Grazing management on commercial cattle ranches: Incorporating foraging ecology and biodiversity conservation principles

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On the Ground

- Sustainable ranch management must consider not only impacts of grazing management on range condition (ecological sustainability) but also on cattle production relative to overhead costs (economic sustainability) and on biodiversity (biological sustainability).
- Rates of growth and reproduction in herbivore populations are determined by access to sufficient high-quality forage and concomitant optimal nutrition during the growing season. By contrast, maintenance of body condition and survival over the dormant season is determined by access to a reserve of adequate-quality forage.
- Rotational grazing systems rely on resting paddocks after grazing for sustaining rangeland productivity and desired species composition, yet a dilemma for managers is forage loses digestibility and nutrient concentration as it matures during rest periods.
- Grazing cattle in large, dense herds, frequently rotated through small paddocks may also compromise nutrition by increasing competition for forage and minimizing adaptive foraging movements. The economic viability of ranches is further compromised by the installation and maintenance costs of fencing numerous small paddocks across a ranch.
- We use foraging ecology principles to highlight how intensive multipaddock grazing systems can compromise cattle production while their infrastructure requirements increase overhead costs of management, thereby minimizing profits. We provide working examples of how these problems can be practically overcome while maintaining ecological sustainability.

Keywords: cattle density, forage maturation, multi-paddock grazing systems, season-long grazing.

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Introduction

Two indispensable goals of commercial cattle ranch management are long-term economic and ecological sustainability.[1,2] Ecological sustainability encompasses rangeland condition and biodiversity. Desired rangeland condition will be attained under appropriate stocking rates and grazing management strategies that yield a high cover of desired grasses for optimal grazing capacity and soil protection,[3,4] while biodiversity will be promoted by creating structural heterogeneity across the ranch through fire, grazing, and their interaction.[5-7] Economic sustainability is an equally important goal, where sustainability is determined by profitability. No matter how excellent cattle management may be in terms of developing optimal grass composition, cover, and productivity on a ranch, if running costs exceed income then the ranch is economically unsustainable and its management approach untenable. There are two key aspects determining if the income from cattle sales exceeds the overall running costs on a commercial cattle ranch (economic sustainability).[2] First, reduced income from poor cattle production will reduce profits and can jeopardize economic viability. Income from cattle production is determined not only by the number of cattle sold but also by their body condition and weight, which affects carcass quality and grading (amount paid per kilogram). This is an important point because if a rancher is having to compensate for poor income per animal by selling more cattle, then the ranching system is inefficient at best (having to sustain more cattle for no extra economic benefit) and economically unsustainable at worst. Moreover, poor body condition will result in low conception and birth rates of breeding herds,[8] undermining the production capacity of the ranch.

Second, the costs of running the ranch, if excessive, will reduce or eclipse profits, thereby undermining the economic viability of the ranch. Running costs are elevated by intensive multipaddock grazing systems requiring a large investment in extensive fencing and water reticulation for numerous paddocks, with associated maintenance costs thereafter.[2,9] Other significant costs arise from intensive multipaddock grazing systems, such as increased vehicle costs (maintenance and fuel) and labor associated with regular movement of cattle.[2] In addition, unintended costs may arise from running very large herds of cattle (>1,000), such as the costs of time and labor to sweep paddocks for lost calves that get separated from their mothers and left behind when the herd is moved to the next paddock (personal observation).

Incurring these elevated costs of intensive multipaddock grazing systems would be justifiable if their perceived advantages translated into improved rangeland condition and better animal production to offset the elevated costs of management. However, neither of these perceived advantages have been detected in meta-analyses of numerous experimental studies.[3] In this article we articulate the mechanisms through which various rangeland management strategies may influence the nutrition of cattle, which in turn influences the economic viability of a ranch through reproduction and weight gain (influencing income), as well as through influences on the running costs of the ranch and ultimately profits (income minus expenses). We outline key concepts and principles in herbivore foraging ecology and biodiversity conservation that if violated by rangeland management strategies are expected to negatively impact cattle production (economic viability) and biodiversity on commercial cattle ranches.

