Introductory Research Essay

Coexistence in Ungulate Communities: Niches, Resource Partitioning, Competition & Facilitation

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Abstract

The coexistence of species is a fundamental concept studied in ecology. Inherent within it are the concepts of a niche and resource partitioning. In this review I will define these basic concepts and examine how they have been studied using ungulates as a model system. Specifically, I will discuss resource use in ungulate systems and how those resources are partitioned across space and time. I will also discuss important factors in studying the coexistence of ungulate communities, namely the roles of physiology, body mass, and landscape variation. I will also briefly go over the newer, genetic methods are now available to answer more in depth questions on the mechanisms maintaining coexistence within these communities.

I.   Introduction

The diversity of life is astounding. Earth holds approximately 8.7 million unique species (Mora et al. 2011). A central question within ecology asks, what maintains this diversity of species? How do so many species coexist? There are different ways to answer this question depending on one's point of view. Some explanations focus on the role of predation in coexistence. Others explore the roles of parasites and viruses. At one level, one can explain coexistence based on availability and diversity of resources. The mechanisms of predation, parasites/diseases and resources are not necessarily mutually exclusive, because for example, predator/prey coexistence may influence intraguild resource-based interactions. Here, I will focus on resource-based theories and the mechanisms behind coexistence at the guild level, ie. species having overlapping resource requirements. I will explore the theoretical background on coexistence, specifically niche theory, wherein I define central concepts such as resource partitioning, spatial and temporal aspects of niche partitioning, and the relative roles of competition versus facilitation. For the main discussion, I will explore how these concepts have been applied to understand intraguild species coexistence patterns of ungulates. Specifically, I will compare and contrast theories and evidence for grazing versus browsing species assemblages and focus on the roles of body size, physiology, and landscape variation in structuring these assemblages.

II.   Niche Theory

The concept of a niche is central to ecological theory yet it has classically had alternative definitions. Grinnell (1917) defined a niche as a species' biogeographic distribution based on several factors such as abiotics, food preferences, and microclimates that are optimal for a certain species survival. Elton (1927) gave niches functional roles, such as the pollination niche of a bee, and thus the Eltonian niche is more related to a species' position in ecosystems and food webs. Hutchinson (1959) theorized a niche based on an n-dimensional space where axes may represent a variety of factors, such as access to water, temperature, season, habitat selection, etc, all of which are required for the species to survive and reproduce. In contrast to Grinnell's niche, Hutchinson takes into account the roles of other species in niche evolution. Essentially, Grinnell's niche can be thought of as the fundamental niche where a species can theoretically be expected to thrive without interference from other species, while Hutchinson introduced the realized niche of a species based on the constraints of other interacting species.

Through natural selection, sympatric species that interact are theoretically expected to evolve niche separation and resource partitioning to reduce competition. Competition is a driving force in the evolution of adaptations that enable niche partitioning and experimental evidence suggests that the more diverse the community the stronger the divergence of character traits, such as body mass. For example, bacterial species tend to evolve more diverse traits when in polycultures compared to monocultures (Lawrence et al. 2012). So a central question is, how similar can multiple species be in their niches and yet avoid competition and maintain stable coexistence? One of the classic dimensions of niche separation is the partitioning of resources by organisms.

III.   Resource Partitioning

What is a resource? A resource can be food, water, light, and breeding places, among other things. Species can partition these resources across space and time. In his review of 81 studies on resource partitioning, Schoener (1974) identified food, space, and time as important niche dimensions enabling coexistence. In general, habitat was the most important, food was second, and time was considered the least important relative to habitat and food.

Darwin's finches provide a well-known example of coexistence via food partitioning based on seed size and corresponding bill shape/length (Grant 1986). Each species of finch has evolved adaptations in the form of beak shape and size to eat certain seed types. So, small finches with small beaks are unable to eat the large seeds which are eaten by larger finches. Five species of marine cave-dwelling mysids appear to coexist stably under resource-poor conditions by a strong pattern of dietary partitioning (Rastorgueff et al. 2011). Two zooplankton predators (*Anisops sardea* and *Tilapia rendalli*) eat the same species of Daphnia, but appear to coexist by differentiating their prey based on size (Lindholm and Hessen 2007) and this was also seen within sardine (*Sardinops sagax*) populations (Espinoza et al. 2009). Herons (*Egreta caerulea*) and Scarlet Ibises (*Eudocimus ruber*) both forage in mangrove swamps, but they prey on different species of crabs (Olmos et al. 2001). These are examples of partitioning different types of food, but animals may also partition food through space and time.

A. Spatial Resource Partitioning.

The partitioning of space in the environment is most often thought of as habitat selection, or where species position themselves in a heterogeneous landscape. Connell's (1961) barnacle studies in the Scottish intertidal zone are classic examples of coexistence via spatial partitioning. He studied the interactions between *Chthalamus stellatus* and *Balanus balanoides* which actively compete for rock space. Both species are limited vertically by desiccation, but *Balanus* is more sensitive to this than *Chthalamus*. *Balanus* is found in the lower parts of the rock face and when experimentally removed, *Chthalamus* rapidly takes over this space showing that *Chthalamus'* realized niche is different than its fundamental niche when in the presence of its competitor *Balanus* (Connell 1961). While this is a classic example of habitat spatial partitioning, interacting species also partition other resources in space. For example, forest floor fungal communities exhibit vertical spatial partitioning in four distinct layers corresponding to how the fungi utilize substrates (resources) (Dickie et al. 2002). Chipmunk (*Eutamias* spp.) communities exhibit spatial habitat and resource use separation along an altitudinal gradient (Heller and Gates 1971). Giant petrels (*Macronectes* spp.) may eat the same foods, but they forage in different locations out at sea (Gonzalez-Solis et al. 2000).

