Although regression of the data plotted in Fig. 1.2 proves significant, it's predictive value is limited because of the outlier for the small bodied Grant's Gazelle (25 kg). From this it would be not be possible to state that animals requiring the least water travel further in relation to their size. Water requirements scale with body weight raised to the power of 0.82 (MacFarlane & Howard 1972) implying that smaller animals have larger water requirements relative to their body size than larger animals. But, it does not necessarily follow that the most water dependent animals, whether that is the largest species, or those with the driest diets, will be found closest to water (particularly for closely spaced water sources, Redfern *et al.* 2003).

Wildlife have a hierarchy of water use, with elephants taking priority at the individual waterhole (Owen-Smith 1996), with bulls dominating breeding groups (Parker 1997). Landscape features (Jarman 1972), dietary and mineral preferences (Weir 1967, Child *et al.* 1971, Ayeni 1977), association with other species, or avoidance of predators and competition (Hitchcock 1996) and tourists (Weir & Davison 1965) and larger or dominant species, especially elephants (Peters 1983, Parker 1997) may all influence where an animal spends most time foraging. An increase in the frequency of waterholes introduces bulk grazing into areas that were previously refugia for more water-independent, and typically rare, species (Owen-Smith 1996). As well as depleting forage resources, the influx brings with it a following of predators. The result is displacement or local extinction of the rare species, as seen for Roan antelope on the northern plains of Kruger National Park, South Africa (P. Funston *pers. comm.*, Owen-Smith 1996).

1.1.5 Spatial impacts

Grass grows by the inch and is ruined by the foot
From a sign in Bekonscot Model Village, Beaconsfield, England

Animals move between places used for feeding and places used for drinking. The localisation of impacts associated with the congregation of animals at water points and the declining grazing pressure with distance from water gives rise to a utilisation gradient termed the *piosphere* pattern (*see* review by Thrash & Derry 1999). The name 'piosphere' was introduced by the Australian Robert Lange when describing

sheep movement in shrubland west of Port Augusta (Lange 1969). In the name he wished to imply an area of influence arising from the need for animals to drink water.

The need to find drinking water is most extreme in arid and semi-arid areas during the dry season when this water is often only available via artificial supply (Ayeni 1975), usually pumped from below ground using wind or oil powered pumps and stored in tanks for release into troughs (*pers. obs.*). If we can represent the watering point as a hub, then distances from the hub can be marked off with concentric rings as shown in Fig. 1.3.
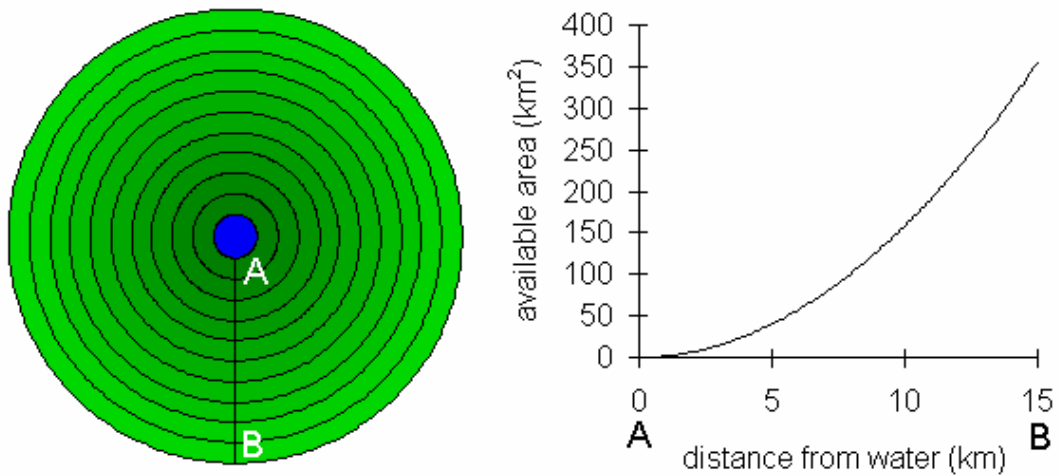

Fig.1.3: The reduction in available foraging area on approaching a watering point.

