

MINI- REVIEW

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

Facilitation versus competition in grazing herbivore assemblages

Randal Arsenault and Norman Owen-Smith

Arsenault, R. and Owen-Smith, N. 2002. Facilitation versus competition in grazing herbivore assemblages. – *Oikos* 97: 313–318.

The importance of facilitation versus competition in structuring herbivore species assemblages is a critical issue in theoretical ecology as well as for practical wildlife management. This paper examines the evidence for facilitation and clarifies our understanding in relation to the mechanisms and the spatial and temporal scales where they occur. Evidence for facilitation through stimulation of grass regrowth during the growing season appears stronger than that for increased resource access through removal of obstructing grass structures during the dormant season. Although facilitation may benefit the nutritional gains obtained by certain species in the short term, these benefits do not appear to be translated into the expected population consequences. We suggest this could be due to seasonal tradeoffs between facilitation and competition, as well as to restrictions on the spatial extent of trophic overlap.

R. Arsenault and N. Owen-Smith, Centre for African Ecology, School of Animal, Plant & Environm. Sci., Univ. of the Witwatersrand, Wits 2050, South Africa (randal@gecko.biol.wits.ac.za).

Trophic interactions among large mammalian herbivores are mediated largely through their grazing and browsing impacts on vegetation (Vesey-Fitzgerald 1960, Bell 1970, Eltringham 1974, Owen-Smith 1985, Murray and Illius 1996, 2000). Competition may arise where one species reduces shared food resources below the level that can be exploited efficiently by another species (Illius and Gordon 1987, Murray and Illius 1996, Prins and Olff 1998). Alternatively, by reducing grass biomass one species may benefit another by facilitating access to forage of a suitable height or quality (Vesey-Fitzgerald 1960, Bell 1970, 1971, McNaughton 1976). The relative importance of these two processes in structuring species assemblages remains unclear. Current

understanding is that competition is reduced primarily through distinctions in body size, and secondarily through adaptations in trophic morphology, leading to differential preferences for grass height and forage quality (Bell 1970, Jarman 1974, Demment and Van Soest 1985, Owen-Smith 1985, Illius and Gordon 1987, Owen-Smith 1989, Prins and Olff 1998). Large species have the ability to utilize high food biomass that is low in quality (Bell 1971, Jarman 1974, Demment and Van Soest 1985, Illius and Gordon 1987). Small species require high forage quality, but can tolerate low food biomass levels. Small species may thus benefit from the grazing impacts of larger species, and potentially out compete the latter when food supplies become reduced

Accepted 18 January 2002

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ISSN 0030-1299

(Illius and Gordon 1987, Gordon and Illius 1989). Furthermore, by selectively grazing on green leaf in taller swards, smaller or more narrow-muzzled species also have the ability to deplete this component to the detriment of forage quality for larger species (Murray and Illius 1996, 2000).

While the joint importance of competition and facilitation in structuring large herbivore assemblages is widely recognized in textbooks and reviews (Owen-Smith 1989, Ricklefs 1990, Krebs 1994, Putman 1996, Dobson 1998, Prins and Olff 1998, Murray and Illius 2000), empirical evidence for effects at the population level remains meagre. Hairston et al. (1960) proposed, provocatively, that the herbivore trophic level is generally predator-limited rather than food-limited, noting the widespread prevalence of much uneaten green vegetation (Hairston et al. 1960). This viewpoint has been firmly rejected for large mammalian herbivores, on the basis that forage of a suitable quality becomes severely limited seasonally (Sinclair 1975). Moreover, herbivore biomass is closely correlated with annual rainfall, and hence with vegetation production (Coe et al. 1976, Fritz and Duncan 1994). But why then is convincing evidence for trophic influences, whether facilitatory or competitive, on population abundance and hence community composition so elusive? How is it that the big species survive, and indeed dominate the biomass within large herbivore assemblages (Bell 1982, Owen-Smith 1988, du Toit and Owen-Smith 1989), despite being supposedly the inferior competitors?