Foraging ecology principles and animal performance

The nutrition-reproduction principle

The effects of nutrition on conception rates of cattle are well recognized and physiologically understood[8] and have been repeatedly experimentally demonstrated.[10-12] Body condition at calving is the principle factor determining how soon a cow will reconceive and also determines the weight and health of a calf.[8] Calf size at birth and calf growth rates are indicators of the future reproductive output of a cow, which is optimized if the calf gains weight at 0.6 to 0.7 kg/day^{-1} (1.3-1.5 pounds per day) and achieves first calving by 2 years old.[8] The probability of conception in cows is optimized by good nutrition, which 1) elevates liver secretion of IGF1 hormone determining growth and maturation of ovarian follicles, 2) elevates leptin which activates the reproductive endocrine system, and 3) reduces blood concentrations of Ghrelin, which inhibits the reproductive endocrine system.[8] Similarly, growth and reproduction in wild herbivores is a function of their intake of energy, protein, and minerals during the growing season, which if not sufficiently attained can negatively affect conception rates, calf size at birth, lactation, calf growth rates, calf survival, and age at first conception.[13-17] The population productivity of wild herbivore populations is most strongly linked to calf survival, which is determined by the quality of the growing season resource.[14,15] Consequently, wild herbivores worldwide select the highest possible quality forage during the growing season, avoiding mature forage and focusing on fresh nutritious regrowth after snowmelt, fire, mowing, or grazing,[17-23] as well as in short grassland in moisture-limited habitats (shallow, upland soils, or saline soils).[19,20,24,25] It is clear, therefore, that the quality of the growing season resource is the major factor driving the productivity of herbivore populations through its effects on animal growth rates, reproduction, and calf survival.

Although we have emphasized the importance of high-quality forage during the growing season for elevating herbivore population productivity (growth and reproduction), access to a reserve of taller adequate-quality forage is essential for maintaining body weight (body stores) during the dormant season and for preventing population collapse during droughts or severe winters.[17,26-30] Access to sufficient adequate-quality forage over the dormant season maintains body weight and is also important for fetus development, because conception occurs at the end of the growing season and the fetus must develop over the dormant season. For cattle, poor nutrition over the dormant season can result in fetus abortion[31] and low calf weights at birth.[32] Thus, although the primary function of the dormant season resource is for maintenance of body stores over the dormant season, it also plays a role in elevating reproduction through its effects on fetus development.

The forage maturation-quality principle

With the understanding that wild and domestic herbivores require access to the highest possible forage quality during the growing season to maintain optimal growth and reproduction,[8,10-20] it is important to understand from a foraging ecology and cattle management perspective how forage maturation affects forage quality. Increasing height and biomass of maturing forage during the growing season results in two key effects, which combine to reduce its quality and ability to meet the elevated nutritional intake requirements of herbivores during the period of growth and reproduction. First, there are concomitant increases in structural compounds for support, such as cellulose and lignin, which reduces the digestibility and consequently the daily intake of forage by herbivores.[27,33] Second, structural carbon increasingly dilutes the concentration of energy and protein in forage (the dilution effect), resulting in less energy and protein absorbed per unit of forage digested.[34] Thus, these two forage maturation effects result in multiplicative depressive effects on daily intake of energy and nutrients—the forage maturation-quality principle (Fig. 1).[27,33,34] Nevertheless, when forage is grazed too short and low in biomass, intake rate is limited by the quantity, not the quality of forage, whereas quality limits intake rate as forage height and biomass increase beyond some optimal level (Fig. 1).[27,33] Although the optimal height and biomass of grassland leading to maximum intake rates for different herbivore species varies according to body size and mouth anatomy,[6,20,21,33] various herbivore species will select the most nutritious and digestible forage they can access, provided that biomass is sufficient to maintain optimal intake rate relative to their body size and mouth anatomy (Fig. 1).

It is important to note, however, that the strength of the negative relationship between forage maturation and forage

