

The nature and modelling of piospheres: a review

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Gradients in utilisation pressure tend to develop around watering points because water dependent herbivores are forced to congregate within a maximum distance of about 10–15 km from water in the dry season. Artificial watering points cause previously migratory or nomadic indigenous large herbivores to become sedentary, so that natural grazing patterns are disrupted. Under this altered grazing pattern, piosphere patterns tend to develop in herbaceous species composition, range condition, grass production, plant biomass, understory cover, standing crop and basal cover. In areas with large populations of elephants the density and canopy cover of trees is directly proportional to distance from watering points. In the absence of elephants an increase in woody plant density and canopy cover tends to occur in a zone just beyond a sacrifice area. Soil erosion, compaction and capping tend to occur at watering points on soils containing clay and silt. Artificial watering points are advantageous to the non-mobile water dependent large herbivore species and disadvantageous to the water independent large herbivore species.

The processes underlying piosphere development and maintenance are numerous and diverse. While being parsimonious treatments of a complex system, conceptual models do provide a reasonable basis upon which to design an improved understanding. The logistic curve has been proposed as a convenient tool for estimating piosphere dimensions, but ignoring the 'best-fit' regression model for a piosphere data set may be an inaccurate practice. A large number of gradient models have been developed, each an attempt to shed some light on the behavioural response underlying what appears to be a complex grazing pattern. Several system models that take piosphere effects into account have been constructed. Some of these produce good simulations of herbaceous material dynamics and especially good simulations of bush dynamics.

Key words: waterholes, watering points, drinking, utilisation, degradation

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Introduction

Lange (1969) coined the word piosphere and defined it as "an ecological system of interactions between a watering point, its surrounding vegetation and the grazing animal." Van der Schijff (1959) considered the most important causes of "local over- and under-grazing" that existed in the Kruger National Park in the nineteen fifties to be inadequate water provision and injudicious rangeland burning. This was before the 'water for game' programme had gained momentum. The available dry season grazing in the vicinity of a permanent watering point determined the population density of large herbi-

vores around that watering point. Also, the distribution of permanent watering points in a vegetation type, rather than the productivity of the vegetation, determined the carrying capacity of that vegetation type (Van der Schijff 1957). Watering points have been linked to desertification (Sinclair & Fryxell 1985) and their development has been called a "critical process" (Belsky 1995).

Uses of piosphere data

Studies of ecological parameters along distance from water gradients are useful for various reasons. Viewing systems as a patch-

work of distance from water annuli has resulted in us gaining a finer scale of understanding of ecological processes (e.g. Belsky 1995). Understanding of the nature of the effects of watering points allows us to plan water provision projects to maximise target parameters (Stafford Smith 1991). Andrew (1988) pointed out that the pattern of placement of watering points can be designed to maximise habitat diversity. The number of watering points can be determined according to economic and ecological principles. These studies are used in locating sampling sites for rangeland condition monitoring, as explained by Foran (1980). Distance from water gradients have also been assumed to represent grazing gradients and used to classify plant species into ecological groups according to their response to grazing. This has been done for various areas (Bosch & Janse van Rensburg 1987; Janse van Rensburg & Bosch 1990; Bosch & Gauch 1991; Bosch & Kellner 1991; Van Rooyen *et al.* 1991; Du Plessis *et al.* 1998). Pickup (1989) describes a method of monitoring range condition by measuring the recovery of vegetative cover after heavy rain along distance from water gradients.

The effects of watering points on rangeland utilisation

The utilisation gradient

Watering points have a marked effect on rangeland utilisation pattern, which in turn, has a large effect on vegetation and soil. According to Graetz & Ludwig (1978) "a piosphere develops as a result of the interaction of the maintenance and social behaviour patterns of herbivores with the vegetated landscape in which the watering point has been established." In the simplest hypothetical case of an isolated watering point in a uniform rangeland type, a gradient of utilisation pressure develops which is greatest near the watering point and decreases as a function of distance from it (see Bosch & Janse van Rensburg 1987; Janse van Rensburg & Bosch 1990; Bosch & Gauch 1991; Bosch &

Kellner 1991). The zone adjacent to the watering point experiences a very heavy (mostly trampling) pressure and is often referred to as the sacrifice area. Conversely, according to Van Wyk & Fairall (1969) and Graetz & Ludwig (1978), areas at distances exceeding that normally travelled by herbivores from water experience the lowest utilisation pressure. Perkins & Thomas (1993a) showed that there is an exponential increase in available grazing with increasing distance from watering points.

Natural rotational utilisation

According to Walker (1979) natural watering points are very seldom permanent in southern Africa and indigenous large herbivores are adapted to undertaking highly irregular and unpredictable movements between forage resources according to the availability of water. The natural system is thus one of long periods of relatively light vegetation utilisation alternating with short periods of fairly heavy utilisation. Artificial permanent watering points and fencing often cause previously migratory or nomadic indigenous large herbivores to become sedentary. Now there is year-round heavy grazing and browsing of range, with consequent increased utilisation pressure and rangeland change.

Relationship with distance from water

Many authors (Glover 1963; Napier Bax & Sheldrick 1963; Savidge 1968; Van Wyk & Fairall 1969; Young 1970; Weir 1971; Spence & Angus 1971; Joubert 1976; Ayeni 1979; Cumming 1981; Kalikawa 1990) have commented on the heavy utilisation of rangeland that occurs around watering points during the dry season when there is no adequate temporary water to entice large indigenous herbivores away from the trampled areas. Van der Schijff (1959) examined the rangeland surrounding watering points in the Kruger National Park and divided it into five zones according to the degree of utilisation by game. The first zone, immediately adjacent to and extending to about 91 m from the

watering point, was trampled to dust (in dry season) and corresponds to the sacrifice area of Graetz & Ludwig (1978). The second zone extending to 1.6 km from the watering point was grazed short and trampled. The third zone extending to 5 km from the watering point was evenly grazed short. The fourth zone extending to 8 km from the watering point was lightly and selectively grazed. The range in the fifth zone, further than 8 km from the watering point, was utilized little or not at all by game during the dry season and accumulation of senescent, unpalatable grass material occurred there (Van der Schijff 1959).