B. Temporal Resource Partitioning

Resource partitioning may be temporally based, often to reduce interference competition or aggressive encounters (Carothers and Jaksic 1984). Ziv et al. (1993) determined that two

sympatric desert gerbil species (*Gerbillus allenbyi* and *G. pyramidum*) coexist via differences in peak activity times by experimentally removing one species and observing a shift in activity times of the other species. The removed species was dominant such that the subordinate species shifted its ideal foraging times to avoid aggressive encounters. Different species of dung beetles emerge from the soil at different times of the day to colonize mammalian dung, and these behaviors may reduce interference competition (Caveney et al. 1995). *Acacia* species differ in the timing of pollen release and the value of nectar rewards which allows temporal partitioning of pollinators (Stone et al. 1996).

IV. Competition & Facilitation

As Hutchinsonian niche theory suggests, species occupy realized niches based on the results of interactions with other species. These interactions may be positive (facilitative) or negative (competition). There are varying mechanisms of competition for resources, such as exploitative competition wherein one species directly depletes resources such that another species can no longer utilize them. When one species makes it difficult or impossible for another species to obtain a resource, this is termed interference competition. Species may also interfere with eachother in aggressive encounters which deplete the energy obtained from resources.

Generally competition has been defined as having three criteria. 1. Species share overlapping resource requirements. 2. Those resources are limiting. 3. The interacting species affect eachother adversely. As Putnam (1996) notes, a competitive interaction may be present if we observe a clear shift in resource use of a species in allopatry compared to sympatry, and even better evidence would be if an inverse relationship could be found between population sizes of a pair of species. But even then, those data are merely correlative and suffer from the classic problem of 'correlation is not causation'. Thus, the concrete existence of competition may be difficult to prove without experimental evidence.

Facilitation may appear in three different types, termed feeding, population or habitat facilitation (Arsenault and Owen-Smith 2002). In feeding facilitation, species assemblages may forage in sequence of eachother, with the first species aiding the second species by making forage more available. Consequently, feeding facilitation should theoretically cause increases in population numbers; this concept is termed population facilitation. Habitat facilitation refers to the changes in vegetation which may be induced by other species. The major difference between the three types of facilitation is that they operate on different time scales, wherein feeding facilitation is the shorter more immediate effect while population and habitat facilitation operate on much larger time scales and are perhaps more difficult to find evidence for. Feeding facilitation has been theorized to be in tradeoff with exploitative competition (Arsenault and Owen-Smith 2002). One species may facilitate the others foraging capabilities during the growing season via different means, but ultimately this leads to decreased resources during the winter or dry season, during which point competition is likely to be a more important force (Arsenault and Owen-Smith 2002). Subsequently, due to the counteracting forces of facilitation and competition, we may not find evidence for population facilitation in some systems. In addition, there is likely an inherent tradeoff between competition and facilitation depending on season and habitat heterogeneity. In general, species are most likely to compete during seasons of low resource abundance (such as during winter or the dry season), with less expected competition and more likelihood for facilitation in the seasons of high resource abundance. Perhaps the most in depth examination of the

tradeoffs between competition and facilitation have been done in plants (eg. Callaway and Walker 1997) where often seedlings may be facilitated through shading by other species, but when they grow larger may actively compete with the species that formerly facilitated their growth.

V.   Niche Theory & Resource Partitioning in Ungulates

I will now apply the above concepts to ungulate systems. How are multispecies ungulate systems separated into niches through resource partitioning? How does the presence of one species affect the realized niche of another species? How do competition and facilitation operate within these systems? Resource partitioning between ungulate species is directly related to differences in body size and physiology. Body size influences how ungulates partition food resources in space and time. Physiology interacts with body size to determine what ungulates will eat. However, the relative weights of these two components are widely discussed and likely are different for grazers and browsers, but further research needs to be done (especially within the browser guild).