The space within each of these areas *between* the rings is the available foraging area at that distance from the water, equal to $\pi x^2 - \pi(x-1)^2$ where x is a discrete distance interval from water. From this it can be seen that the available area decreases rapidly on nearing the watering point (Perkins 1991) and as animals move in towards it, their cumulative foraging effort becomes concentrated into less space. The result is a gradient of stocking pressure, which is greatest nearest the watering point and decreases as a function of distance from it (Andrew 1988). For herbivores, along with the gradient of stocking pressure comes a gradient of grazing intensity, greatest at the centre and least at the furthest distance from water an animal may travel during the period before returning to drink. This defines the extent of the piosphere (Graetz

& Ludwig 1978). This is a maximal model for available foraging area at distance from water. Real-life examples are more likely prone to restriction by landscape features, *e.g.*, aspect, fences, watercourses and other boundaries, and may not conform to geometric prediction (*e.g.*, Weir 1971) because of variations in the animal behavioural response to wind, topography and spatially heterogeneous vegetation (Nash *et al.* 1999).

By definition then a piosphere may occur at any point in the landscape where there exists a focal point for animal convergence. This has been mostly documented for artificial watering points in semi-arid livestock systems (*e.g.*, Foran 1980, Andrew & Lange 1986a, 1986b, Stroleny & Mentis 1989) and naturally occurring waterholes in wildlife systems (Goodman 1982, Thrash *et al.* 1991, Gaylard *et al.* 2003), but for large herbivores generally and livestock in particular, similar patterns occur around other foci, for example, shady trees, rest sites and saltlicks (Andrew 1988). Smaller animals may add to the piospheres of larger animals, or create their own, like the areas surrounding rabbit warrens, prairie dog towns, termitaria, nesting colonies of rooks and reefs that shelter tropical fish, to name but a few (Andrew 1988). As animals tend to frequent particular watering points along rivers, most probably due to ease of access, semi-circular piospheres also occur along their banks.

The utilisation gradient in forage biomass provides feedbacks for animal foraging and intake, and the redistribution of nutrients and seeds in the landscape (*see* Thrash & Derry 1999 plus Redfern *et al.* 2003). In addition to foraging activity, trampling exposes topsoil by destroying canopy structure and disturbing litter, increasing soil compaction and reducing infiltration of rainwater (Kelly *&* Walker 1976, Thrash 1997). Reduced microtopography limits collection of runoff water and nutrients (Nash *et al.* 2003) and increases bare soil by removal of plant-soil interactions that maintain vegetated patches (Rietkerk *et al.* 2000). Exposed topsoil dust is eroded by wind action or fixed by rainwater into a soil crust (Andrew & Lange 1986a), further reducing infiltration and increasing run-off (Beukes & Ellis 2003, Thrash 1997). Soil dust collects on leaf surfaces where it inhibits stomatal closure or photon entrapment and absorption, and thus photosynthesis and transpiration (Andrew & Lange 1986a).

At the centre of the piosphere, experiencing the highest herbivore pressure, trampling usually generates an area reduced to nothing but mud (Thrash & Derry 1999) called the *sacrifice zone* (Graetz & Ludwig 1978). Defecation and urination elevate nutrients (Fig. 1.4), affecting herbaceous production (especially phosphorus-availability gradients, Turner 1998a, 1998b) or to levels above the toxicity tolerance of plants (Perkins & Thomas 1993a). Nutrient levels are also higher because trampling of lichen crusts reduces nitrogen fixation (Andrew & Lange 1986a) as a function of distance from water (Hodgins & Rogers 1997).

a)

b)
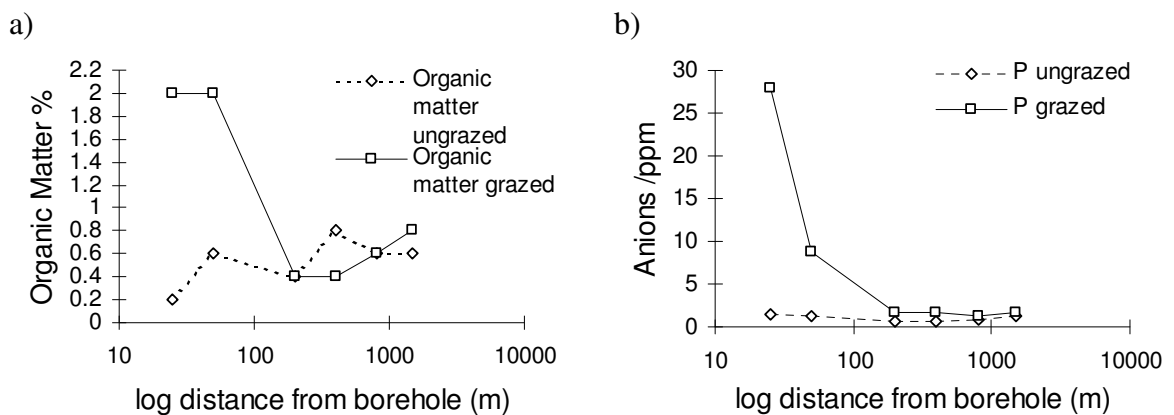
(*Data source* Perkins 1991)