Perkins & Thomas (1993a) identified similar zones on cattle ranches in the Kalahari (also see Perkins 1996). The grazing pressures were higher on the cattle ranches than in the Kruger National Park and Perkins & Thomas divided the sacrifice area into two zones. The first (0–50 m from the watering point) was a zone of irreversible degradation caused by nutrient enrichment to the point of toxicity. The second zone (0–400 m from the watering point) corresponded with the sacrifice area of Van der Schijff (1959). The third zone (200–800 m from the watering point) corresponded to the second zone of Van der Schijff (1959), but the fourth zone (200–2000 m from the watering point) was the bush densification zone and was not found by Van der Schijff (1959) in Kruger National Park. The fifth zone (> 2000 m from the watering point) corresponded to the fifth zone of Van der Schijff (1959). The absence of Van der Schijff's (1959) third and fourth zones can be explained by cattle not grazing as far out from water as indigenous large herbivores.

A few studies have provided quantitative evidence to substantiate the qualitative observations given above. Negative relationships between indices of herbivore utilisation and distance from water have been shown for livestock (Lange 1969; Andrew & Lange 1986a, Hart *et al.* 1991; Pinchak *et al.* 1991; Hart *et al.* 1993) and indigenous large herbivores (Young 1970; Child *et al.* 1971;

Weir 1971; Senzota & Mtahko 1990; Thrash *et al.* 1993a, 1995; Hunter 1996).

An interesting point is that Thrash and co-workers (Thrash 1993; Thrash *et al.* 1993b; Thrash 1998a) studied piospheres in the Kruger National Park about thirty years after Van der Schijff (1957) and found that only the first and second zones identified by Van der Schijff were evident. During the nineteen fifties, when Van der Schijff (1957) did his studies, large parts of the Kruger National Park were beyond 16 km from permanent water and therefore not utilised in the dry season. Since the 'water for game' programme (Joubert 1986) has been completed, however, the situation has changed completely. Thrash & Biggs (1993) used data collected during an aerial survey and a Geographic Information System to show that very little (0.009 %) of the Kruger National Park was more than 10 km from a permanent water supply in 1992. All of the national park was therefore within reach of mobile water-dependent herbivores.

Maximum distance

Collinson (1983) has classed indigenous large herbivores according to the frequency that they require drinking water. Water dependent herbivores are forced to congregate within a certain distance from watering points in the dry season. This has been stated to be 10–15 km in Amboseli by Western (1975), 12–16 km in Kruger National Park by Van der Schijff (1957) and 10 km in Mkuzi Game Reserve by Goodman (1982) and Pilanesberg National Park by Collinson (1983). The reason for the variation within areas and between areas is probably that wild herbivores in conservation areas very seldom use only one watering point (Young 1970). The movement between watering points complicates the assessment of the distance from water to which they can forage. The temperature, humidity, moisture content of the forage and the physical condition and physiology of the animals all affect this distance and all vary considerably. Another factor is the scarcity of areas beyond the reach

of water dependent herbivores. Du Toit (1990) found that some water independent browsers (e.g. giraffes) may also be attracted to the heavily utilised woody vegetation near watering points for nutritive reasons.

Trampling effect

The impact caused by trampling is higher than that caused by grazing in the immediate vicinity of watering points (Senzota & Mtahko 1990). When herds are large and watering points few and there is competition for drinking space, animals mill around and trampling is severe and causes the sacrifice area (Young 1970; Zambatis 1980).

Effect of watering points on herbaceous vegetation

Species composition

The concentration of herbivore utilisation in the vicinity of newly constructed watering points has been found to lead to the decline of various intolerant groups of herbaceous plant species. Spence & Angus (1971), Edroma (1981) and Friedel (1988) found that the tall, sour, fire climax grasses (e.g. *Cymbopogon* spp.) are eliminated. Riney (1982) was of the opinion that the particularly palatable species that are selected by grazing herbivores decline. The erect palatable grasses such as *Pennisetum*, *Themeda* and *Digitaria* have been found to decline (Friedel & Blackmore 1988; Smit & Rethman 1989; Van Rooyen *et al.* 1990) and smaller leaved, prostrate grasses such as *Cynodon dactylon* to increase (McNaughton 1984; Friedel & Blackmore 1988; Cowley & Rogers 1995; Navie & Rogers 1997). According to Weir (1971), Kelly & Walker (1976), Walker (1980), Riney (1982), Tolsma *et al.* (1987), Stroleny & Mentis (1989), Georgiadis & McNaughton (1990), Bastin *et al.* (1993) and Cowley & Rogers (1995) the annual species : perennial species ratio increases. Stride (1997) found that chloridoid grasses increased and andropogonoid grasses decreased near water.

Weeds (e.g. *Tribulus terrestris*) become dominant near the water (Tolsma *et al.* 1987; Andrew 1988; Stroleny & Mentis 1989; McClaran & Anable 1992). Species diversity has been found to decline near watering points (Tolsma *et al.* 1987) in Botswana, whereas seedbank species diversity near watering points was high in a semi-arid subtropical Australian rangeland (Navie *et al.* 1996). Thrash *et al.* (1993b) found no consistent relationship between distance from water and herbaceous species diversity. This lack of consistency is both unusual in the piosphere literature and difficult to explain. Further research on this aspect is probably required.

Areas that are naturally waterless in the dry season provide only summer grazing for water dependent large herbivores. When watering points are constructed in these areas, the range out to about 10 km from water is grazed and trampled more than before. Smuts (1972) dealt with the changes that occur in these areas. He found that this practice leads to changes in the herbaceous vegetation species composition. Pioneer annuals, such as *Tragus berteronianus* and *Urochloa mosambicensis* become more dominant over the whole area and perennial species, such as *Themeda triandra* and *Digitaria* spp., decline (Smuts 1972). The effect of watering point construction in previously waterless areas is under-researched and is fertile ground for further research.