A. Physiology & Body Size in Ungulates

Early on people observed different groups of ungulates (Hofmann and Stewart 1972). Some fed predominantly on grasses (grazers) while others ate woody plants, shrubs, fruits and leaves (browsers). Intermediate types varied between these two types of forage. Hofmann (1989) suggested physiological adaptations that were underlying the differences in food-type selection and he gave them new, perhaps more relevant, names (Figure 1). Grass/roughage eaters are capable of tolerating relatively poor quality food as they have large rumens allowing them to ferment and break down the cell walls within highly fibrous food such as grass. In comparison, ungulates with smaller rumens are less able to tolerate low quality food and so must maintain higher quality (low ratios of carbon to nitrogen) diets (such as shrubs, fruits, and leaves) and are termed concentrate selectors. The intermediate classification remains the same; these animals are much more flexible in their diets and often rely on what is available seasonally. Differences in salivary glands between the three classes are likely an evolved adaptation to plant defenses against herbivory. Salivary gland weight as a proportion of body weight is largest in concentrate selectors/browsers, medium in intermediate feeders, and smallest in grass eaters/grazers (Hofmann et al. 2008). This may indicate decreased need for production of tannin-binding salivary proteins in grazers since grasses contain very little or no tannins (Hofmann et al. 2008). In addition, microbial floras likely play a large role in how ruminants digest and glean nutrients from food. Empirical data and modeling suggest that microbial adaptations and plant chemistry maintain diet selection strategies between species (Gordon and Illius 1996). Physiological differences also influence how often ungulates need to drink water (Cain et al. 2012). Physiology hence plays a large role in maintaining ungulate species niches, in that some species are not adapted to utilize certain resources, allowing access for the one(s) that is/are adapted for it.
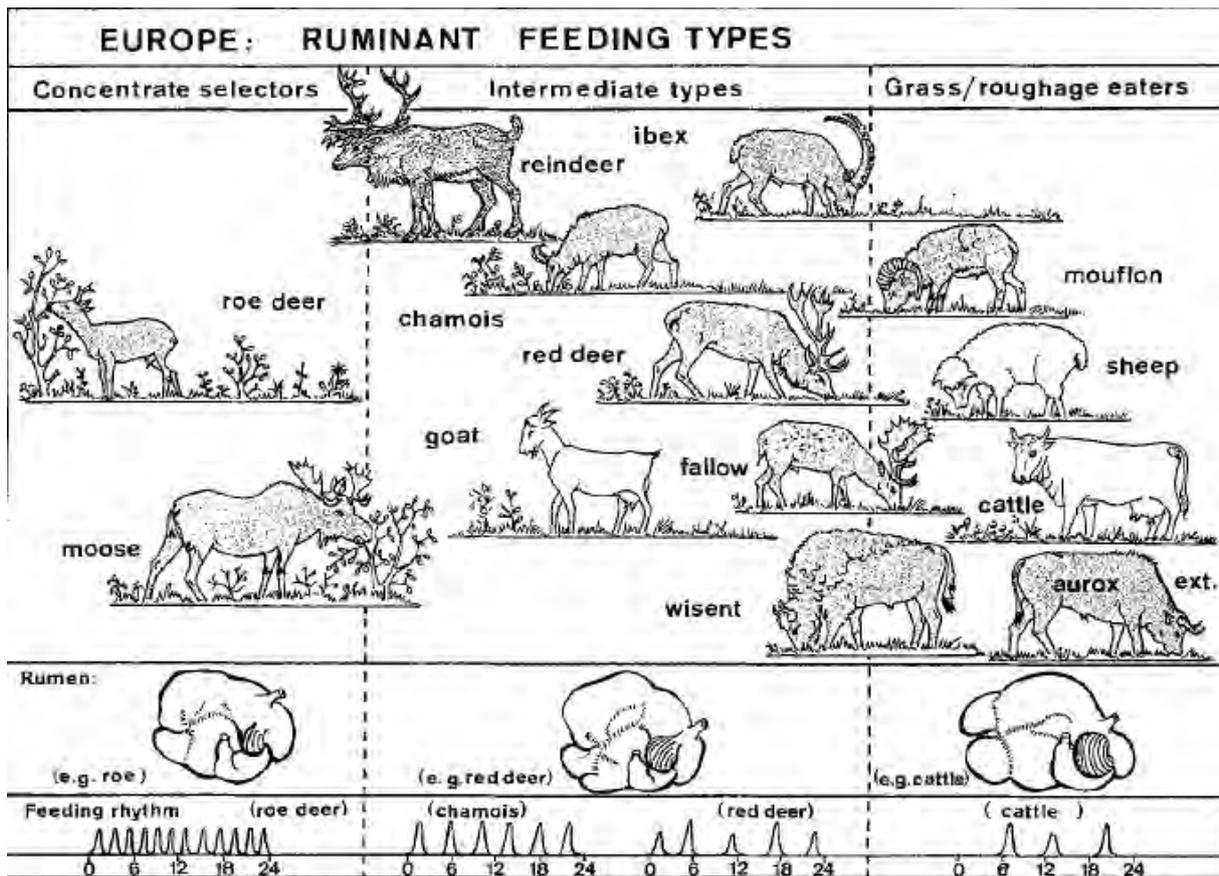
Figure 1. Classification of European Concentrate selectors, Intermediates and Grass/roughage eaters. Excerpted from Hofmann (1989).

Figure 1 is only based on ruminants. Yet, there is an important aspect of ungulate physiology that has not been discussed yet. Non-ruminants (also called hind-gut fermenters) are mostly comparable to roughage eaters (Kleynhans et al. 2011). Ruminants ferment their food in their stomachs to break it down, while non-ruminants have no fermentation system or one that is located in the caecum. Thus, non-ruminants have a faster throughput rate than ruminants, but ruminants are considered to have a more efficient system for extracting nutrients from food (Duncan et al. 1990).

In addition to gut morphology, ungulates may also have evolved to specialize on certain functional plant types based on mouth anatomy. Muzzle shape, size of mouth opening, teeth, and tongue morphology differ markedly between concentrate selectors, mixed feeders, and grass/roughage eaters. Differences in mouth anatomy allow for different levels of selectivity for certain grasses and browse, as well as differences in lengths of feeding bouts and total forage intake (Hofmann 1989).

When animals are subject to poor quality diets over long periods of time, increased body mass may be evolutionarily selected for, resulting in decreased food competition (Gordon and Illius 1996). Allometric theory is behind this logic, which states that metabolic rate declines disproportionally with increasing body mass (Kleiber 1933), while the length of the digestive tract is proportional to body mass. This means that smaller species have higher metabolic rates and energy needs than larger species and thus smaller species are more constrained by diet quality (Belovsky 1997). The logic is relatively simple in that smaller species have less room within their guts to process food than larger species, yet due to their disproportionally high metabolic rate, they must consume high quality/ high energy foods. In comparison,