Fig. 1.4: Elevated soil nutrients are a product of defecation and urination. Organic matter (a) and Phosphorous (b) are examples of this.

Both univariate (*e.g.*, Graetz & Ludwig 1978) and multivariate (*e.g.*, Perkins 1991) techniques have been used to analyse these data. Ordination (ter Braak & Prentice 1988) and Principal Components Analysis (Jongman *et al.* 1995) can show which environmental variables have dominant effects by separating species-by-site data from environmental data (*e.g.*, distance from water, soil moisture and nutrients. *e.g.*, Fernandez-Gimenez & Allen-Diaz 2001, Heshmatti *et al.* 2002).

1.1.6 Plant response

Plant response within the piosphere is a local effect, largely determined by edaphic and environmental factors (Kalikawa 1990, Makhabu *et al.* 2002). The dynamics of savanna vegetation depend on the competition between plants for light and space to grow in, soil nutrients and soil water, whereas compositional changes depend on the life histories of individual plant species present and on their location along the

gradient of grazing pressure (Lailhacar *et al.* 1993). Therefore, disturbances by herbivores bias this competition according to plant life histories (Lailhacar *et al.* 1993). For example, the growth of some grasses is promoted by grazing but reduced in others (Andrew *&* Lange 1986b). Species may be described as 'increasers' or 'decreasers' or unaffected (*e.g.*, Rogers & Stride 1997). Landsberg *et al.* (1997) found Australian biota evenly split into 38% increasers and 33% decreasers. The result is that, a grazing gradient will not only be expressed via a defoliation gradient but also by a change in the composition of the vegetation. As a result, piospheres have been used (Moleele 1994, Hosten & West 1995, Fernandez-Gimenez. & Allen-Diaz 1999, Lind *et al.* 2003) to test Clementsian succession (Connell & Slatyer 1977), State and Transition (Westoby *et al.* 1989) and nonequilibrium models (Ellis & Swift 1988) of rangeland vegetation dynamics (see Section 5.5.2). Within the herbaceous layer, poor quality, hardier (centripetal) increaser grasses will be favoured by the high grazing pressure towards the centre, displacing higher quality, less hardy (centrifugal) decreasers to the perimeter of the piosphere (Perkins & Thomas 1993a). Near the centre one might expect to find a short sward of annual grasses, moving out to a taller stand of annuals with some perennials, and open grassland of decreasers farthest away, being predominantly perennials (Fig. 1.5). This is a rule of thumb, an aid to a conceptual model, for which some studies are in good agreement (*e.g.*, Friedel 1988, Thrash *et al.* 1993), and others contradict wholly (*e.g.*, Stroleny & Mentis 1989, van Rooyan *et al.* 1994, Nangula & Oba 2004), or at least in part (*e.g.*, Foran 1980, Andrew & Lange 1986b, Heshmatti *et al.* 2002). Proximate sites experiencing similar grazing pressures may differ in plant composition through soil differences (*e.g.*, sandveld pans versus clay pans, Makhabu *et al.* 2002) without the effect of distance from water within sites.

All piospheres do not match the conceptual model because of complicating factors such as grazing-induced vigour (Andrew & Lange 1986b). Clearly, the community response to disturbance is complex (Perkins & Thomas 1993a). In addition, 'palatability' is often used in association with diet quality, but is subjective, based on our assumptions about the desirable qualities of forage, and the comparative qualities

of proximal forage (Illius *et al.* 1996a). A mechanistic understanding of animal diet is better interpreted in terms of nutritional optimality (*e.g.*, Owen-Smith 1994).