Range, condition, biomass and cover

A belt of land devoid of vegetation in the dry season, develops around watering points (Van der Schijff 1959; Delany & Happold 1979; Senzota & Mtahko 1990) and is called the sacrifice zone (Stoddart *et al.* 1975) or sacrifice area (Graetz & Ludwig 1978). Range condition (Foran 1980; Barker *et al.* 1989), grass production (Edroma 1989), plant biomass (Andrew & Lange 1986b), understory cover (Bastin *et al.* 1993; Cowley & Rogers 1995; Pickup & Bastin 1997; Ringrose *et al.* 1996), standing crop and basal cover (Thrash 1998a) have all been

found to be directly proportional to distance from water. Even though large herbivores prefer natural to artificial watering points (Hitchcock 1996), the impact of artificial watering points is not significantly different from that at natural permanent watering points (Thrash 1998b). When watering points are placed in areas naturally only used for wet season grazing however, the change to year-round utilisation of the herbaceous vegetation causes the basal cover out to about 10 km from the water to decline (Smuts 1972; Delany & Happold 1979; Riney 1982; Thrash *et al.* 1991a).

Nutritional quality was found to be higher near (50 m) watering points than farther (800 m) from it (Georgiadis & McNaughton 1990). This was due to increased dry season utilisation pressure, causing a change in species composition and soil nutrient content. This improved nutritional quality is probably of little importance to herbivores, however, as the vegetation in close proximity to the watering points is not grazed in the wet season and consists of annual plants only.

Effect of watering points on woody vegetation

Species composition

On browsing gradients away from watering points woody plants that are vulnerable to browsing or trampling suffer increased mortality. Near the watering point where browsing pressure is highest these tend to be replaced by plants adapted to withstand browsing. Andrew & Lange (1986b) and Bastin *et al.* (1993) found this on livestock stations in arid Australia, whereas Ross (1995) reported similar results from the succulent Karoo of South Africa. Friedel (1988) found that *Dicrostachys cinerea* relative abundance is inversely proportional to distance from watering points and *Acacia tortilis* and *Acacia karroo* relative abundances are directly proportional to distance from watering points. The changeover of species may lead to one association being replaced by

another. For example, the *Sclerocarya birrea* / *Acacia nigrescens* savanna association in the central Kruger National Park is gradually replaced by a browsing resistant *Acacia tortilis* / *Dicrostachys cinerea* savanna association under the high browsing pressures at watering points (Coetzee 1983; Du Toit 1988).

Woody plant density and cover

Overgrazing of the herbaceous stratum, resulting in reduced competition for moisture and reduced intensity of fires, near watering points tends to result in an increase in woody plant density in areas in which elephants do not occur (Van Vegten 1983; Tolsma *et al.* 1987; Friedel & Blackmore 1988; Ringrose *et al.* 1996). In areas with large populations of elephants however, such as the Kruger National Park, destruction of trees by these animals occurs at watering points (Young 1970; Lason 1979; Eltringham 1980; Van Wijngaarden 1985; Thrash *et al.* 1991b). This results in a decrease in tree density near watering points (Van Wyk & Fairall 1969; Delany & Happold 1979; Van Wijngaarden 1985; Thrash *et al.* 1991b). An increase in scrub growth near water and decreasing away from it occurs in the Kruger National Park (Van Wyk & Fairall 1969; Smuts 1972; Thrash *et al.* 1991b). In the Kalahari, there is a decline in shrub canopy cover in the immediate vicinity (<400 m) of watering points (Perkins & Thomas 1993a). This accompanies an increase in canopy cover in a zone beyond the sacrifice area (about 400 m to 1500 m), after which shrub canopy cover is unaffected by the watering point.

Impact of elephants

Megaherbivores can have a major impact on woody vegetation. Du Toit (1988) found that elephants are the primary agents of woody stratum change near surface water in the Kruger National Park. According to the findings of Van Wyk & Fairall (1969) the utilisation of woody plants by elephants in the Kruger National Park is inversely propor-

tional to distance from water and the state of the grass cover. The greatest damage of the habitat by elephants is also in the vicinity of rivers and permanent watering points (Napier Bax & Sheldrick 1963; Laws 1970; Weir 1971; Bromwich 1972; Anderson & Walker 1974; Afolayan 1975). Excessive utilisation of the herb stratum by grazers is implicated as the primary reason for increased browsing activity and destruction of the woody strata by elephants in the Kruger National Park (Van Wyk & Fairall 1969). Woody plant destruction by elephants is usually selective according to species (Van Wyk & Fairall 1969; Weir 1971; Field 1971) and favoured species tend to decline in abundance.

Effect of watering points on soil

Herbivore trampling gradients, indexed by track development, have been shown by Lange (1969) and Andrew & Lange (1986a) to radiate from watering points. Soil compaction and capping tend to occur at watering points (Lason 1979; Walker 1980; Riney 1982; Van Wijngaarden 1985; Andrew & Lange 1986a, but not on almost pure sands (Perkins & Thomas 1993a). Capping is caused by the removal of the protective plant cover and the resulting splash erosion (Rauzi 1963) as well as the trampling of the soil surface when moist by large animals (Van den Berg *et al.* 1976). The infiltration capacity of soils has been shown to be inversely proportional to the grazing pressure (Rhoades *et al.* 1964; Van den Berg *et al.* 1976) and the rate of water infiltration into the soil is directly proportional to distance from watering points (Kelley & Walker 1976; Dunn 1977; Riney 1982; Van Wijngaarden 1985; Andrew & Lange 1986a; Thrash 1997). This is especially important on heavier textured soils (Walker 1980) and may be negligible on very sandy soils such as those of the Kalahari (Perkins & Thomas 1993a).

The loss of herbaceous cover and increased run-off at watering points result in a higher rate of soil erosion (Young 1970; Lason 1979; Edroma 1981; Perkins & Thomas

1993a). Venter (1990) estimated that 2.55 million tonnes of soil had been lost by wind erosion at a single watering point in the Kruger National Park. The finer fractions of the soil are lost first (O'Connor 1985). The texture of the soil would therefore be expected to change along a grazing gradient away from a watering point, although this is not always evident (Thrash 1997).

The deposition of nutrients in dung in the vicinity of water causes a high concentration of nutrients to develop at watering points (Weir 1971; Georgiadis 1987; Tolsma *et al.* 1987; Perkins & Thomas 1993a). According to Georgiadis (1987) nutrient effects on soil only become evident after extremely high utilisation intensities.

Effect of watering points on large herbivores

Migration patterns

When artificial watering points are placed in areas previously waterless in the dry season, naturally migratory large herbivore populations may become sedentary (Young 1970; Smuts 1972; Joubert 1976).