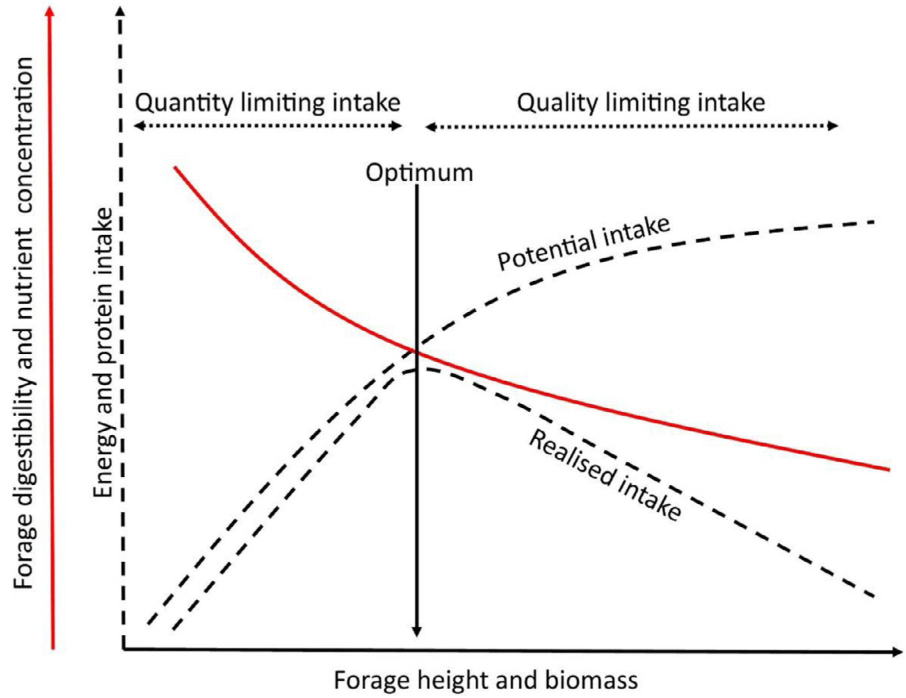

Figure 1. Conceptual model of the effect of forage maturation (increasing height and biomass) on potential food intake, digestibility, and tissue nutrient concentration (energy and protein) of forage, which affects protein and energy intake by herbivores.[27,33,34] Using the food intake model,[33] the optimal grass biomass for a 450-kg cow is estimated to be 156 g/m^2, which is well below the production potential of most grasslands, except those on shallow, dry soils.

quality is determined by grassland productivity, as influenced by the duration of plant available soil moisture over the annual cycle. Grassland productivity increases with increasing mean annual rainfall or increasing soil moisture availability through hydrological processes associated with landscape features, such as bottomlands, wet meadows (dambo's, vlei's) and floodplains,[20,35,36] with the result that grasses growing in higher rainfall regions or in poorly-drained grassland are of lower quality.[19,20,36-38] Thus, the need to facilitate higher quality grazing for cattle through burning, mowing, or grazing, which removes old stems and litter and stimulates new growth (immature, high-quality forage), increases with increasing grassland productivity (Fig. 2). For example, grazing by prairie dogs increased digestibility and protein content of grasses in short-grass steppe only at a site with above-average rainfall, whereas at lower rainfall sites their grazing effects reduced grass biomass well below the optimal level for cattle (Fig. 1) while not improving forage quality much.[37] By contrast, burning or grazing of more productive grasslands results in increased forage quality and improved animal production.[37-41] Therefore, there is increasing need for maintaining grassland in a short, immature phase by fire, grazing, or mowing (facilitation of high-quality forage) with increasing grassland productivity. This provides a general predictive principle for determining whether cattle ranches require facilitation of grazing (Fig. 2). For example, in high rainfall grasslands (>700 mm [27.6 inches]), such as tallgrass prairie (United States) or sourveld (South Africa and Zimbabwe), cattle are likely to experience decreased growth and reproduction if they are continually moved between paddocks where grasses have been allowed to mature during a recovery period of several months before grazing (Figs. 2 and 3A). Although less of a priority than in high-rainfall areas, cattle will also benefit from facilitation of high-quality forage through fire, grazing, or mowing in semi-arid areas with intermediate rainfall (400-500 mm [15.7-19.7 inches]),[41] while in arid regions (<300 mm [<11.8 inches]) fire, grazing, or mowing may even reduce cattle performance because forage quantity becomes the major factor limiting intake (Fig. 1).[37]

The functional resource heterogeneity principle

Exclusive emphasis on factors influencing foraging decisions at the local scale during the growing season excludes consideration of how foraging decisions are influenced across seasons and years. Inherent environmental gradients, such as spatial variation in aspect, elevation, annual rainfall, geology, and topography/hydrology influence soil texture, soil fertility, and soil moisture availability, with associated effects on grassland phenology, height, and productivity.[18-20,35-38,42] In turn, these environmental gradients influence spatial heterogeneity across landscapes in the quantity and quality of forage (digestibility, energy, protein, and minerals), its seasonal availability and greenness, forage species composition, and plant diversity, which provide functional resource heterogeneity and associated adaptive foraging options for herbivores.[18-20,24,25,36] Short, high-quality forage is found in moisture-limited habitats, such as low rainfall saline areas and shallow soils in uplands, whereas taller reserves of forage for the dormant season are found in more productive