Mere overlap in resources utilized by individual animals does not necessarily constitute competition. The outcome depends on the extent to which these resources limit population abundance (Wiens 1989, Putman 1996). Grass resources may appear to be superabundant during the growing season, but only a fraction of this potential food may be nutritionally acceptable and accessible (Wilmschurst et al. 1995, Prins and Olff 1998). During the non-growing season, grasses become dormant and forage is progressively depleted. At this time of the year herbivores of different species tend to segregate into distinct habitats, or concentrate on different resource types (Jarman and Sinclair 1979, Owen-Smith 1982, Owen-Smith and Novellie 1982, Gordon and Illius 1989). But such segregation does not necessarily imply a lack of competition, as one species may be excluded from habitats or resource components that it would have otherwise utilized but for the feeding impacts of another (Rosenzweig 1981). From a broader perspective, we may observe only the "ghost of competition" (Connell 1980) in the form of assemblages of species that compete weakly or only intermittently, because strong competitors were eliminated in the evolutionary past.

We suggest that greater clarity about the relative roles of competition and facilitation in structuring large herbivore assemblages could be obtained if more recog-

nition was given to (1) the effective mechanisms through which these processes operate, (2) contrasting effects during different seasons, and (3) spatial heterogeneity in the available resources. We explain our case, and present supporting evidence, below, with a focus on facilitation in particular. We distinguish between feeding facilitation, population facilitation and habitat facilitation, outline potential seasonal tradeoffs between facilitation and competition, and suggest how this perspective helps explain observed patterns of spatial partitioning among herbivore species.

Feeding facilitation

Feeding facilitation may arise in two different ways: (1) when grazing by one species makes more grass accessible to another species, e.g. by reducing grass height and removing stems (Vesey-Fitzgerald 1960, Bell 1970, 1971), or (2) when grazing by one species stimulates grass regrowth, thereby enhancing the nutritional quality of forage for another species (Vesey-Fitzgerald 1974, McNaughton 1976, Gordon and Illius 1988).

Increased resource access

Facilitation through increased access to resources was described qualitatively by Vesey-Fitzgerald (1960), in terms of a grazing succession. His observations were made in tall floodplain grasslands in the Rukwa Valley in Tanzania, where trampling and feeding by elephants (*Loxodonta africana*) exposed medium-height grasses to buffalo (*Syncerus caffer*), which in turn generated shorter grass exploited by topi (*Damaliscus lunatus*).

Further evidence supporting the grazing succession concept was provided by Bell (1970, 1971), who studied the distribution of resident buffalo, zebra (*Equus burchelli*), wildebeest (*Connochaetes taurinus*), topi and Thomson's gazelle (*Gazella thomsonii*), across the catenary sequence of grasslands in the western Serengeti. All species concentrated on the highest ground during the wet season, where short grasses offering the best quality forage dominated. Towards the end of the wet season, species moved in order of decreasing body size towards lower ground, where medium-tall but poorer quality grasses occurred (with the exception of topi, which left before the larger wildebeest). Furthermore, Bell (1971) observed migratory populations of three of these species (zebra, wildebeest, Thomson's gazelle) moving through his study area, and recorded that they likewise moved in order of body size in relation to changes in grass height.

Recent authors have questioned Bell's (1970, 1971) interpretation of these patterns of species association as representing grazing facilitation (Sinclair and Norton-Griffiths 1982, Illius and Gordon 1987, de Boer and

Prins 1990, Putman 1996, Prins and Olff 1998). The movement of larger species from the upper catena could readily be explained as a consequence of grass height reduction, once the grass had stopped growing. (Illius and Gordon 1987). Whether the smaller species benefited in any way from the grazing impacts of the larger species was unclear.