Species composition

Artificially induced changes in water distribution cause a change in the temporal and spatial patterns of utilisation of the vegetation. This is to the advantage of the non-mobile water dependent species (e.g. cattle, warthog, impala and waterbuck) and to the disadvantage of the water independent species (e.g. red kangaroo, common reedbuck and eland) (Newsome 1965, 1971; Goodman 1982; Collinson 1983). Rapid population increases of non-mobile water dependent species necessitates culling of these populations (Goodman 1982). Rapid population increases of mobile water dependent Burchell's zebra and blue wildebeest populations followed the construction of artificial watering points on the north eastern Lebombo plains of the Kruger National Park

(Joubert 1976). This resulted in increased competition with the vulnerable roan antelope population during the nineteen-eighties, causing a decline in the latter (Viljoen 1995).

Some species produce altricial young and require stands of tall grass to hide them. These species include sable and roan antelopes and common reedbeek. When large herds of grazers spend the dry season in an area, their grazing shortens the grass. When watering points are placed so that no area is farther than about 10 km from permanent there are no areas where large herds of water dependent grazers cannot forage and the large herbivores that require tall grass are expected to decline (Collinson 1983). Joubert (1976) recommended closing down all but a few selected artificial watering points in otherwise prime roan antelope habitat in the Kruger National Park.

Indigenous large herbivores versus livestock

Indigenous large herbivores do not remain close to watering points after drinking (Young 1970; Senzota & Mtahko 1990). In one study about 80 % of Burchell's zebra and 90 % of blue wildebeest spent less than three minutes there (Senzota & Mtahko 1990). Lions have been shown to concentrate their hunting activities around watering points (Smuts 1978). Livestock, on the other hand, tend to remain in the vicinity of watering points, chewing the cud or resting in shade. The utilisation of range close to water is therefore different for indigenous herbivores and livestock (Werger 1977).

Effect of watering points on biodiversity

One of the variable determinants of habitat diversity is distance from water and the resulting spatial variations in herbivore utilisation. Another is the intensity and frequency of fires (Collinson 1983). Plant species diversity is expected to peak at some intermediate point along the gradient of distance from water (Andrew 1988). Hypothetically the construction of a few, relatively sparsely

distributed, artificial watering points in a large area (such as the South Australian arid zone in which, previously, there were no permanent watering points) increases the diversity of habitats (Andrew 1988). A general supply, however, of a large number of uniformly distributed watering points results in a heavy uniform herbivore utilisation pressure and a uniform cover of short sparse annual grasses, so that habitat diversity and ecosystem stability are reduced (Goodman 1982; Collinson 1983; James *et al.* 1999). For this reason, Collinson (1983) and Owen-Smith (1996) recommend that artificial watering points should not be placed closer than 30 km apart and 15 km apart, respectively, in a large national park (the difference between these two recommended distances stems from a difference in the estimates of the distance that water dependent herbivores will travel from water, Collinson worked with 10 km and Owen-Smith with 5 km). Goodman (1982) and Joubert (1986) suggest that artificial watering points should also be placed close to existing rivers and other natural permanent and semi-permanent watering points for minimum disturbance of natural foraging regimes.

Effect of watering points in arid areas

Watering points in arid wildlife areas have less impact because the herbaceous vegetation is mostly annual and the herbivores are less water dependent (Mills & Retief 1984; Knight *et al.* 1988). Child *et al.* (1971) and Van Rooyen *et al.* (1990, 1994) found little impact on the vegetation in the Kalahari (mean annual rainfall of 200–250 mm). No consistent relationship between primary production (measured using satellite imagery), and distance from water was found around wells used by cattle in the Sahel (mean annual rainfall of 200–400 mm) (Hanan *et al.* 1991). The resolution in this study was low (1.1 km) however and there may have been undetected sacrifice areas around these watering points. Of all the large herbivores in the Kalahari Gemsbok National Park the movements of only the blue wildebeest

population was affected by closure of watering points (Mills & Retief 1984).

Effect of linear versus point water sources

Linear water sources include canals, rivers, running streams and bore drains. Point water sources include troughs, pans and small dams. Cowley & Rogers (1995) compared the effects of sheep at bore drains (linear sources) with point water sources in the Mulgalands of Australia. They found that the hypothetical gradient in stocking density with distance from water is less severe with linear water sources. The impact of point water sources is thus greater than linear water sources (Cowley & Rogers 1995). Unfortunately, livestock (Cowley & Rogers 1995) as well as indigenous large herbivores tend to concentrate at particular points along linear water sources so that the impact is similar to a string of point water sources. The drinking behaviour of livestock and indigenous large herbivores at perennial rivers in the dry season requires research as this seems to be a gap in our knowledge.

Water provision for various management objectives

Water provision for maximum range condition

Van der Schijff (1957) made recommendations for the management of the Kruger National Park. He considered the number of watering points at the time to be inadequate because there was "under-utilised" range beyond the reach of water dependent large herbivores in the dry season. He also warned however, against placing watering points too close to one another, so that they serve the same grazing area. He considered watering points 8 km apart too close as degradation of the rangeland resulted. The Kruger National Park is no longer managed for maximum range condition (Joubert 1986) however, and having some "degradation" and some "under-utilised" range is probably desirable

as it maintains biodiversity and natural ecological processes.

Water provision for maintenance of biodiversity and natural processes

Most national parks have the maintenance of biodiversity and natural processes as the chief management objective (e.g. Joubert 1986; Goodman 1982). Although it is not desirable that lightly utilised (under-utilised) rangeland dominates a national park, it should be viewed as a habitat type that should be allowed to persist. Artificial watering points in most conservation areas have been placed so uniformly, however, that very few areas are now farther than about 10 km from water and this lightly utilised habitat, with the herbivores and plants that are adapted to it, is threatened (Thrash & Biggs 1993). This habitat type remains hypothetical however and its study should be a priority.

Water provision for maximum large herbivore production

Water has an indirect effect on carrying capacity in that availability of water often affects large herbivore home ranges. For maximum sustained production of large herbivore biomass it is necessary to utilise each area of the property to the maximum possible without degradation. This can only be achieved with an even distribution and adequate number of watering points (Walker 1979) so that the large herbivore carrying capacity is determined solely by the productivity of the vegetation (Zambatis 1985a). The objectives of the property thus determine the water provision strategy to be employed.