Compositional changes detected using multivariate analysis and direct measurements tend to negatively reflect increasing grazing pressure towards water (*e.g.*, Thrash *et al.* 1993), reaching a maximum at distances from the watering point where the piosphere is not detectable through subsequent measurement of species.
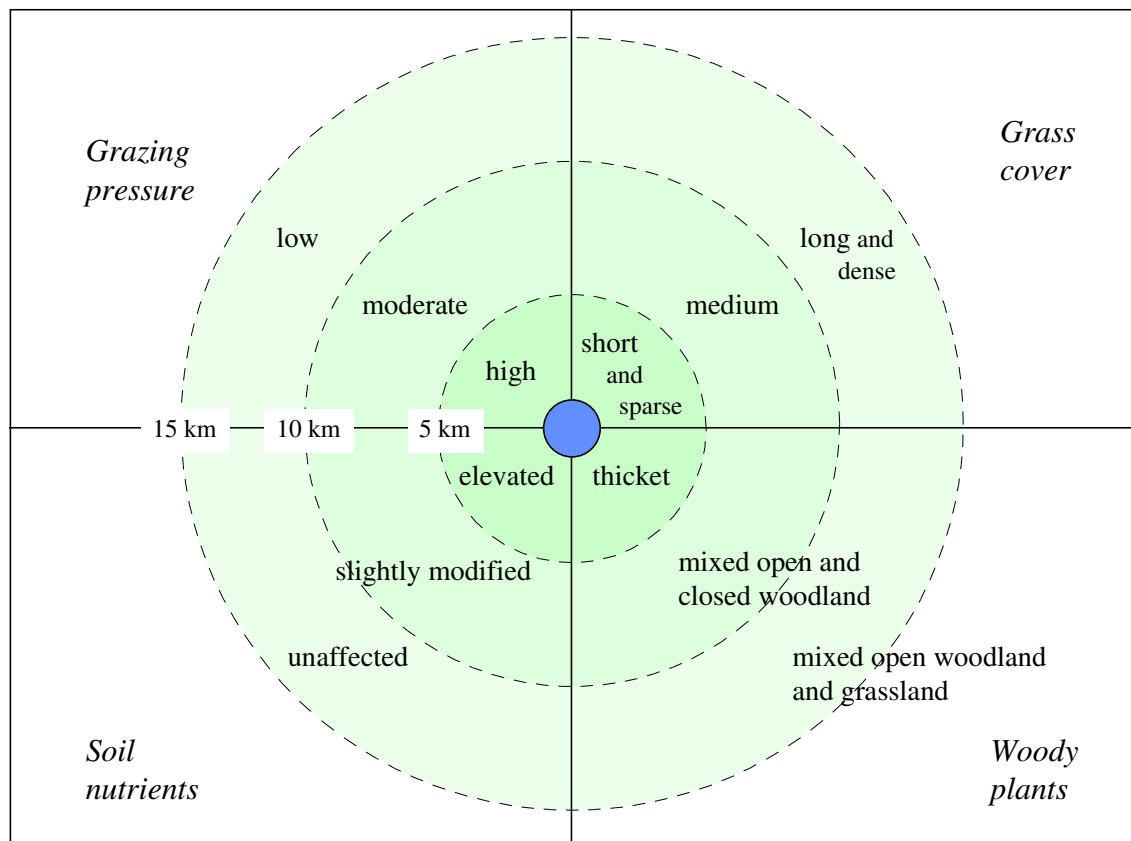

Fig. 1.5: Diagrammatic illustration of how distance from permanent water is an important determinant of the habitat diversity of an area. Adapted from Collinson (1983).

The extent of the impact as reflected by the response of a measured variable, and our interpretation, depends upon which variable is being measured (Fernandez-Gimenez & Allen-Diaz 1999), when it is being measured (*i.e.*, in which season and the age of the site) and where it is being measured (*i.e.*, dependencies on climate and vegetation type). For example, a gradient may be generated in soil surface characteristics up to only a few tens of metres away from a watering trough (Andrew & Lange 1986a), whereas trends in herbaceous plant basal cover may be detected up to 7 km from the

focal point (Thrash *et al*. 1991), and 'desert patches' (areas of exposed soil around well sites) have been reported to have radii of 30 km and 50 km (Glantz 1977 and Rapp 1976, respectively, cited in Hanan *et al*. 1991).