Although movements of the migratory populations of zebra, wildebeest and Thomson's gazelle appeared to be associated with changing grass height, substantial numbers of resident wildebeest remained in the area throughout this time. The reduction in grass height that occurred before the arrival of migratory wildebeest could have been due to the grazing of resident wildebeest, rather than that of migrant zebra. Furthermore, subsequent observations failed to support Bell's contention that the migratory wildebeest followed behind the zebra in their migrations (Sinclair and Norton-Griffiths 1982, Sinclair 1985).

Increased quality of resources

McNaughton (1976) provided convincing evidence that Thomson's gazelle were attracted to areas where prior grazing by wildebeest improved the quality of the grass sward on the Serengeti plains. Concentrations of migratory wildebeest removed 85% of the green biomass of a *Themeda-Pennisetum* tall grassland over a 2–3 week period. This stimulated leafy grass regrowth and increased the green biomass concentration. In contrast, green biomass declined as grass became senescent in nearby areas protected from wildebeest grazing. Thomson's gazelle maintained their preference for areas previously grazed by wildebeest up to 6 months after the passage of the wildebeest, well into the dry season. McNaughton (1984) demonstrated furthermore that grassland productivity, as well as the green leaf concentration within swards, was enhanced by quite high levels of grazing. However, Wilmshurst and Fryxell (unpubl.) found that there was a subsequent competitive impact on gazelles, as a result of the reduction in grass standing crop brought about by the grazing impact of the wildebeest.

Working on the Isle of Rum, Scotland, Gordon (1988) found that areas grazed by cattle (*Bos taurus*) during winter had a significantly higher standing crop of green vegetation in e spring, and had proportionately more green than dead material, than areas protected from cattle grazing. He observed that red deer (*Cervus elaphus*) in spring preferred to feed in areas that had been grazed previously by cattle during the preceding winter.

Hobbs et al. (1996) investigated the effects of winter grazing by elk (*Cervus elaphus canadensis*) on cattle grazing during spring and early summer in sagebrush grasslands in Colorado. The study was conducted ex-

perimentally using exclosures with elk stocked at different densities. Prior grazing by elk enhanced the nitrogen content and digestibility of the forage available to cattle, and the nitrogen content of cattle diets. However, under high elk stocking density, the improvement in dietary quality was counterbalanced by a substantial reduction in the daily dry matter, digestible energy and protein intake of the cattle, as a consequence of reduced carryover of dead perennial grass from year to year (Hobbs et al. 1996). Notably, spatial partitioning in patch use was precluded.

In summary, evidence suggests that feeding facilitation can occur through the improved forage quality of grass regrowth, rather than simply through increased resource access through the removal of obstructing grass structures. Such facilitation would therefore occur during the growing season for the vegetation.

Population facilitation

Both Vesey-Fitzgerald and Bell implied that feeding facilitation would translate into improved population performance for species grazing later in the succession. Vesey-Fitzgerald (1960) suggested that the presence of elephants promoted greater numbers of medium-sized herbivores in the Lake Rukwa region, while Bell (1970) postulated that a decline in zebra abundance in the Serengeti ecosystem could lead to a reduction in wildebeest numbers. Changes in herbivore populations in the Serengeti over the past 25 years have not supported the latter expectation. Wildebeest have increased almost four-fold, while zebra numbers have remained stationary (Sinclair and Norton-Griffiths 1982, Dublin et al. 1990, Putman 1996), indicating little or no interdependency.

Although feeding facilitation was demonstrated to benefit Thomson's gazelle in the short term (McNaughton 1976), the large increase in wildebeest in the Serengeti ecosystem has also not resulted in an increase in the Thomson's gazelle population (Sinclair and Norton-Griffiths 1982, Dublin et al. 1990).

Following the recent elimination of buffalo from the northern and western regions of the Serengeti National Park through poaching, topi, impala (*Aepyceros melampus*), and possibly oribi (*Ourebia ourebi*), have increased in abundance. Thus competition rather than facilitation is suggested, although the population changes of the smaller species could also be due to release from predation (Sinclair 1985).