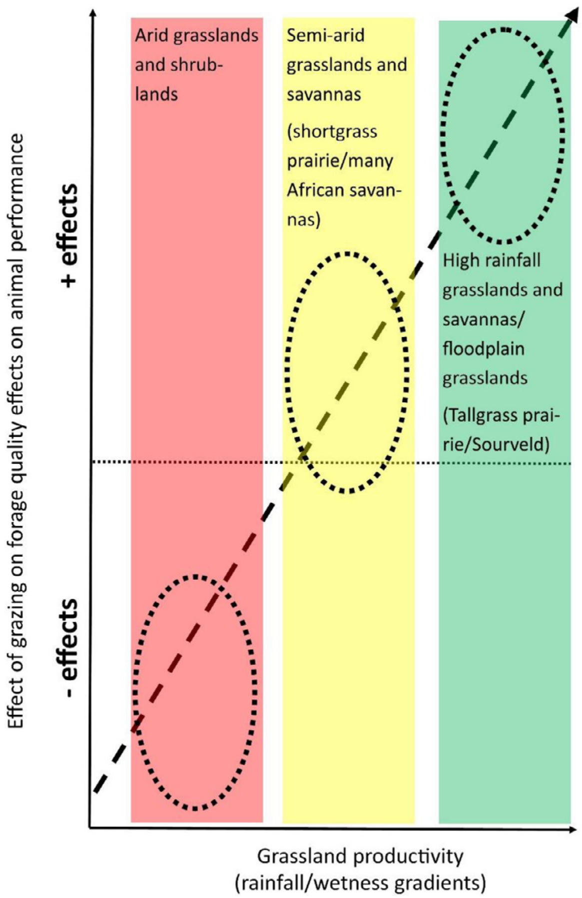

Figure 2. The effect of grassland productivity on the need to use fire, grazing, or mowing to prevent grassland maturation and severe loss of forage quality (grazing facilitation) with an associated negative impact on cattle weight gain and conception rates.

wetter habitats, such as in valley bottomlands, wet meadows (dambo's, vlei's), and floodplains.[18-20] Additional variation is introduced by transient environmental factors, such as patchy rainfall, fire, and grazing events and snowmelt waves on altitudinal and aspect gradients, which create immature, high-quality forage.[18,21-23,39-41] Functional resource heterogeneity facilitates adaptive foraging options for herbivores in the face of seasonal and inter-annual variability in forage resources and seasonal variability in their resource intake requirements. Consequently, functional resource heterogeneity ensures that herbivore populations can grow to high levels through access to short, high-quality forage to meet elevated demands for energy, protein, and minerals during the growing season when females are pregnant and lactating or calves are growing.[17,27,28] During the dormant season herbivores can maintain body stores through access to reserves of taller adequate-quality forage during adverse periods, such as in severe winters or during the hot late dry season and droughts of tropical and subtropical savanna environments.[17,19,20,24,25,28] In this regard, a central aspect of functional habitat/resource heterogeneity is grassland structural heterogeneity, which represents a continuum from short, high-quality grassland for maximizing intake of energy and nutrients for growth and reproduction over the growing season to taller, adequate-quality grassland as a reserve of forage for the dormant season and droughts. Adaptive foraging over the annual cycle along this continuum of grassland structural states results in more productive and stable herbivore populations.[26-30]