In addition to herbaceous vegetation changes, high grazing and trampling intensities towards the centre deplete grass cover of shorter species allowing shrub and tree growth to encroach in those areas fuelled by the centripetal carriage of shrub and tree seed in fæces (Perkins & Thomas 1993a). Changes in herbaceous cover tend to be more consistent across all studies, essentially because of the sacrifice zone. Woody cover is more variable between regions of differing climate, soil and vegetation types, and management (*e.g.*, compare the Kalahari, Tolsma *et al*. 1987, with Kruger National Park, Gaylard *et al*. 2003). Cattle ranching can produce piospheres that feature a band of shrubs in the near vicinity of a borehole (Kalahari 20-400 m , Perkins 1991; Tanzania 300-2500m, Tobler *et al*. 2003). For savanna, encroachment may displace palatable leaf-succulent shrubs in favour of unpalatable woody species (*e.g.*, in the Kalahari, Moleele & Perkins 1998 and in the Succulent Karoo, Riginos & Hoffman 2003). A wildlife equivalent typically lacks a central woody band because the effect of elephants and other browsers is to override this bush encroachment and open up the area. This in itself leads to a gradient in shrub density (extending to 2.8 km from the watering point, Brits *et al*. 2002) or tree damage (Gaylard *et al*. 2003). Cowley (2001) found quite different rates of woody cover change for separately stocked sheep and kangaroo compared to mixed stock. Bush encroachment may also be suppressed anthropogenically around settlements (Fernandez-Gimenez & Allen-Diaz 2001). Anti-herbivory responses may reduce effective forage availability (Cooper & Owen-Smith 1986). Although not reported to occur in response to the grazing gradient of the piosphere, increased chemical protection (Whitham *et al*. 1991) and spinescence (Dangerfield *et al*. 1996) occur in woody species under concentrated grazing.

The processes that generate, maintain and modify utilisation gradients are dependent on temporally dynamic quanta (*e.g.*, rainfall volume and animal density, van Rooyan *et al*. 1990, Parker & Witkowski 1999). This would be expected to give rise to

temporal variation in piosphere extent and the shape of the response, but not sufficient to restore the system to its previous state (Parker & Witkowski 1999, Rietkerk & van de Koppel 1997, Rietkerk *et al.* 1997). However, Perkins has consistently argued that the Kalahari is more resilient to permanent modification, and that restoration is possible (*e.g.*, Perkins & Thomas 1993b). For example, bush encroached zones may revert to open savanna (Perkins 1996), even though they have been noted to spread outwards during development (Perkins 1991). During the dry season some of the piosphere characteristics, such as the amount of defoliation of the forage will reach its maximum. The nature of some of those relationships will then change for the wet season; for example, grass growth will increase the herbaceous cover and therefore decrease the amount of bare soil (van Rooyan *et al.* 1994). So although there will be an overriding tendency for the piosphere to grow out, depending on climate and stocking rates (Heshmatti *et al.* 2002), there will also be a seasonal flux in piosphere dimensions, and complexity from site-specific sensitivity to degradation (Perkins & Thomas 1993b), making it difficult to assess the extent of impact. It is therefore unfortunate that no long-term piosphere data exists but only a few years of basal cover measurements made at artificial watering points in the Kalahari (van Rooyan *et al*. 1990, 1994; Parker & Witkowski 1999 was not a gradient analysis), which generally followed rainfall levels suggesting that when monitoring the piosphere effect it is important to account for climate (KNP 1997).

1.1.7 Management

Justification and siting of artificial water sources, especially in Game reserves and other protected areas within semi-arid regions, has never been a more contentious issue in Africa than at present. Some sites have undergone a holistic re-evaluation of water resource management (*e.g.*, Kruger National Park), for which managers have had to account for the external pressures that also tax the water supply, *i.e.*, rivers running in to game reserves get tapped and depleted by human intervention (H.Biggs *pers. comm.*, Braak 1997). Decisions then taken to supplement that inadequate supply must be informed with respect to the consequences of supplementary water provision (Braak 1997). Central to this discussion is the large-scale damage to the landscape from water provision characterised as the