Stafford Smith (1991) suggested evening out the impact of large herbivores around widely spaced (5–20 km apart) watering points by increasing the number of watering points. This results in smaller sacrifice areas, decreased travelling times for the large herbivores and increased persistence time for forage.

What constitutes an adequate number of watering points is vague in the literature and probably depends on the behaviour of the particular type of large herbivore involved. According to Zambatis (1980), for maximum herbivore productivity, watering points should be spaced so that little or no overlap of home ranges of herbivores occurs. Cattle readily forage out to only about 500 m from water (Pinchak *et al.* 1991; Hart *et al.* 1991), whereas African elephants, Cape buffalo and Burchell's zebra readily forage out to about 5 km from water (Young 1970). Zambatis (1980) advised game ranchers not to place watering points less than 5 km apart. Many game ranches are far too small to allow this however. A flexible approach, in which a high density of controllable watering points is provided is recommended. Periodic assessments, are made so that watering points are closed on a rotational basis and heavily utilised rangeland is rested.

Modelling of piospheres

Simplification of a complex system

Antagonistic to any generalised piosphere modelling effort is the range of responses that have been found for vegetation and soil properties with distance from water across different study sites. That is to say, the piosphere effect is a multivariate system response, further complicated by its particularity to the site of interest.

The spatial extent of vegetation impact is largely determined by soil and vegetation type—Kalikawa (1990), gives example of variation between sites with description of two boreholes in the Central Kalahari Game Reserve. Thus, assessing the extent of the impact, as reflected by the response of a measured variable, depends upon which variable is being measured, 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.* 1991a), and 'desert patches' (areas of exposed soil around wells) have been reported to have radii of 30 km and 50 km (Glantz 1977 and Rapp 1976, respectively, cited in Hanan *et al.* 1991). However, within the detectable extent of impact for any given site, characteristic zones of compositional change in the vegetation and particularly in the tree-grass ratio may be recognised. This has enabled the representation of the individual piosphere as annuli in the form of conceptual models in the presence (Collinson 1983) and absence (Perkins & Thomas 1993a) of woody layer mediation by browsers.

Conceptual models

Whilst being parsimonious treatments of a complex system, the conceptual models do provide a reasonable basis upon which to design an improved understanding, (e.g., one that includes temporal dynamics).

Changes in composition with time depend on the life histories of individual plant species present and on their location along the gradient of grazing pressure (Lailhacar *et al.* 1993). A notional pattern displaces less hardy (centrifugal) species, from the centre, outwards, towards the perimeter, and replaces them with hardier (centripetal) species. This is a rule of thumb, an aid to the conceptual models, for which some studies are in good agreement (e.g., Friedel 1988; Thrash *et al.* 1993b), and others contradict wholly (e.g., Stroleny & Mentis 1989; Perkins 1991; Van Rooyen *et al.* 1994), or at least in part (e.g., Foran 1980; Andrew & Lange 1986b). Why all piospheres do not conform to the concept may be due to complicating factors such as grazing-induced vigour (Andrew & Lange 1986b), implying a complex community response to disturbance (Perkins & Thomas 1993b).

Further abstraction allows these models to be used as units of landscape management

(Foran 1980). Incorporating knowledge about livestock behaviour and patterns of home-range use (e.g., dietary preference, wind direction) and paddock design, will highlight areas most susceptible to impact (Pickup & Stafford Smith 1987). Consideration of these areas allows the construction of management strategies for optimal rangeland use and minimal degradation (Cridland & Stafford Smith 1993). Application to wildlife areas involves additional levels of complexity. These include notions regarding the stabilising qualities of heterogeneity on system dynamics (Goodman 1982), wet and dry season ranges (e.g., Funston *et al.* 1994), and the importance of maintaining rare species refugia in the landscape (Owen-Smith 1996).

The general logistic model

The piosphere effect that underlies the conceptual models is the pattern that results from the amalgamation of animal impacts and the separate graded responses of vegetation and soil characteristics. The separate responses fall into two categories; those in which there is a concomitant increase in the level of the variable with distance from water, and those that decrease. Graetz & Ludwig (1978) recorded vegetation and soil data that appeared sigmoid when plotted against distance from water. This led them to the suggestion that a generalised regression model could be used to describe both the increasing and decreasing response types in terms of a logistic curve. Their choice in the logistic curve was sensible when one considers its pliability of form through manipulation of its parameters. Furthermore, its parameters can be used to partially quantify the zones of the piosphere depicted by the conceptual models. In addition to proving to be an acceptable fit for their own data collected in the Australian chenopod shrubland of New South Wales, the generality of Graetz & Ludwig's model is supported by its subsequent use in southern Africa, now with an additional term to account for nonzero y-intercepts (Thrash 1998a; Verlinden *et al.* 1998). An exponential decay model, offering

similar interpretation by its parameterisation, was favoured for the change in cover with distance from water for a site on the Nullarbor Plain, Australia (Cridland & Stafford Smith 1993).

The use of the logistic model in rangeland management

Although the logistic curve is a convenient tool to estimate piosphere dimensions, by adopting the logistic equation and not selecting the 'best-fit' model for a piosphere data set, the loss in estimator precision may outweigh the logistic curve's usefulness. Conversely, the process of selecting the most suitable model will have some bearing on what we may infer from the analysis (Buckland *et al.* 1997). For example, one dimension of a piosphere that may be estimated using this graphical model is the distance to the extent of its impact as measured by the abscissa upon negligible change in the asymptotic gradient (e.g. Thrash 1998c). This value would be useful to managers when trying to assess the spacing of watering points. Keys of 3 models; exponential, logistic and Gompertz, were fitted to compositional data collected at 9 sites in Kruger National Park (Thrash *et al.* 1993b). Whilst there was no overall effect on estimating the impact extent by selecting the logistic curve in favour of a 'best-fit' alternative if one existed ($t_{0.05,8} = -0.16$; $P \gg 0.05$), the error in doing so for individual sites ranged between approximately a fifth (0.18) and nearly four times (3.91) the distance estimated by selection of the 'best-fit' model, and on average the distance estimated by the logistic equation was over twice (2.06) that estimated by the 'best-fit' model (Derry & Morris *unpubl.*).

