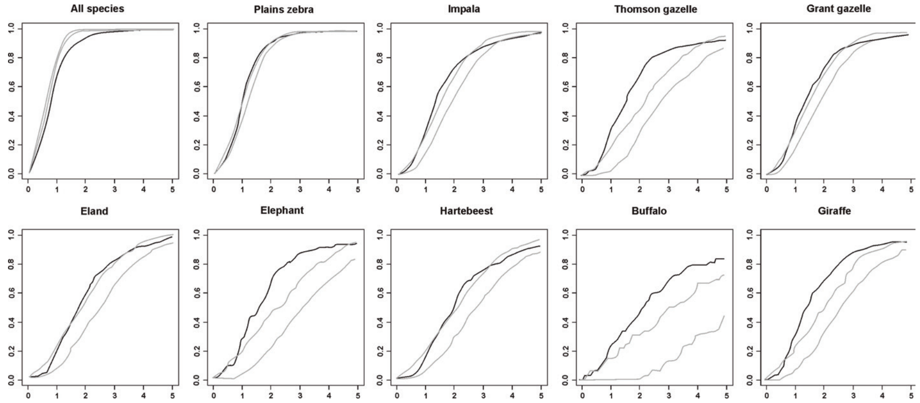

Figure 3.8. *The estimated* $\hat{G}_{\bullet}(r)$ *-function for* $X_{\bullet}$, *the combined data, and the* $\hat{G}_i(r)$ *-functions (solid lines) for the nine animal species with envelopes (dotted lines) for testing for spatial randomness. Coordinates along the horizontal axis are in km. Figure numbering is from a (top left) to j (bottom right). All species show an aggregated pattern, with the exception of the plains zebra, which displays a random distribution. The pattern of all species, on the contrary, is more regularly distributed*

$G_i(r)$-function results for each species treated individually also show a tendency for aggregation in all cases, except the most abundant species, plains zebra, but only at intermediate values for r (Figure 3.8). For impala, Grant's gazelle, eland and hartebeest, departure from CSR was never marked, while Thomson's gazelle, elephant, buffalo and giraffe display clearly aggregated distributions. In contrast to all results presented above, the $\hat{G}_{\bullet}(r)$ -function plot for the combined data for all 9 species shows a significantly more regular pattern than CSR (Figure 3.8) at radii between 0.5 and 5 km.

The $\hat{F}_{\bullet}(r)$ -function plot for $X_{\bullet}$, the combined population of species drops below the lower bounds of CSR at a distance of approximately 0.5 km, showing that the pattern of herds is significantly aggregated beyond this distance (Figure 3.9). The individual $\hat{J}_i(r)$ -functions for the plains zebra and the giraffe (Figure 3.9) become significantly aggregated at r = 0.7 km, whereas for other species this occurs at greater values of r (r = 0.8 – 1 km). For most species the trend is relatively smooth but the pattern for elephant and to a lesser extent buffalo appears stepped at r = 1. This may reflect the tendency for these species to occur in stable groups that are spatially aggregated for social reasons.