larger species can still extract enough energy from larger portions of low quality/low energy food. Larger species are thus able to tolerate lower quality food based on their size (Figure 2) and they consume larger total amounts of forage in order to maintain their large size; this is also known as the Jarman-Bell Principle (Bell 1970, Geist 1974, Jarman 1974, Demment and Vansoest 1985). However, large species should still chose high quality food if it is available (Wegge et al. 2006). For example, some megaherbivores (>1000 kg) do not appear to follow the Jarman-Bell Principle in that they have been shown to consume higher quality diets than expected based on their size (Makhabu 2005, Kleynhans et al. 2011). Smaller ungulates may be less tolerant of low quality food for other reasons such as they may be more susceptible to the detrimental effects of plant secondary metabolites due to dosage effects. Thus, based on size and classification, we might expect the smallest grass/roughage eaters to be the most selective in their diets in comparison to other members of the grazer guild and the same expectation has been held for the browser guild. However, Kerley et al. (2010) found that small browsers broadened their diet to include up to 51% grass when their preferred browse was cleared away, which is perhaps counter to the body size constraint hypothesis, although they may have been very selective in their choices of certain grass species or grass parts.
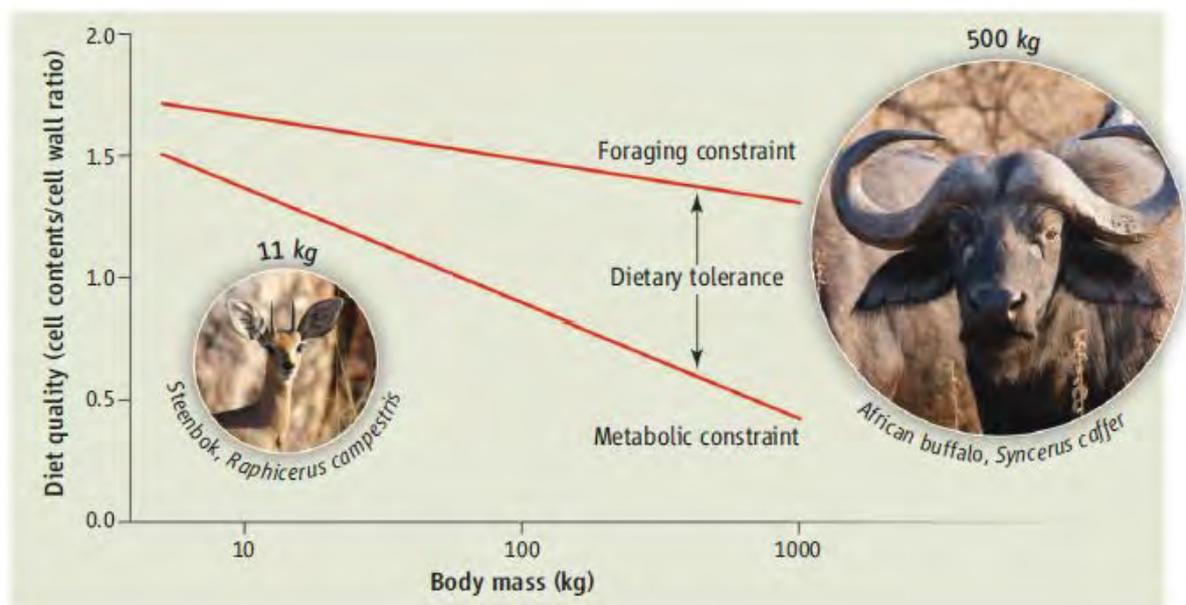

Figure 2. A graphical illustration of the Jarman-Bell Principle. Herbivores have an upper limit of what they can extract from the environment (foraging constraint) and a lower limit of what they need to survive (metabolic constraint). Along a body mass continuum, this represents dietary tolerance (du Toit 2011).

There is a debate as to the relative roles of body size and physiology in determining ungulate dietary partitioning (Clauss and Hummel 2005). Some, such as Hofmann (1989) claim that physiology is the most important, if not only, factor influencing the diversity of resource use among ungulates. However, after adjusting for the effects of body mass, Gordon and Illius (1994) found very little difference in digestive strategy between African ruminants. Most likely, digestive physiology and body mass interact in determining ungulate niches and species coexistence (Illius and Gordon 1992).

B. Spatial Resource Partitioning & Body Mass

Spatial niche partitioning in ungulate systems likely occurs via differences in species patch selection. Landscape variation allows for patches of differing food quality, but this varies seasonally (Macandza et al. 2012). Some geographical features allow for herbivores to hide from potential predators and are often unevenly distributed. Water is also an important resource, especially when it is limiting, and it influences how ungulates partition space (Cain et al. 2012). Body mass is expected to influence how ungulates partition space (eg. Figure 3). Larger body mass often indicates dominance in interspecific interactions (Ceacero et al. 2012). Differential species patch selection may be a result of interference competition (Ferretti et al. 2011b). In addition, because of their expected ability to eat lower quality food, larger ungulate species are hypothesized to utilize a broader range of habitats than smaller species, and larger species are expected to forage at the coarsest of scales. Cromsigt et al. (2009) found that smaller ruminants tend to have patchy distributions within the landscape, whereas larger ruminants and all sizes of non-ruminants tended to be more evenly distributed; the latter result indicates an interaction between body size and physiology. However, experimental testing of patch-selection showed the larger species (zebra and white rhino) graze at the fine-grained plots and smaller species (warthog and impala) chose the coarse-grained plots (Cromsigt and Olff 2006). This may show that other factors are in effect such as predation risk, wherein the smaller species may select the larger plots for better predator awareness. This also indicates that grazers tend to partition the landscape at multiple spatial scales (Cromsigt 2006) but the effect of body mass is not fully clear. Comparatively, there are few studies on space use and patch-selection within browser guilds, other than research into interference competition between roe and fallow deer (Ferretti et al. 2011a, Ferretti et al. 2011b). More research into spatial partitioning of species of divergent body mass and feeding type will likely better elucidate mechanisms of coexistence between ungulate species (Richard et al. 2012).
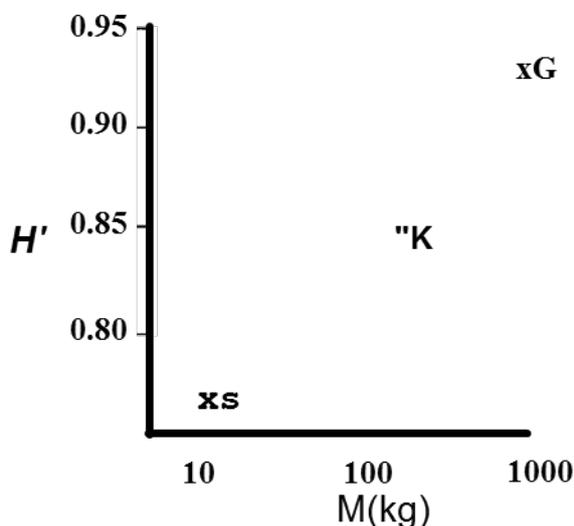

Figure 3. Body mass influences how ungulates utilize space. Y-axis is diversity of habitat use and X-axis is mass for three species of browsing ruminants: S = steenbok, K = kudu, G = giraffe (du Toit and Owen-Smith 1989).