Regression models

Semiarid environments exhibit high temporal and spatial variability (Ellis *et al.* 1993), this spatial heterogeneity being found at a range of spatial scales, locally, within plants, through the whole plant communities and up to landscape and regional scales (Kotliar &

Weins 1990). Foraging animals respond to the spatial heterogeneity of their environment by making diet selection decisions that need to account for the distribution of their forage resource (Laca & Demment 1991). A grazing gradient occurs where there exists a relationship between foraging behaviour and a trend in this spatial distribution. At the landscape scale, animal distributions are the simplest method we have to study the behavioural response. Relating direct measurements of animal density to watering point location can show species interaction, especially wildlife displacement by livestock. These measurements analysed using statistical modelling techniques (e.g., kriging) can also highlight the impact zones associated with animal distributions along grazing gradients (Verlinden *et al.* 1998).

The prediction of animal grazing pattern

A large number of models have been developed, each an attempt to shed some light on the behavioural response underlying what appears to be a complex grazing pattern. Techniques that have been employed include, regression analysis (e.g., Senft *et al.* 1983), probability densities (e.g., Arnold & Maller 1985) and GIS (e.g., Wade *et al.* 1998). Disquietingly, Stafford Smith (1990) achieved realistic results from an elementary random-walk model of sheep movement. The only adjustments made were to keep animals within the scope of the paddock, motivate them through previously utilised areas, and probabilistically tailor their movement with respect to wind direction.

Remote sensing of gradients

More analytically, the flux of animal movements to and from watering points has been captured by using a convection-diffusion process calibrated with remote-sensing measurements (Pickup & Chewings 1988; Pickup 1994). Remotely-sensed Landsat images of vegetation cover are typically translated into animal distributions via the design of a filter that accounts for vegetation growth and temporal variation in vegetation

cover. The filter incorporates growth, originally modelled as an exponential decay of a growth peak following satisfactory rain, however since then more sophisticated rainfall-driven growth models have been devised (Pickup 1995). Additional terms account for natural decline in vegetation cover, and species gradient effects (compositional changes) assumed to reduce forage quality under heavy stocking. Animal density is then assumed proportional to the depletion of vegetation cover and can be modelled using families of inverse Gaussian distribution functions. The approach is effective in extrapolating information from satellite imagery and linking animal densities to range utilisation. This has proved a useful method for the prediction of herbage production and the subsequent distribution of animals along a grazing gradient. It is also effective for the monitoring of rangeland (Pickup *et al.* 1994) and estimation of rangeland degradation (Pickup *et al.* 1998). To date the approach lacks a two-dimensional treatment, and requires further development of the biological component for application to other sites (Stafford Smith 1990). It is noteworthy that this remote sensing technique uses defoliation as a predictor of animal distribution. Heterogeneity in rangeland utilisation is assumed equivalent to spatial difference in the removal of vegetation cover related to distance from the nearest watering point.

Productivity gradients

General relationships between animal densities and primary production (e.g., Coe *et al.* 1976; Fritz & Duncan 1994) might imply an alternative predictor of animal distribution and thus herbivore impacts. Gradients may be found in standing crop biomass as well as vegetation cover (Cridland & Stafford Smith 1993), and appropriately, herbage production may be estimated using remotely-sensed data (Pickup 1995). However, animal responses to gradients of primary production do not fully reflect large-scale dependencies. Functional responses may be complex (Spalinger & Hobbs 1992). Van de Koppel *et*

al. (1996) detected reduced foraging efficiency in tall, dense grasses at the upper end of a productivity gradient. To model this, negative relationships between plant density and consumption rate, and plant density and digestion efficiency are introduced into a typical predator-prey formulation to reduce the herbivore numerical response. The model predicts a maximal grazing pressure at intermediate levels of standing crop. Under these conditions, multiple stable states may occur for systems of intermediate productivity. Under high productivity, there is a potential for unchecked domination by vegetation. Utilisation thresholds in tall, dense swards are due to dietary and other factors. Reduced digestibility and palatability of plant material, reduced intake of structural tissues and increased vertical resource partitioning constrain diet quality and quantity. Other effects are physical impediment (e.g., impenetrable swards of *Cenchrus ciliaris*, Tuli Block, South Africa, *pers. obs.*), increased threats of predation through obstructed vigilance (Lamprey 1963), and substitution of foraging time to heightened vigilance (Illius & Fitzgibbon 1994).

System models

Simulation models seek to emulate ecosystem behaviour by the integration of system components (sometimes packaged in sub-models) by various means (e.g., Starfield & Bleloch 1991; Baltzer 1998; Derry 1998), allowing independent dynamics (e.g., growth) as well as interaction (e.g., competition). The representation of the need, to differing degrees, for animals to drink water, depends largely on a model's iteration interval and the nature of the animal component. At one extreme, highly mechanistic, spatial models that attempt to predict foraging behaviour within small time steps may simulate animal movements that are responsive to physiological stress. Constraint within a home range as a function of water requirement becomes a model output. Simpler models that are not so concerned with the fundamentals of spatial impacts may simply super-

impose a grazing gradient over the modelled region.

A grid-based model of a single piosphere

Jeltsch *et al.* (1997) considered the question of piosphere reversibility and spread using a grid-based simulation model of 2 separate borehole sites in the Kalahari thornveld. They succeeded in generating similar variability in piosphere size, as determined by changes in grazing pressure, to that observed by Perkins (Perkins & Thomas 1993a). Fundamental piosphere responses are recognisable in the model's output for herbaceous and woody cover. While this exercise provides invaluable insight into the generation and maintenance of piosphere responses in vegetation cover, the rule-based algorithms comprising the model do not extend to include foraging behaviour. This means that the grazing pressure was constantly levied according to location along the extent of a preconceived, exponential grazing gradient. Reduction of phytomass in random grid cells conforms to this grazing pressure. Perhaps then, accumulated depletion is likely to give rise to a herbaceous layer that reflects a deterministic gradient. Possibly more impressive is the model's simulation of bush densification.

