CHAPTER 3B

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

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The famous statement "Lies, damned lies, and statistics" is attributed to Benjamin Disraeli (1804 – 1881), British Prime Minister for the Conservative Party. When he made that pronouncement, he possibly referred to one of the original meanings of statistics, namely, the (quantitative) description of nation states. In the 19th century, the three developmental lines merged of what we now call 'statistics', that is to say, the quantitative description of societies, the study of sets of objects and the analysis of probabilities. Statistics became the quantitative investigation of equal elements or objects belonging to one set. At that time, two major ways to test hypotheses emerged; one was the experimental way (which became dominant in physics and chemistry) and the other was the statistical way, where a theory or hypothesis was confronted with observations (typical for biology and medicine). Finally, statistics developed into a powerful tool to discover underlying mechanisms that explain variation in patterns or processes.

Alfred Stein and Nicholas Georgiadis (Chapter 3) were apparently motivated by two of these meanings of 'statistics'. First is the quantitative description of equal elements (in their case 'herds' of animals) belonging to one 'set' (all herds in Laikipia District, Kenya; for more information on that area, see, e.g., Heath 2000). The second is the discovery of possible underlying mechanisms that could explain the observed distribution of 'herds' in a landscape.

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Their quantitative description of the ‘herds’ of Laikipia is an exciting one, even though it has some obvious problems. The first problem is that they use the term ‘herd’ very loosely; not a “group of individuals of the same population that form a socially coherent unit over time and space” but merely as “one or more animals at a given location”. Note that ‘location’ is not defined in the text, but we may infer perhaps that it could be a cell with a radius of 250 m. Because Stein and Georgiadis do not use a biological definition of ‘herd’, their analysis is, by definition, not able to make a statement about these biological social units. Their analysis, however, may make statements about what normally is just called a ‘group’ (in their case this would be about “groups of individuals of the same species that are observed within a certain (here not reported) distance of each other”. Because they chose to use the term ‘herd’, their conclusion may be suspect. Indeed, harem size of plains zebra is normally about 7 individuals (Voeten 1999); it is unclear to us what biological unit the mean herd size of 30-odd zebra (their Table 4.1) could represent. Likewise, while a ‘herd’ size of buffalo of 23 (*loc. cit.)* can occur in nature (e.g., Prins 1996), one wonders whether lone bulls and herds of buffalo cows were all taken together under the term ‘herd’. We would not advocate that, since ‘bachelor bulls’ often select different terrains and have a different spatial use than herd animals (Sinclair 1977; Prins 1989a; 1989b; 1996).

A second problem is about the contrast between easily observable animals and ones that are difficult to spot from the air. The chapter of Stein and Georgiadis assumes that all individuals and all species in all terrain types are equally well-spotted; indeed, they state that their work is based on a ‘total count’. Yet, we know from other studies that this is not realistic: small animals are more difficult to spot than big ones, greyish animals more difficult than reddish-brown, and it is easier to get a realistic count of animals on grasslands than of those occurring in thickets (e.g., De Leeuw et al. 1998; Said 2003). Conclusions about patterns of spatial use of animals have to take into account the distribution of the substrate in which they occur: in other words, the spatial patterns of randomness or aggregation may have been caused by vegetation patterns, but the authors do not provide information on these.

Problems aside, the true contribution of this chapter is the development of tools to describe spatial patterns of elements or objects. Stein and Georgiadis show how the F, G and J functions can be used to describe and analyse how animals are distributed in a spatial context. This is useful, because a full description of the exact locations where each individual occurs does not yield insight: one would not see the wood for the trees. Of course, these functions can also be used to describe and analyse other spatial patterns, e.g., the occurrence of large trees in a savanna landscape, water points in an arid environment, camp sites of nomadic people, etc., etc. Stein and Georgiadis point the way, and we think it is a way that should be followed.

In their analysis of the patterns of spatial occupancy of the different species, they find, by-and-large, that groups and singletons of plains zebra, impala, Grant’s gazelle, eland and hartebeest were randomly dispersed, but that groups and singletons of elephant, buffalo, giraffe and Thomson’s gazelle were distinctly aggregated. They then started searching for explanations for these patterns. Here they use the second important function of statistics, namely, the unearthing of possible underlying mechanisms that explain an observed distribution. Thus, statistics can function as a heuristic tool for the development of testable hypotheses. In their search for testable hypotheses that potentially explain their observed result, they tested whether feeding style, dependence on drinking water, mating system or tendency to migrate could explain the dichotomy between the two groups of ungulates. They did not find such a simple factor that could explain why, for example, in September 1996 (when their data were collected) Thomson's gazelle occurred aggregately and Grant's gazelle randomly. We think this lays bare two things. First, explaining an observed (or 'discovered' pattern) without a preconceived hypothesis, is not simple and can rapidly develop into a hunt for the notorious needle in a haystack. Second, because there is no clear underlying hypothesis data 'happened' to be collected in September (which is the middle of the dry season) and sampling at the end of the dry season (or for that matter at the end of the wet season) could have yielded two different sets of species of which individuals are dispersed randomly across the landscape versus species of which the individuals aggregate at a particular scale of observation. The work of, for example, Voeten (1999), Voeten and Prins (1999), Ottichilo (2000), Ottichilo et al. (2001), Oindo (2001), Oindo et al. (2001) or Said (2003), shows how dynamic wild herbivores use these landscapes in time and space. In other words, Stein and Georgiadis should not have made deductions on an analysis of data from a single time of the year: it is much more likely that repeated sampling should have yielded the desired 'explanatory factor'. We hope that Nick Georgiadis will be able to collect simultaneous GPS data (using 10 aircraft!) of the wild herbivores in Laikipia over different seasons.