C. Temporal Resource Partitioning: Seasons of Plenty and Limiting Resources

Ungulate diet partitioning varies throughout the year. Many studies show that dietary overlap is highest during seasons of plenty, whereas dietary partitioning more likely occurs during the season where resources are limiting (Mysterud 2000, Kleynhans et al. 2011). For example, depending on the season, cattle and mule deer in British Columbia are expected to have varying levels of dietary overlap, with the highest probability of competition in May, when mule deer eat large proportions of grass (Willms et al. 1976, Willms and McLean 1978). However, over time as resources become limiting, cattle and deer become more specific to their own niches. Cattle continue to eat primarily grass towards the end of summer whereas deer prefer to feed on shrubs such as willow (Willms et al. 1980). Differential overlap in browse: graze ratios within ungulates depending on season and availability of food has also been noted within Indian populations of chital, sambar, gaur and elephant (Ahrestani et al. 2012) and Spanish populations of red and fallow deer (Azorit et al. 2012). If we look at another resource (water), zebra and sable showed temporal differences in frequencies of returning to watering holes (Cain et al. 2012).

VI.   Competition & Facilitation: Grazing Successions, Browsing Successions?

In ungulate systems, diets often overlap to large extents, in that sympatric species often consume similar plant species and plant parts and often forage at similar times and patches. This may suggest that ungulate assemblages are actively competing, but dietary overlap does not necessarily give evidence for competition. High overlap may suggest competition, but only if resources are limiting. On the contrary, high overlap may also suggest a lack of competition in that the assemblage of species may be coexisting via an alternative partitioning of niche-space. Competition may only become apparent in the case of introduced species, wherein there is a lack of evolutionary history between the species (see refs on the introduced Chinese muntjak in England: Chapman et al. (1985), Chapman et al. (1993)).

Grazing successions have been observed in many systems and are the classic examples of facilitation in ungulate systems (Vesey-Fitzgerald 1960, McNaughton and Georgiadis 1986, Gordon 1988). For example, cattle-deer relationships have been well studied by Willms *et al* in south central British Columbia and show evidence for facilitation. Willms and McLean (1978) observed deer with diets of high proportions of grass during early spring (March-May). They found a distinct preference by mule deer for Sandberg bluegrass (*Poa sandbergii*), with less use of bluebunch wheatgrass (*Agropyron spicaturm*). Both grass species have similar green-up times and nutrition content, but the wheatgrass species tends to have tillers over old-growth making barriers to the more palatable new growth. Willms et al. (1979) found that mule deer will prefer to feed on fields abundant with wheatgrass when the fields had been grazed by cattle the previous fall. This indicates a grazing succession and facilitation in that the cattle consume the roughage parts of the grass, facilitating deer consumption of the more palatable growth the following spring.

Competition and facilitation may be operating in the same system yet have differing weights depending on the season. In an African system, wild ungulates compete with cattle during the dry season wherein there are limiting resources, yet they facilitate cattle during the wet season of plenty (du Toit 2011). This was evidenced through experimental treatments with only cattle

(C), cattle and wild ungulates without megaherbivores (WC), and cattle with wild ungulates and megaherbivores (MWC). Cattle weight gain decreased in the WC and MWC treatments during the dry season, but increased in the same treatments during the wet season (Odadi et al. 2011). A similar tradeoff between competition and facilitation during the alternating wet and dry seasons has been proposed in a Nepalese system of ungulates, but has not been tested empirically (Wegge et al. 2006).

The browsing literature has very little discussion of facilitation, despite the notion that facilitation in browsing guilds may be easier to find evidence for since shrubs and trees are discrete units, making patches easier to define. The main difficulty in observing and quantifying browsing behaviors in multispecies assemblages is the lack of visibility in forests. There is some evidence for facilitation within the browsing guild (albeit from cross taxa). Dawson et al. (1990) found in two distinct sites that Rocky Mountain mule deer in their winter range prefer foliage from more mature Douglas fir trees with stem diameters greater than 25 cm over regeneration sized trees less than 5 cm in stem diameter. Similar observations have been noted for Columbian black-tailed deer (Silen et al. 1986). A reason for this preference could be related to plant chemistry in that regeneration sized trees may have higher concentrations of secondary metabolites (Swihart and Picone 1998). This preference has led other researchers to hypothesize on a potential facilitatory role of Red Squirrels (*Tamiasciurus hudsonicus*) for mule deer. Red Squirrels are likely to supply a winter source of clipped Douglas-fir twigs to mule deer (and other ungulates) through their own foraging and clipping of twigs for buds and cones (Rea et al. 2011). However, mule deer may have to compete for this preferred forage when other large herbivores are present. In a captive dietary study (albeit with low sample size), mule deer ate disproportionately low amounts of their preferred food source when in the presence of moose and elk, which may be indicative of dominance interactions in the wild as well (Rea et al. 2011).

In Fennoscandia there is much less research into browsing competition and facilitation, but there are some indications of it (Mysterud 2000). Such as, browsing may increase primary production through compensatory regrowth, possibly facilitating future herbivory (McNaughton 1983). But, intense browsing may decrease cover for hiding neonates (Loft et al. 1987). Moose may facilitate smaller species, such as roe deer, by providing trails in the snow. Roe deer have been observed using moose trails in particularly harsh winters (Cederlund et al. 1980).