On the Isle of Rum, Gordon (1988) found that red deer produced more calves per female after 1971, when cattle were introduced, than over the period from 1957 to 1971 while cattle were absent. Improved calf production could potentially lead to higher population abundance, but this was not demonstrated.

In another temperate zone study, Putman (1996) assessed evidence for competition or facilitation within a species assemblage including cattle, ponies (*Equus caballus*), red deer, sika deer (*Cervus nippon*), fallow deer (*Dama dama*), and roe deer (*Capreolus capreolus*) in the New Forest, England. Changes in fallow deer numbers were negatively related to the numbers of cattle and ponies pastured in the forest in the previous year, clearly negating any population-level facilitation from these larger grazers.

Although facilitation has been widely accepted as an important structuring force of grazing ungulate communities, we found no evidence that feeding facilitation has anywhere been translated into an increase in population abundance.

Habitat facilitation

The vegetation changes induced by the feeding and destructive impacts of megaherbivores, (species weighing > 1000 kg as adults) can alter habitat structure, to the benefit or detriment of other species. Notably, the cascade of extinctions throughout northern Eurasia and the Americas during the late Pleistocene encompassed not only all megaherbivores, but also many medium-sized mammalian herbivores less vulnerable to human hunting pressure (Alroy 2001). This suggests that the medium sized species may have benefited from the habitat structure promoted by megaherbivore impacts on vegetation (Owen-Smith 1987).

The propensity of elephants to transform savanna woodlands into either open parkland or shrubland, depending on underlying soil type, is well known (Laws 1970, Bell 1981). The vast increase in elephants in the Tsavo region of Kenya during the 1960s, and consequent opening of dense shrubland, was followed by increases in the abundance of grazers like oryx (*Oryx gazella*) and zebra, while browsers such as lesser kudu (*Tragelaphus imberbis*) and gerenuk (*Litocranius walleyi*) declined (Parker 1983). Declines by some grazing ungulates, plus increases by browsers, in the Hluhluwe Game Reserve in South Africa were attributed to habitat thickening following the extermination of elephants a century earlier (Owen-Smith 1989).

Grazing hippopotamus (*Hippopotamus amphibius*) and white rhinoceros (*Ceratotherium simum*) can likewise transform tall grass grasslands into extensive grazing lawns (Olivier and Laurie 1974, Owen-Smith 1988). Elimination of hippos from the Mweya Peninsula region of the Queen Elizabeth National Park, Uganda, was followed by a substantial increase in elephant, buffalo and waterbuck (*Kobus ellipsiprymnus*), species favouring tall grass, after the lakeshore grassland had recovered from the short state maintained by hippo grazing (Eltringham 1974). Following the recovery of

the hippo population, numbers of these three species reportedly declined in this region. The increase in white rhino abundance in the Hluhluwe-Umfolozi Park in South Africa was associated with declines by reedbuck (*Reduca arundinum*) and waterbuck, both dependent on tall grass (Owen-Smith 1988). Species preferring short grass, specifically wildebeest, zebra, impala and warthog (*Phacochoerus aethiopicus*) have maintained or increased their abundance.

Wild ungulates the size of buffalo (ca 600 kg) and smaller do not appear responsible for large scale habitat changes in African savanna ecosystems, except in situations where predators were eliminated, movements confined by fencing to small areas, or locally in the vicinity of water points (Cumming 1982). This generalization does not apply to domestic cattle stocked at high densities by sedentary pastoralists (du Toit and Cummings 1999). Nevertheless, hare (*Lepus europaeus*) browsing was found to slow the succession of shrubs for > 25 years, benefiting the grazing of Brent geese (*Branta bernicula bernicula*) (van der Wal et al. 2000).

Hence, there seems to be sufficient evidence demonstrating population responses by herbivores in response to facilitative habitat alteration by other species, in some situations. However, habitat facilitation is not restricted to the major vegetation impacts caused by the very largest herbivores.