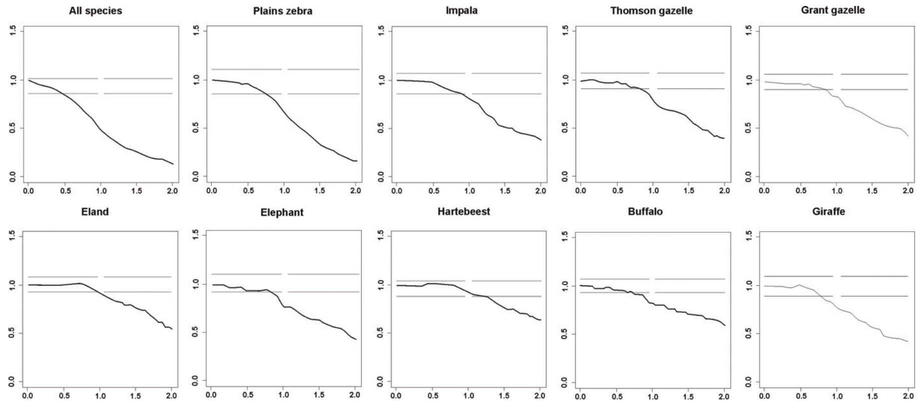

Figure 3.9. *The estimated* $\hat{J}_{\bullet}(r)$ *-function for* $X_{\bullet}$ *the combined data and the* $\hat{J}_i(r)$ *-functions (solid lines) for the 9 animal species with envelopes (dotted lines) for testing for spatial randomness. Coordinates along the horizontal axis are in km. Figure numbering is from a (top left) to j (bottom right). These J-functions indicate randomness for distances up to 0.4 km (for all species) and to distances between 0.7 km and 1 km for individual species. Beyond that distance, herds are distributed in a more aggregated way*

DISCUSSION

The nine species featured in this study are subject to all forces that influence spatial aggregation: habitat specificity, social structure and organisation, philopatry, predator avoidance, and limited dispersal. Based on *F*- and *J*- function results, all displayed aggregated distributions. By contrast, some of the same species displayed random distributions under the *G*-function. Comparison of results from the different functions used to estimate dispersion is instructive about spatial patterning at the landscape level. The area also has some fencing, but although this may lead to lower densities, it is not considered to be very important for the spatial-pattern study.

Results from the *F*-functions were derived from points selected randomly over the entire study area, and are therefore influenced not only by natural forces affecting herd dispersion (such as those listed above), but also by 'unnatural' factors, such as displacement of wildlife by humans, cultivation and livestock. By excluding wildlife from large sectors of the study area, these factors accentuate observed degrees of aggregation and may partly account for the consistently aggregated dispersion patterns displayed in *F*-function plots for all species, relative to CSR. In ecosystems such as this, therefore, where wildlife are displaced from some areas by humans and livestock, all species are likely to violate the assumption of random dispersion patterns typically made when sample counting.

Comparison of results from the F-, G- and J-functions used to estimate dispersion is instructive about spatial patterning

A way to reduce the influence of these ‘unnatural’ factors on the analysis of dispersion would be to excise human-occupied sectors from the study area, and repeat the *F*-function analysis. However, the *G*-function provides a more efficient way of reducing ‘unnatural’ influences because randomly chosen herds comprise foci for analysis, and areas lacking herds are automatically excluded from the analysis. By this measure, herds of plains zebra, impala, Grant’s gazelle, eland and hartebeest were dispersed in a random, or only slightly aggregated fashion, whereas herds of elephant, buffalo, giraffe and Thomson’s gazelle were distinctly aggregated (at least at values of r between 1 and 4 km). These results support the widely held view that herds of elephant and buffalo are likely to be too aggregated to be effectively censused by sample counting with regularly spaced transects, even in a ‘natural’ context.

Comparison of *G*-function results among species yielded no clear association between dispersion pattern and feeding preference (grazer, mixed feeder or browser), dependence on drinking water, mating system or tendency to migrate. Factors that have a potentially organising influence on herds within species, such as territoriality (impala, Thomson’s gazelle, Grant’s gazelle, hartebeest), or intraspecific competition, may have been operating, but were evidently not strong enough to cause regular patterns of dispersion within species in this landscape. Strong social bonds within and between herds are known to influence elephant herd associations (McComb et al. 2001), possibly accounting for the extreme aggregation displayed by this species. By contrast, plains-zebra harems are known to associate and disassociate on a daily and seasonal basis (Rubenstein pers. comm.), but this evidently does not result in significant aggregation at the landscape level. At least in this woodland-dominated habitat, ‘exogenous’ forces such as patchiness of preferred habitat are more likely to account for aggregations of Thomson’s-gazelle herds, which prefer open, short grassland.