Are the relative roles of competition and facilitation in ungulates driven by differences in body size or physiology? Mysterud (2000) tested this in the browsers of Fennoscandia and found no relationship between the degree of dietary overlap and body mass, but there was a tendency for differences in feeding type (physiology) to be correlated with degrees of dietary overlap. Since these data are only on overlap, competition is only suggested, but not proven. For better resolution of this system, other niche axes likely need to be taken into account such as the roles of spatial and temporal partitioning and the fitness of individuals with and without competing species. For grazing systems, competition and facilitation are perhaps better studied. The nutrition content of grasses decreases with height (Mattson 1980) and analyses of the grazing succession in the Serengeti report that the larger species consume proportionally more lower quality food such as grass stem than higher quality food such as leaf, which is preferred by the smaller species (Makhabu 2005). These findings spawned the theory that the larger species may facilitate smaller species by consuming all the roughage from above, revealing higher quality forage below for the smaller species. However, in some cases the height at which animals graze does not seem to be related to body mass (Arsenault and Owen-Smith 2008).

Smaller species have also been hypothesized to be superior competitors because they may be able to subsist on sparser, shorter vegetation. Thus, the question of competition or facilitation gets turned around in that it may be that the smaller species are consuming the higher quality foods from below, pushing the larger species to eat the lower quality foods located above. For a browsing system, the tallest species (giraffe) were found to forage proportionally longer in the upper parts of the canopy despite that they can reach the lower parts as well (Woolnough and Du Toit 2001). Facilitation was ruled out in this system because the giraffe bites were far beyond the reach of the smaller species; instead the smaller species took smaller, more selective bites in the lower canopy, making it less profitable for a giraffe to also forage in this layer (Woolnough and Du Toit 2001). In another African study, browsers and mixed feeders of differing sizes tended to take selective bites lower in the canopy, but when those were depleted, they shifted their bites upward (Makhabu 2005). As an example of this, Figure 4 depicts a browsing line in an African system. In reality, there is likely to be a mix of both small species outcompeting larger species for the higher quality forage down below as well as larger species consuming larger amounts of lower quality food from above and potentially facilitating the smaller species.

Figure 4. Browse line in an African system. Photo credit: Göran Spong.

VII. New Study Methods

In general, interspecific dietary overlap complicates foraging studies and determination of species niches. Each species requires its own management and conservation plan, thus determination of species specific dietary preferences and requirements is necessary, but often in the field it is difficult to partition these preferences between species, especially within the browser guild (Krannitz and Hicks 2000, Serrouya and D'Eon 2008). This is where browsed twig environmental DNA (biteDNA) could play a powerful role by disentangling the preferences of individual browser species as well as definitively placing foraging locations, currently not feasible via pellet, telemetry and tracking studies (Nichols et al. 2012). The biteDNA method is relatively simple, wherein twigs that have been bitten or browsed by ungulates (Figure 5) are collected from the environment and taken back to the laboratory where DNA is extracted and amplified, ultimately identifying which species ate that specific twig. While faecal and rumen analyses have yielded extensive data on classifying diets, they still do not reveal where the animals actually forage. Thus, new data via browsed twig environmental DNA promises to give new insights into browsing dynamics of multispecies assemblages (Nichols et al. 2012). With this more detailed knowledge about interspecific dietary overlap and the degrees of spatial and temporal partitioning among ungulate species, more informed management strategies can be implicated.

Figure 5. An example of a twig that is collected for biteDNA analysis. The top 2-3 cm are collected for DNA extraction and amplification to determine which ungulate species ate the twig. Other site specific data are also collected. Photo credit: Vera Steinberg.

VIII. Conclusion

In this review I have discussed coexistence in terms of the partitioning of resources across space and time using ungulates as a model system. Inherent in using this system, I have examined the importance and evidence for the roles of body mass and physiology which interact across space and time to determine the patterns of resource partitioning. The main message is that animal communities are constantly in flux and niche spaces are thus multi-dimensional and highly dynamic. Positive and negative interactions (facilitation and competition) are constantly changing and shaping the animals and their niche spaces through time (seasons) and space (habitats). Of course, no two species or model systems are alike, but by looking at the underlying rules of one thoroughly studied system, one might be able to generalize to other animal systems. Specifically, by utilizing new methods (eg. biteDNA) we can ask new questions that may reveal these underlying rules.

References

Ahrestani, F. S., I. M. Heitkönig, and H. H. Prins. 2012. Diet and habitat-niche relationships within an assemblage of large herbivores in a seasonal tropical forest. Journal of Tropical Ecology **28**:385-394.

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

Arsenault, R. and N. Owen-Smith. 2008. Resource partitioning by grass height among grazing ungulates does not follow body size relation. Oikos **117**:1711-1717.

Azorit, C., S. Tellado, A. Oya, and J. Moro. 2012. Seasonal and specific diet variations in sympatric red and fallow deer of southern Spain: a preliminary approach to feeding behaviour. Animal Production Science:-.

Bell, R. H. V. 1970. The use of the herb layer by grazing ungulates in the Serengeti. Pages 111-124 *in* A. Watson, editor. Animal populations and relations to their food resources. Blackwell, Oxford.

Belovsky, G. E. 1997. Optimal foraging and community structure: The allometry of herbivore food selection and competition. Evolutionary Ecology **11**:641-672.

Cain, J. W., N. Owen-Smith, and V. A. Macandza. 2012. The costs of drinking: Comparative water dependency of sable antelope and zebra. Journal of Zoology **286**:58-67.

Callaway, R. M. and L. R. Walker. 1997. Competition and facilitation: A synthetic approach to interactions in plant communities. Ecology **78**:1958-1965.

Carothers, J. H. and F. M. Jaksic. 1984. Time as a niche difference - the role of interference competition. Oikos **42**:403-406.

Caveney, S., C. H. Scholtz, and P. McIntyre. 1995. Patterns of daily flight activity in onitine dung beetles (Scarabaeinae: Onitini). Oecologia **103**:444-452.

Ceacero, F., A. J. Garcia, T. Landete-Castillejos, J. Bartosova, L. Bartos, and L. Gallego. 2012. Benefits for Dominant Red Deer Hinds under a Competitive Feeding System: Food Access Behavior, Diet and Nutrient Selection. Plos One **7**.