The location and depth of bush densification zones in the near vicinity of the "virtual borehole" are similar to those measured by Perkins (1991), and were found stable for simulation times in excess of a century after removal of grazing pressure. The bush dynamics are a product of increasing the grazing pressure upon nearing the water point, leading to extinction of herbaceous cover within local grid cells, and subsequent colonisation of those grid cells by a woody species.

Perkins (1991) carried out his experiments in the eastern Kalahari, where precipitation levels (~ 450 mm/yr) might be expected to generate rooting patterns that seek to partition the water resource (Mordelet *et al.* 1997). Deep surface sands proffer a low storage capacity for infiltration (Mazor 1982) which

shallow herbaceous roots access before percolation to the deeper placed roots of the woody vegetation. It is reasonable therefore that the foundation for bush densification is considered the depletion of grasses by the high herbivore utilisation intensity near the borehole.

Fire is included in the model as a function of fuel load was previously identified as having an important influence on the model's results (Jeltsch *et al.* 1996). Perkins (1991) originally identified the exclusion of fire by the continuous grazing of the herbaceous layer, which reduces the available fuel load, along with seedling establishment following favourable rainfall patterns, as cofactors in the promotion of the woody layer (Perkins 1991).

Grid-based models of animal densities

Another Kalahari-based model (Starfield *et al.* 1982) moves 3 species of wildlife between blocks along a section of river according to an index of attractiveness that captures diet preferences and water dependence, including drought tolerance. The model was successful in predicting basic animal movements and population dynamics in response to water location and accumulated defoliation in blocks hosting a watering point, but is not configured to model piosphere patterns.

The Paddock utility in RANGEPACK (Stafford Smith 1988; Stafford Smith & Foran 1990; Cridland & Stafford Smith 1993) provides a user interface for the specification of paddock characteristics, such as watering point location, fencelines, and wind direction (an influence on sheep movement). The exponential decay model is used to impose a grazing gradient, the slope of which is determined by watering point salinity and a vegetation preference index, also influenced by watering point salinity, thereby introducing an element of animal physiology. The model can be used to test sketched paddock designs against predicted spatial impacts for multiple watering point systems,

and is being developed to accept real paddock data via GIS input.

Modelling the physiology of foraging behaviour

Mechanistic models move away from the grazing gradient approach towards predictions of animal movement whilst accounting for physiological constraints. To model animal movement with respect to water requirements, the balance between acquirement via drinking and dietary moisture content, and losses via respiration, sweat, urine, and faeces need to be considered.

Loza *et al.* (1992) include all of these factors in a physiological submodel, and specify the location of a watering point and shade in a landscape submodel. An hourly iteration interval sees animals making daytime decisions conditional on their physiological status, derived from thirst, respiration and hunger indices. Animals are mobilised towards water or shade according to the strength of the corresponding index, and if sufficiently hungry, will forage en route. A priority is set for drinking, over shade, over eating. During winter, animals were predicted to spend roughly a half of each day near water. During warmer months animals were predicted to suffer higher water loss, spend longer drinking, and spend more time near shade. Increasing the distance between water and shade reduced the time spent near water in favour of travelling to shade after drinking requirements had been satisfied. The representation of the landscape is coarse. Water and shade are located in, and separated by, adjacent kilometre-wide blocks with movement in 0.5 km units. Forage growth is not dynamic, daily growth being input as a value independent of consumption. Hence, impacts are not recorded.

Distance to water versus animal energy expenditure

SAVANNA (Coughenour 1993) does not simulate animal water balance but does take account of energy expenditure in travel

undertaken to satisfy water requirements. The iteration interval is a week. Animals are distributed across the grid-based landscape in relation to an index of habitat suitability, assessed in terms of distance to water along with forage abundance and tree cover. Watering points may be either, seasonal wells, permanent wells or perennial streams, each classifiable as either a mineral or fresh quality. The level of seasonal wells are dependent on the previous three months' rainfall, whilst loss from permanent wells is dependent on the previous 12 months' rainfall. Discharge rates and distance to water are input as maps. Animals that cannot be supported at current discharge rates disperse to other areas containing excess water. A maximum animal density may be set for each grid cell. Plant growth is related to soil moisture and transpiration rate. Trees are classified into size classes. Grazing and browsing impacts are registered on the corresponding phytomass in each cell. Whilst, the model has been successfully applied to predicting large-scale vegetation dynamics and animal distributions (Kiker 1998), an assessment of the model's capacity to simulate piosphere dynamics is in progress (Derry & Kiker *pers. comm.*).

Piospheres and the socio-economics of large herbivore production

An additional dynamic component important to sustainable rangeland management arises from market forces. Piosphere dynamics in the Kalahari are inextricably linked with socio-economic (Perkins 1991) and now political factors (Perkins 1996). A benefit function in ORIA (Optimal Rangeland Integrated Assessment model, Duraiappah & Perkins, *unpubl.*) is used to encapsulate the income from livestock sales, the cost of shipment from the cattlepost to the abattoir, the gain of milk, draught power, hides and prestige by retaining animals and the loss of these benefits by selling animals. The analytical model also includes the cost of restocking, the provision of supplementary food, labour costs and effort. Borehole density for the modelled region is limited within bounds

to avoid overlap of neighbouring piospheres. The cost of borehole establishment and maintenance are also charged. Additional boreholes are drilled if the current quantity of boreholes cannot support the current head of livestock. Stock numbers fluctuate with available forage. Vegetation dynamics are modelled for grass and browse within 2 concentric zones surrounding the boreholes, and a grazing reserve beyond the outer annuli. The level of bush densification is assumed to be an exponential function of distance from a borehole once grass levels fall below a threshold. Forage intake is balanced against energetic requirements for maintenance and travel. Vegetation is trampled in proportion to animal density and affects grass more than browse. Substitution of herbaceous forage with browse is constrained to reflect digestive constraints in cattle. The model seeks to maximise the benefit function net costs limiting sales to levels that do not result in a smaller herd size than the initial herd.