Temporal tradeoffs

Beneficial effects of grazing impacts on grass production, green leaf concentrations, sward bulk density and nitrogen cycling have been convincingly demonstrated (McNaughton 1984, 1985). The consequent enhancement of energy flow through improved forage quality may have contributed to the high abundance of wildebeest in the Serengeti ecosystem, and of white rhinos in the Hluhluwe-Umfolozi Park, through their own grazing impacts (i.e. self facilitation) (Owen-Smith 1988). Why have positive consequences for population levels of other large herbivore species not been found?

One possible explanation is the confounding effect of predation, where for example higher wildebeest numbers in the Serengeti promote greater predator abundance, thereby having a negative impact on the population levels of zebra and Thomson's gazelle (McNaughton 1984, 1985, Sinclair 1985).

An alternative explanation that we propose involves the seasonal tradeoff between facilitation and competition. The grazing impacts of white rhino and wildebeest promote improved grass quality for other grazing herbivores during the wet season, enhancing reproductive performance. However, as a consequence less grass remains to support the latter species through the dry season, restricting population levels.

Klein (1965) noted that for deer (*Odocoileus* spp.) in North America, population abundance is determined primarily by the amount of food remaining during late winter, affecting over-winter survival. In contrast, food quality during early summer governs individual growth and physical condition, and consequently reproductive success (Klein 1965). Owen-Smith (1990) found that the calving success of greater kudu under African savanna conditions was determined largely by rainfall over the preceding wet season, possibly promoting the production of high quality forage in the form of forbs. On the other hand, the overall population density of browsers like kudu is determined largely by the amount of forage retained through the late dry season (Owen-Smith 2002).

Hence, we suggest that interspecific competition predominates during the dormant (winter or dry) season, when forage of adequate quality becomes progressively depleted. The effects of such competition can be ameliorated by feeding facilitation arising from enhanced food quality during the growing season, improving recruitment success. The overall demographic consequence depends on the balance between these temporal tradeoffs. Thus, although evidence for either feeding facilitation or competition may be found at one time of the year, the anticipated population consequences need not necessarily follow. We do not exclude the possibility that "apparent competition" mediated through shared predators may be an additional influence. Susceptibility to predation can, however, be dependent largely on nutritional status (Sinclair and Arcese 1995).

Spatial partitioning of resources

Trophic interactions among herbivore species of differing body size take place within a complex spatial mosaic, most especially for grazing ungulates within African savannas (McNaughton 1983, 1989). Small species could potentially out-compete larger species within the habitat types they occupy, through their feeding effects on resource abundance or quality during the dormant season. However, small herbivores tend to be localized in their distribution, because of their need for high-quality forage, while large species forage less selectively across a range of vegetation types (du Toit and Owen-Smith 1989). The effect of competition by smaller species on the forage quantity and quality obtained by larger species is thus restricted in its spatial extent. Moreover, because large species forage through the high quality patches favoured by small species while sufficient food remains on offer, they reduce the amount of food left to support smaller species through the dormant season. Hence, competition is a two-way process, but somewhat localized in its occurrence.

Conclusions

Feeding facilitation arises mainly during the growing season, when grazing by larger species may stimulate vegetation regrowth and hence temporarily improve forage quality for other species. Improved reproductive success may result. Counterbalancing this is a reduction in the amount of forage remaining to support populations through the dormant season, with mortality heightened as a result. While competition and facilitation may be manifested through short term consequences for foraging efficiency, the effects on population dynamics may be suppressed through seasonal tradeoffs and spatial localization. The population outcome depends on the overall regime over the annual cycle. We conclude that feeding facilitation in the growing season can act to ameliorate the exploitative competition that comes into operation during the dormant season, and that this is an important mechanism promoting species coexistence within grazing herbivore assemblages.

Acknowledgements – We acknowledge helpful comments, suggestions and criticisms on previous drafts of this manuscript from Andrew Illius, John Wilmshurst, Iain Gordon and Johan du Toit, and in review by Herbert Prins and John Fryxell.

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