Cederlund, G., H. Ljungqvist, G. Markgren, and F. Sålfelt. 1980. Foods of moose and roe deer at Grimsö in central Sweden. Swedish Wildlife Research **11**:167-247.

Chapman, N. G., K. Claydon, M. Claydon, P. G. Forde, and S. Harris. 1993. Sympatric populations of muntjac (muntiacus-reevesi) and roe deer (capreolus-capreolus) - a comparative-analysis of their ranging behavior, social-organization and activity. Journal of Zoology **229**:623-640.

Chapman, N. G., K. Claydon, M. Claydon, and S. Harris. 1985. Distribution and habitat selection by muntjac and other species of deer in a coniferous forest. Acta Theriologica **30**:287-303.

Clauss, M. and J. Hummel. 2005. The digestive performance of mammalian herbivores: Why big may not be that much better. Mammal Review **35**:174-187.

Connell, J. H. 1961. Influence of interspecific competition and other factors on distribution of barnacle Chthamalus stellatus. Ecology **42**:710-&.

Cromsigt, J., H. H. T. Prins, and H. Olff. 2009. Habitat heterogeneity as a driver of ungulate diversity and distribution patterns: interaction of body mass and digestive strategy. Diversity and Distributions **15**:513-522.

Cromsigt, J. P. and H. Olff. 2006. Resource partitioning among savanna grazers mediated by local heterogeneity: an experimental approach. Ecology **87**:1532-1541.

Cromsigt, J. P. G. M. 2006. Large herbivores in space: Resource partitioning among savanna grazers in a heterogeneous environment. University of Groningen, Wageningen.

Dawson, R. J., H. M. Armleder, and M. J. Waterhouse. 1990. Preferences of mule deer for Douglas-fir foliage from different sized trees. Journal of Wildlife Management **54**:378-382.

Demment, M. W. and P. J. Vansoest. 1985. A nutritional explanation for body-size patterns of ruminant and non-ruminant herbivores. American Naturalist **125**:641-672.

Dickie, I. A., B. Xu, and R. T. Koide. 2002. Vertical niche differentiation of ectomycorrhizal hyphae in soil as shown by T-RFLP analysis. New Phytologist **156**:527-535.

du Toit, J. T. 2011. Coexisting with Cattle. Science **333**:1710-1711.

du Toit, J. T. and N. Owen-Smith. 1989. Body size, population metabolism, and habitat specialization among large african herbivores. American Naturalist **133**:736-740.

Duncan, P., T. J. Foose, I. J. Gordon, C. G. Gakahu, and M. Lloyd. 1990. Comparative nutrient extraction from forages by grazing Bovids and Equids - a test of the nutritional model of Equid Bovid competition and coexistence. Oecologia **84**:411-418.

Elton, C. 1927. Animal Ecology.

Espinoza, P., A. Bertrand, C. D. van der Lingen, S. Garrido, and B. Rojas de Mendiola. 2009. Diet of sardine (Sardinops sagax) in the northern Humboldt Current system and comparison with the diets of clupeoids in this and other eastern boundary upwelling systems. Progress in Oceanography **83**:242-250.

Ferretti, F., G. Bertoldi, A. Sforzi, and L. Fattorini. 2011a. Roe and fallow deer: Are they compatible neighbours? European Journal of Wildlife Research **57**:775-783.

Ferretti, F., A. Sforzi, and S. Lovari. 2011b. Behavioural interference between ungulate species: Roe are not on velvet with fallow deer. Behavioral Ecology and Sociobiology **65**:875-887.

Geist, V. 1974. On the relationship of social evolution and ecology in ungulates. Integrative and Comparative Biology **14**:205-220.

Gonzalez-Solis, J., J. P. Croxall, and A. G. Wood. 2000. Foraging partitioning between giant petrels Macronectes spp. and its relationship with breeding population changes at Bird Island, South Georgia. Marine Ecology-Progress Series **204**:279-288.

Gordon, I. J. 1988. Facilitation of red deer grazing by cattle and its impact on red deer performance. Journal of Applied Ecology **25**:1-9.

Gordon, I. J. and A. W. Illius. 1994. The functional significance of the browser-grazer dichotomy in african ruminants. Oecologia **98**:167-175.

Gordon, I. J. and A. W. Illius. 1996. The nutritional ecology of African ruminants: A reinterpretation. Journal of Animal Ecology **65**:18-28.

Grant, P. R. 1986. Ecology and evolution of Darwin's finches.

Grinnell, J. 1917. The Niche-Relationships of the California Thrasher. The Auk **34**:427-433.

Heller, H. C. and D. M. Gates. 1971. Altitudinal zonation of chipmunks (Eutamias) - Energy budgets. Ecology **52**:424-&.

Hofmann, R. R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia **78**:443-457.

Hofmann, R. R. and D. R. M. Stewart. 1972. Grazer or browser: a classification based on the stomach structure and feeding habits of East African ruminants. Mammalia **36**:226-240.

Hofmann, R. R., W. J. Streich, J. Fickel, J. Hummel, and M. Clauss. 2008. Convergent evolution in feeding types: salivary gland mass differences in wild ruminant species. J Morphol **269**:240-257.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or Why Are There So Many Kinds of Animals? The American Naturalist **93**:145-159.

Illius, A. W. and I. J. Gordon. 1992. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. Oecologia **89**:428-434.

Jarman, P. J. 1974. Social-organization of antelope in relation to their ecology. Behaviour **48**:215-&.

Kerley, G. I. H., M. Landman, and S. de Beer. 2010. How do small browsers respond to resource changes? Dietary response of the Cape grysbok to clearing alien Acacias. Functional Ecology **24**:670-675.

Kleiber, M. 1933. Size of animals and utilization of food

Tiergrosse und Futterverwertung. Biedermanns Zentralblatt. B. Tierernahrung **5**:1-12.

