can, as well as other rangelands[1,6]. Further work is required to identify the nature and limits of these effects.

Wildlife is increasingly viewed as a natural resource which merits sustainable use rather than extermination in pastoral grazing systems[7]. For this to succeed, a fuller understanding is required of the natural and human factors regulating the densities, and particularly the productivities, of wild and domestic large herbivores in these ecosystems.

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McNaughton *et al.* reply — Fritz and Duncan conclude that African pastoral and natural systems have similar carrying capacities for large herbivores. According to the data in the sources they cite, wild herbivore–soil–rainfall data are on a local basis in game reserves, while livestock–soil–rainfall data are national averages. This will tend to inflate the density of wild ungulates and to deflate the abundance of livestock substantially. This is because areas chosen for game reserves naturally tend to have abundant wildlife, and much of the total land areas of most African countries will not support livestock owing to tsetse fly, lack of reliable water, inadequate amounts or quality of forage, vegetation types which are not conducive to livestock raising, and so on.

In addition, the assignment of a single value for rainfall and soil fertility to an entire nation is highly suspect, particularly given the regional climatic and edaphic heterogeneity of Africa. Vast areas within an African nation may be covered with miombo or desert, where livestock densities approach zero, while livestock herds are confined to only a small portion of the nation. We conclude that the data presented by Fritz and Duncan are biased and cannot be used to test the effect of animal husbandry on carrying capacity at a regional scale.

The method used by Fritz and Duncan to assess soil fertility is too coarse and subjective to answer quantitative questions about the importance of soil fertility and precipitation on carrying capacity. This classification basically states that volcanic soils are fertile, those derived from 'basement' rock are infertile, and the others are in between. Quantitative assessments of soil fertility comparable to those of precipitation are feasible and should be used to study this important issue.

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Remembering landmarks

Sir — Because the position of an almost infinite number of objects specifies the same point in space, and memory capabilities of animals are probably limited, one expects memory of only a few landmarks to specify points in space for animals. Much current research focuses on the characteristics of such landmarks, and what form the memory takes. Biegler and Morris[1] report an interesting and carefully designed experiment which they claim reveals a fundamental rule used by animals when deciding which landmarks to remember ("if it moves, don't use it"), and that by applying this, animals extract spatial invariance from their environment. Although the hypothesis is plausible, and their results are suggestive, additional controls are needed before this conclusion should be drawn.

For half the rats in Biegler and Morris's experiments, the goal was specified by two distinct landmarks, the locations of which were fixed relative to a square arena. For the other rats the goal was specified by the same two landmarks, in the same geometrical array, but the whole array was randomly positioned in the arena before each trial. For both groups ('fixed' and 'varied', respectively) the arena was kept stationary within a square room. When the animals had been trained to find the goal (a buried food dispenser) they were given tests with either the landmark array, or the food dispenser, removed from the arena. When the landmarks were removed, both groups searched randomly in the arena, suggesting that cues external to the arena were not guiding animals to the goal. When the food dispenser was removed, there was a marked difference between the two groups. The 'fixed' group searched mostly at the goal, whereas the 'varied' group searched mostly around the nearest landmark to the goal. Biegler and Morris concluded that landmark stability is a prerequisite for spatial learning and memory.

However the animals began trials from the midpoints of the sides of the square arena. Thus, subjects in 'fixed' experienced four "starting viewpoints" of the landmark array. By contrast, subjects in 'varied' experienced up to 196 (there were 49 possible locations of the array in the arena). Consequently, 'varied' subjects were frequently experiencing novel starting viewpoints of the landmark array, and even from starting viewpoints that they had seen before, they would have had much less practice than 'fixed' subjects (up to 1/49).

The ability to reach a goal from a novel viewpoint is thought to require special processing abilities[2,3]. It should not be assumed to be a trivial task, or unlikely to improve with practice. There are thus two explanations for Biegler and Morris's result — theirs, and that 'varied' animals were simply less practised from each starting viewpoint. There are several ways to distinguish between these interpretations. One would be to see if the tendency of 'varied' rats to use the rule "move towards the triangular landmark and search around it" declines with practice. Because landmark stability and starting viewpoint can be manipulated independently, a better way would be to make them independent factors; this would allow their relative effects to be determined.

There are two other reasons for interest in Biegler and Morris's conclusions. First, experiments on insects[4,5], birds[6] and rodents[7,8] show, contrary to their conclusions, that animals do learn and remember the precise location of a goal using an unstable landmark array. Second, many ecologically important points for animals remain fixed relative to unstable landmark arrays (mouths, nectar and cheese in rat traps spring to mind), and one might expect animals to have evolved the cognitive ability to remember the precise location of such points. Extracting spatial

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