G-function results for each species treated separately, showing random or aggregated patterns, contrasted strikingly with results from the pooled data for all species, which showed that wild herbivore herds were arrayed across the landscape in a significantly regular fashion. This result implies that factors causing individual species to be aggregated or randomly dispersed either (1) complement each other when combined across space, or (2) are organised by factors that exert their influence on the entire community. As an example of the first possible cause, which we refer to as ‘habitat-preference complementarity’, we expect that animals that are abundant are more randomly dispersed (often called habitat generalists) than rare species (habitat specialists). While the two most abundant species (plains zebra, impala) showed random *G*-function distributions, there was no overall association between rank of relative abundance and dispersion pattern ($P > 0.065$). By contrast, we expect habitat specialists to be found within preferred habitat patches, to display lower herd densities in transitional

Species aggregation is caused by factors that complement each other or that exert their influence on the entire community habitats, and to be absent from unsuitable habitats. When the data of all species are pooled, the net effect is for herds to become regularly spaced across the landscape.

Clear differences in the distribution of groups emerged. For example, habitat preference results in grouping that is closely linked to the location of available habitat, whereas this relationship between consumer presence and resources is affected by the presence of competitors. Further details concerning the ecological explanation of the observed patterns have to be worked out in the future, as this extends the scope of this chapter (see Box 3.2).

Box 3.2 *Testable hypotheses for future research*

Hypothesis 1. Based on 'habitat preference complementarity', we expect that abundant species are more randomly dispersed (i.e., habitat generalists) than rare species (habitat specialists).
Hypothesis 2. We expect habitat specialists to be aggregated within preferred habitat patches (in fact, one then tests whether these habitat patches are aggregated in the landscape), to display lower herd densities in transitional habitats, and to be absent from unsuitable habitats.
Hypothesis 3. As is shown in this chapter, herds become regularly spaced across the landscape when the distribution data of all species are pooled. This brings us to the following hypothesis: abundant animals tend to be dispersed randomly in contrast to rare species. The rare species mutually exclude each other because they are habitat specialists and, thus, do not occur in the same habitat. The over-layering of these patterns results in a 'regular' pattern.

As an example of the second possible factor referred to above, which we refer to as 'prey preference complementarity', predators are hypothesised to have a disaggregating effect on dispersion of preferred prey herds (although it is hypothesised that predators lead to increased herd size, i.e., 'safety in numbers', see Krause and Ruxton 2002), which, when the data of the prey species are pooled, is manifested as an organising effect by predators on the dispersion of preferred prey. Herds of preferred prey species, which could be aggregated in the absence of predation, react to the presence of predators by moving apart, becoming less aggregated, and alleviating pressure exerted by predators. Since the presence of predators is cued to multiple prey species, the net effect on combined prey herds is to cause a more regular pattern of dispersion.

G-function results for individual species in this study appear to conform to expectations of both habitat and prey preference complementarity in ways that are hard to separate. In the former, we observe large-sized species (elephants, giraffe and buffalo) preferring habitats featuring high vegetation biomass, small-sized species (Thomson's gazelle) requiring open habitats with low biomass, and mid-sized species (eland, plains zebra, hartebeest, impala and Grant's gazelle) distributed across a variety of savanna habitats featuring grasslands associated with a range of tree densities. Because extreme habitat types, featuring either high or low vegetation biomass, are likely to be rarer and more patchy than intermediate habitat types, herbivore species preferring extreme habitat types are likely to display more aggregated distributions than are species preferring intermediate habitat types.

Similarly, for prey-preference complementarity, herds of mid-sized prey species (eland, plains zebra, hartebeest, impala and Grant's gazelle), which are more likely to be preferred by the dominant predators in this ecosystem (hyenas, lions and leopards), are expected to display less aggregated (even random) distributions. By contrast, herds of large-sized species (elephant, giraffe and buffalo) are expected to experience lower predation pressure (Sinclair et al. 2003, although buffalo has quite a high predation rate, see Prins and Iason 1989), and are thus expected to be more aggregated. Herds of the smallest-sized species (Thomson's gazelle) conform to the expectation of an aggregated distribution, although they experience high predation pressure.