Kleynhans, E. J., A. E. Jolles, M. R. E. Bos, and H. Olff. 2011. Resource partitioning along multiple niche dimensions in differently sized African savanna grazers. Oikos **120**:591-600.

Krannitz, P. G. and S. L. Hicks. 2000. Browsing of antelope bitterbrush (Purshia tridentata : Rosaceae) in the south Okanagan valley, British Columbia: Age preferences and seasonal differences. American Midland Naturalist **144**:109-122.

Lawrence, D., F. Fiegna, V. Behrends, J. G. Bundy, A. B. Phillimore, T. Bell, and T. G. Barraclough. 2012. Species interactions alter evolutionary responses to a novel environment. PLoS Biology **10**.

Lindholm, M. and D. O. Hessen. 2007. Competition and niche partitioning in a floodplain ecosystem: A cladoceran community squeezed between fish and invertebrate predation. African Zoology **42**:158-164.

Loft, E. R., J. W. Menke, J. G. Kie, and R. C. Bertram. 1987. Influence of cattle stocking rate on the structural profile of deer hiding cover. Journal of Wildlife Management **51**:655-664.

Macandza, V. A., N. Owen-Smith, and J. W. Cain Iii. 2012. Dynamic spatial partitioning and coexistence among tall grass grazers in an African savanna. Oikos **121**:891-898.

Makhabu, S. W. 2005. Resource partitioning within a browsing guild in a key habitat, the Chobe Riverfront, Botswana. Journal of Tropical Ecology **21**:641-649.

Mattson, W. J. 1980. Herbivory in relation to plant nitrogen-content. Annual review of ecology and systematics **11**:119-161.

McNaughton, S. J. 1983. Compensatory plant growth as a response to herbivory. Oikos **40**:329-336.

McNaughton, S. J. and N. J. Georgiadis. 1986. Ecology of African grazing and browsing mammals. Annual review of ecology and systematics **17**:39-65.

Mora, C., D. P. Tittensor, S. Adl, A. G. B. Simpson, and B. Worm. 2011. How Many Species Are There on Earth and in the Ocean? PLoS Biol **9**:e1001127.

Mysterud, A. 2000. Diet overlap among ruminants in Fennoscandia. Oecologia **124**:130-137.

Nichols, R. V., H. Königsson, K. Danell, and G. Spong. 2012. Browsed twig environmental DNA: diagnostic PCR to identify ungulate species. Molecular Ecology Resources:no-no.

Odadi, W. O., M. K. Karachi, S. A. Abdulrazak, and T. P. Young. 2011. African wild ungulates compete with or facilitate cattle depending on season. Science **333**:1753-1755.

Olmos, F., R. Silva E Silva, and A. Prado. 2001. Breeding season diet of scarlet ibises and little blue herons in a barazilian mangrove swamp. Waterbirds **24**:50-57.

Rastorgueff, P. A., M. Harmelin-Vivien, P. Richard, and P. Chevaldonné. 2011. Feeding strategies and resource partitioning mitigate the effects of oligotrophy for marine cave mysids. Marine Ecology Progress Series **440**:163-176.

Rea, R. V., D. P. Hodder, and I. Luecke. 2011. Douglas-fir clippings by American red squirrels (Tamiasciurus hudsonicus): a potential winter food source for mule deer (Odocoileus hemionus). Northwestern Naturalist **92**:72-76.

Richard, E., C. Calenge, S. Saïd, J. L. Hamann, and J. M. Gaillard. 2012. Studying spatial interactions between sympatric populations of large herbivores: A null model approach. Ecography.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science **185**:27-39.

Serrouya, R. and R. G. D'Eon. 2008. The influence of forest cover on mule deer habitat selection, diet, and nutrition during winter in a deep-snow ecosystem. Forest Ecology and Management **256**:452-461.

Silen, R. R., W. K. Randall, and N. L. Mandel. 1986. Estimates of genetic-parameters for deer browsing of Douglas-fir. Forest Science **32**:178-184.

Stone, G., P. Willmer, and S. Nee. 1996. Daily partitioning of pollinators in an African Acacia community. Proceedings of the Royal Society B: Biological Sciences **263**:1389-1393.

Swihart, R. K. and P. M. Picone. 1998. Selection of mature growth stages of coniferous browse in temperate forests by white-tailed deer (Odocoileus virginianus). American Midland Naturalist **139**:269-274.

Wegge, P., A. K. Shrestha, and S. R. Moe. 2006. Dry season diets of sympatric ungulates in lowland Nepal: competition and facilitation in alluvial tall grasslands. Ecological Research **21**:698-706.

Vesey-Fitzgerald, D. F. 1960. Grazing succession among East African game animals. Jour Mammal **41**:161-172.

Willms, W. and A. McLean. 1978. Spring forage selection by tame mule deer on big sagebrush range, British-Columbia. Journal of Range Management **31**:192-199.

Willms, W., A. McLean, and R. Ritcey. 1976. Feeding-habits of mule deer on fall, winter, and spring ranges near Kamloops, British-Columbia. Canadian Journal of Animal Science **56**:531-542.

Willms, W., A. McLean, R. Tucker, and R. Ritcey. 1979. Interactions between mule deer and cattle on big sagebrush range in British-Columbia. Journal of Range Management **32**:299-304.

Willms, W., A. McLean, R. Tucker, and R. Ritcey. 1980. Deer and cattle diets on summer range in British-Columbia. Journal of Range Management **33**:55-59.

Woolnough, A. and J. Du Toit. 2001. Vertical zonation of browse quality in tree canopies exposed to a size-structured guild of African browsing ungulates. Oecologia **129**:585-590.

Ziv, Y., Z. Abramsky, B. P. Kotler, and A. Subach. 1993. Interference competition and temoral and habitat partitioning in 2 gerbil species. Oikos **66**:237-246.