The model manages to simulate various aspects of Kalahari piospheres. These include, temporal dynamics such as bush densification, spatial effects such as essential winter grazing being limited to the outlying grazing reserve, and animal behaviour such as mixed diets during summer. It also provides a test of optimal herd sizes and national agricultural policy, finding in support of an 8km spacing of boreholes. Ecologically sustainable stocking rates (carrying capacity) were found in excess of economically sustainable stocking rates, dependent on cattle prices and borehole costs. Losses from trampling were found to be large enough to justify investment in more boreholes to diffuse herd intensity.

Miscellaneous models

Aspects of other models lend themselves to solving some of the problems envisaged during development of a comprehensive piosphere model. A few examples are given here.

Fryxell (1998) has generated a central-place foraging model of beaver resource depletion that effectively generates a piosphere pat-

tern. The model accounts for the effects of forage abundance and nutritional quality on beaver forage preference and subsequent handling and retention times. The pitfall with beaver foraging behaviour, when comparing it to e.g., livestock, is that beavers restart their foraging excursions from a central position on each occasion. Each food item is located relative to the central point rather than with respect to the previous food item, lending itself well to the Markovian Chain approach adopted, but requiring modification if to be applied in a piosphere modelling context.

Pennycuik (1979) provided a useful allometric energetics model of animal mobility to calculate 'foraging radius', the home range of the free-ranging animal, the determinant of piosphere extent.

Effective and economical artificial water provision is partly dependent on the type and dimensions of the water container (Zambatis 1985b), and this could be included in bio-economic system models of watering points. Evaporation is related to surface area, therefore, water loss from rectangular troughs is proportional to the length of their perimeter, whilst water loss from circular pans increases exponentially with their diameter. Insufficiently sized pans (<10m diameter) tend to become mud wallows. This deters drinking. Sufficiently sized pans (>25 m diameter) lose 16.7 times more water to evaporation (919.8 m³ per annum) than that lost from a 15 m trough (55.1 m³ per annum) holding 6300 litres, deemed a minimal capacity for daily wildlife water provision.

Synopsis and extension

There has been a considerable amount of work done on piospheres in the past 30 years. Within the piosphere literature there is remarkable consistency between areas and sources with respect to their nature. There are however, several aspects of the subject that have been neglected and require research. One of these aspects is the recovery of piospheres when the watering

point is closed. This information would have great practical value for national parks where more natural water provision methods are being adopted. It could also be used to investigate the potential for rotational water provision. On a theoretical level this information could be used to test hypotheses derived from succession theory and disequilibrium theory. Piospheres would be especially good for these purposes because there is a range of levels of degradation. Thresholds of degradation for example, should be easy to detect using piospheres. Most piosphere research has, for obvious reasons, concentrated on the area in the vicinity of watering points. Completely neglected are the areas far enough away from permanent water to be unutilised by water dependent large herbivores in the dry season. Hypothetically these areas should exist in large national parks and communal grazing areas with sparse water supplies. These areas may be structurally very different from dry season grazing areas and may provide habitat for rare species. Only one study has dealt with linear water sources. Many properties have rivers flowing through them. A fertile ground for research is the movement patterns of large herbivores that drink at rivers and the size of the piospheres that form around popular drinking sites along rivers. These data will be useful for inclusion in models for areas with rivers. Indigenous browsers being virtually water independent, it is understandable that piosphere studies in savanna areas have concentrated on herbaceous vegetation gradients. More research is needed on woody vegetation gradients however, especially in areas where elephants occur.

The location of animal drinking water has been identified as an important factor in determining patterns of rangeland use, and yet models of the piosphere response are scarce. Ecosystem modelling efforts tend to concentrate on the prediction of animal distributions, as a simple function of distance from water. Although animal movement may be based on simple rules, complexity is evident in the piosphere response and the consequences that this will have on animal utilisation of rangeland. Animal distribution

models that do account for water location fail to account for piosphere dynamics, confining grazing impacts to within appropriate limits. Models that do simulate spatial impacts have not investigated the significance of the many other factors that may be contributing to the grazing pattern, including animal response, and assume a gradient of grazing intensity to be a sufficient predictor of piosphere generation and dynamics. The advantages of including an economics component have been recently demonstrated, although the structuring of this will vary with application. Animal effects omitted from mechanistic modelling efforts include trampling, defecation and urination. Trampling exposes topsoil by destroying canopy structure and disturbing litter. Such effects reduce infiltration (Kelly & Walker 1976). Exposed topsoil dust can either be eroded by wind action or fixed by rainwater to form a soil crust, reducing infiltration and increasing run-off (Thrash 1997). A potential destination for a soil dust particle is a leaf surface where it may impede photosynthesis and transpiration (Andrew & Lange 1986a). Where present, the trampling of lichen crusts will reduce nitrogen fixation, thereby exacerbating another repressor of plant productivity, the toxic concentration of dung and urine.

Hydrology has been ignored as a factor in causing spatial vegetation growth patterns around watering points. Natural waterholes are points of collection for rainwater and retain water longer than at equivalent soil depths in the surround. Slow release of leaked water from natural pans, and even artificial, concrete-lined pans (by way of cracks in their bases) will bolster local soil water content. In contrast, the pumping of boreholes causes an inverted cone in the aquifer, a 'drawdown' of the water table, which expands with increased use. The withdrawal of groundwater reduces pore-water pressure and collapse of the soil structure, leading to subsidence (Hsi *et al.* 1994). No work has been reported that relates this phenomenon to piosphere dynamics around pumped sites. Drawdown of groundwater also occurs at much reduced hydraulic

potentials than those generated by pumping when evapotranspiration exceeds precipitation (Hosty & Mulqueen 1996). The recharge of subterranean water reserves also requires consideration. For the Kalahari in particular, each year, the amount of rainfall reaching the water table has been thought negligible due to impedance by surface sands, causing enough delay for eventual loss to evapotranspiration during winter. This widely accepted sequence of events does not account for the levels of recharge activity subsequently measured in Kalahari groundwater (Mazor 1982), implying the need for a re-evaluation of water flow in these soils.

It is impossible to predict whether increasing the number, and detail, of mechanisms simulated in a model of piosphere dynamics will improve its performance. However, as we improve our comprehension of the factors that generate piospheres, it will become possible to evaluate their relative influences on the piosphere response, potentially via the use of models. Perhaps then we may expect improvements in our models of rangeland use, and elicitation of the role of gradients in rangeland degradation and utilisation.

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