Finally, Stein and Georgiadis make another tantalising observation for which they have no good explanation. If they group the nine different species, and they run their F, J and G tests on the amalgamated observations of the spatial occurrence of groups and singletons of all species in Laikipia District, they find that these "wild herbivores are arrayed across the landscape in a significantly regular fashion". We call this 'tantalising', because we have our doubts about their explanation that predation could explain this. Repeated sampling is crucial for the confirmation of this pattern that was observed only once. Their idea that predation could explain this, is not shared by us. There are several reasons to be hesitant.

First, the 'safety in numbers hypothesis' does not predict regular spacing but predicts (unpredictable) aggregation in space. *Second*, studies of the association between species in the face of predation in East Africa do not suggest regularity across the landscape. Parts of Laikipia look like parts of the Serengeti, and Sinclair and Norton-Griffiths (1982) observed significant associations between species, while in Manyara, De Boer and Prins (1990) found randomness in the association between species on the scale of tens of hectares. Detailed observations of Voeten (1999) in Tarangire of wildebeest and plains zebra show very similar habitat requirements of these species at certain times of the year, leading then to strong spatial association, but dissociation and dissimilar requirements at other times of the year. *Third*, Stein and Georgiadis are cushy when ascribing the patterns they find to predation. They state "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 (hyena, lion and leopard), 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". They concede that buffalo can experience very high predation pressure (Prins and Iason 1989), and acknowledge that the small Thomson's gazelle (about 25 kg; see for body mass of different ungulates Kingdon 1982) does not fit their expectation either, so two out of nine species do not agree with their hypothesis. But why classify eland (about 470 kg) as mid-sized together with, e.g., Grant's gazelle (55 kg), but buffalo (630 kg) or giraffe (600 kg) together with elephant (3550 kg)? Further, are predation data known for Laikipia? In Timbavati (South Africa), for example, 55% of the annual mortality was caused by predation in case of impala, but for giraffe this was 34% (Hirst 1969): is this difference really big enough to support the dichotomy as envisioned by Stein and Georgiadis? In the Serengeti, Sinclair and Norton-Griffiths (1982) found that between 13 and 21% of the annual mortality of wildebeest was caused by predation, while Sinclair (1985) reported 30%, but Hirst (1969) found it to be 96% in Timbavati, and Mills (1984) found a figure of 93% for the Kalahari. Perhaps Laikipia has more of the appearance of the Serengeti than of the Kalahari, but does it function like the Serengeti? Without a study of predation pressures in Laikipia itself, how well supported are Stein and Georgiadis' thoughts about the relation between body mass, predation and level of aggregation of the individuals in their study? *Fourth*, where Stein and Georgiadis expect aggregation in the case of giraffe, a study on individuals in the Masai Ecosystem of northern Tanzania by Van der Jeugd and Prins (2000) reveals much randomness. *Fifth*, from a natural-selection point of view one would expect also spatial patterns to reflect fitness maximization strategies of individuals of the nine different populations of herbivores. It would make sense to test a hypothesis based on the ideal free distribution of these individuals, but a hypothesis based on predation by several predator species resulting in more regularity across the landscape of groups and individuals of several species of prey, could, to our taste, easily lead to group-selectionist type arguments (*sensu* Wynne-Edwards 1962), which makes us very weary of accepting predation by several predators as a potential explanatory factor for the regular distribution of individuals of several ungulate species.

In conclusion, we think that statistics is very important to describe patterns concisely and precisely. Stein and Georgiadis' statement how useful certain statistical techniques are, is amply demonstrated by their paper. On the other hand, we are less enthusiastic about statistics as a heuristic tool for finding explanatory factors, although we fully acknowledge its use. We think that potential explanatory factors should be firmly grounded in existing theories and linked-up with hypotheses that have been tested. Finally, we think that one needs more observations on the (ir)regularity of herbivore distributions, of single species or of pools of species, at different times of the year, and with a better understanding of the associated resource distribution patterns before one jumps to conclusions.