Attempting to discriminate between these alternatives, further *G*-function analyses were performed on the combined data for large- and small-sized (habitat specialist or 'non-preferred' prey) species, and on the combined data for the mid-sized (habitat generalist or 'preferred' prey) species. If habitat preference complementarity is operating, the result should be a tendency by both groups to shift towards a more regular dispersion pattern. If prey preference complementarity is operating, the result for the non-preferred prey group should be to remain aggregated, while the preferred prey group should become regularly spaced. Results (Figure 3.10) tend to support habitat preference complementarity, in that the 'non-preferred' prey group is randomly dispersed, and while the 'preferred' prey group tends towards a regular dispersion pattern, this is far less marked than the result for all species combined (Figure 3.8).

These results do not rule out the possibility that both mechanisms – habitat and prey preference complementarity – have been operating in this landscape over such a long evolutionary time that experimentation is required to detect their separate effects. Recent evidence of the effects of reintroduced wolves on prey in North America shows that predators can greatly affect movements, local densities and sizes of prey herds (Hebblewhite et al. 2002; Hebblewhite and Pletscher 2002; Kunkel and Pletscher 2001; Ripple et al. 2001). However, explicit evidence of disaggregating effects by predators on prey herd dispersion is lacking. There is also growing evidence that predators affect the presence of other predator species (e.g., Durant 1998; Creel 2001). Spatially explicit models of predator–prey dynamics have tended to oversimplify responses of predators and prey to each other (Lima 2002), but are beginning to examine the effect of predators more realistically (Cosner et al. 1999; Abrams 2000; Alonso et al. 2002; Connel 2000; Forrester and Steele 2000; Křivan and Vrkoč 2000; Pitt and Ritchie 2002; Vucetich et al. 2002).

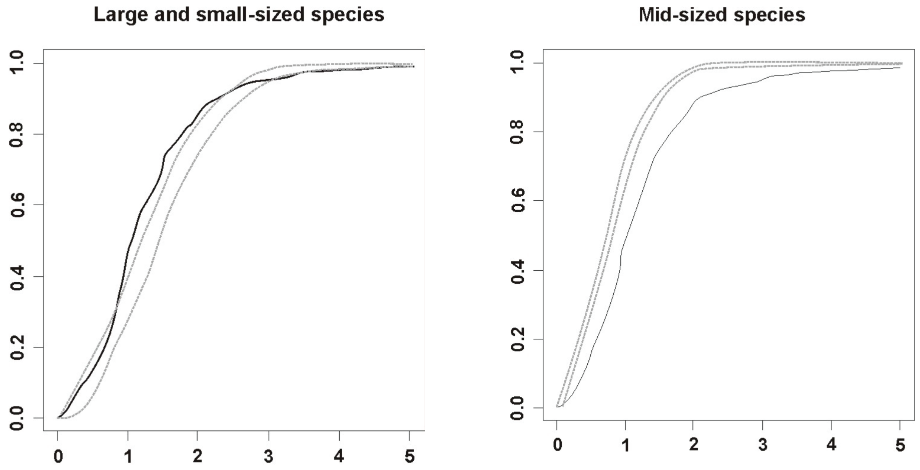

Figure 3.10. *The estimated* $\hat{G}(r)$ *function for large- and small-sized species (left-hand side) and mid-sized species (right-hand side). Coordinates along the horizontal axis are in km*

SYNTHESIS

Combination of GPS technology with spatially explicit statistical techniques, such as plots of the *F*-, *G*- and related *J*-functions, yields novel ways of characterising wild-herbivore dispersion patterns. In particular, the striking contrast between aggregated or random patterns displayed by species analysed separately and the regular pattern observed with pooled data from all species, reveals an emergent and unexpected property of the herbivore community that demands further explanation. This issue and some other hypotheses for future research are formulated in Box 3.2.

Further, the applied value of the spatial analysis of these total count data is, for example, the potential to correct systematic bias in the sample survey methodology. Further studies should reflect the degree to which violation of the assumption of random distribution affect the estimate and which species are mostly affected by this.

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