The herd size/density–nutrition principle

Apart from forage maturation, three additional factors, 1) foraging at high densities, 2) small paddocks, and 3) rapid rotations between paddocks (short occupancy period), are also predicted to reduce diet quality for cattle. Across a range of herbivore species it has been shown that increasing herbivore density beyond some critical level results in increasing competition for quality forage, which is a result of increasing probability of encountering forage plants already consumed, trampled, or fouled by another individual as well as by interference in the ability to move away from competitors to find unoccupied patches (Fig. 3B).[43-45] Searching time is buffered by chewing time up to some critical herbivore density beyond which searching time exceeds chewing time and forage intake is reduced.[44] A strategy of forcing cattle to forage at high density in small paddocks is, therefore, expected to reduce forage intake. Density values for where forage intake and growth rates of cattle have been observed to be negatively impacted are 6.4 steers per hectare (~3 steers per acre) under short duration grazing compared with 0.8 steers per hectare (~0.3 steers per acre) under continuous grazing in high-rainfall tallgrass prairie in Oklahoma,[46] and in lower rainfall shortgrass prairie the densities were 1.6 steers per hectare (~0.6 steers per acre) under rotational grazing compared with 0.16 steers per hectare (~0.06 steers per acre) under continuous grazing.[47] Paddock sizes can be highly variable between ranches using rotational grazing strategies, varying with ranch size and ranging from 60 ha (148 acres) on small ranches in Colorado to several hundred hectares on larger ranches.[47] In Botswana an 18,800 ha (46,456 acres) ranch managed under holistic planned grazing is divided into 64 paddocks of 293 ha (724 acres) each but these are grazed by a herd of around 2,000 cattle providing a density of 6.9 animals per hectare (~2.8 animals per acre), similar to the Oklahoma example but at considerably lower rainfall (831 mm vs. 430 mm [32.7 inches vs. 16.9 inches]).[48] Although a 293-ha paddock may sound large, in the flat and uniform environment of the Kalahari landscape, several thousand-hectare size paddocks may be more effective at incorporating functional resource heterogeneity, whereas in more hilly and variable regions paddocks of several hundred hectares may be sufficient. The key point is that functional resource heterogeneity decreases with decreasing paddock size,[49,50] which thereby limits adaptive foraging and increases negative density dependent effects of stocking rate on animal performance (Fig. 3C).[49-51] It is also plausible that short periods of occupation in paddocks limit time for cattle to make adaptive foraging decisions in relation to their temporally shifting needs for specific resources (Fig. 3D). For example, where a desired forage resource is restricted to sections of a paddock, cattle may miss an opportunity to select

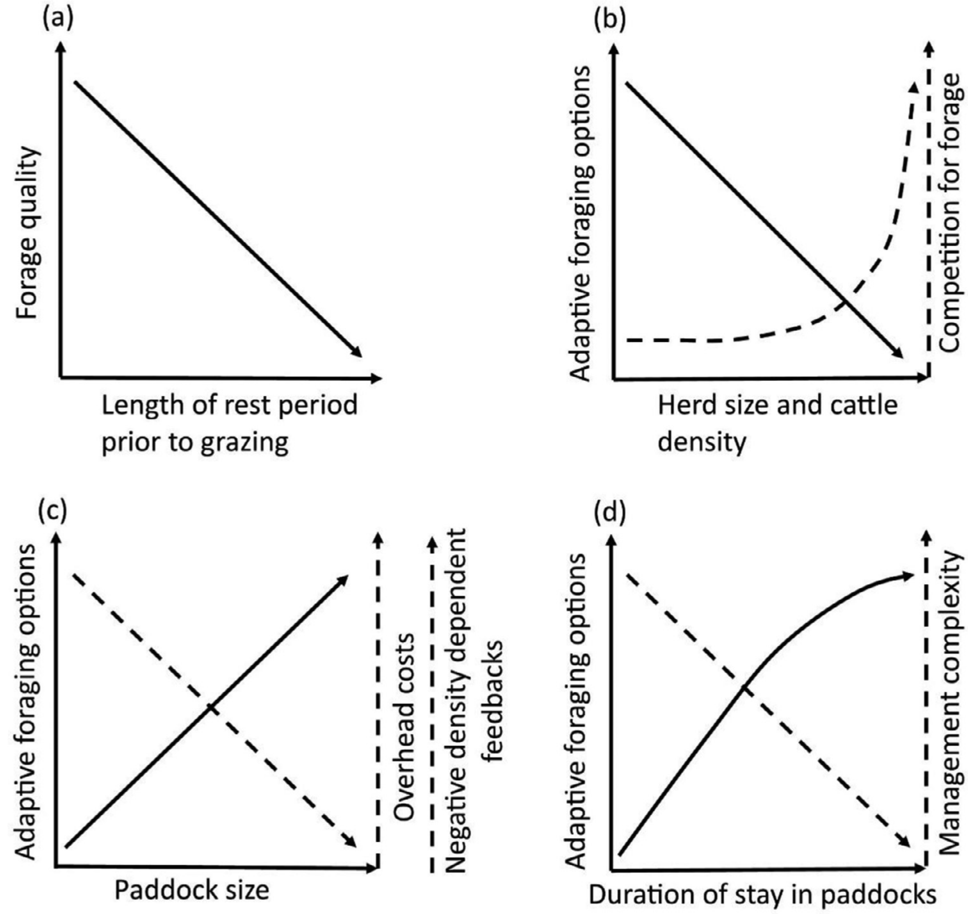

Figure 3. Conceptual model of the effect of key rangeland management variables on access to forage resources, adaptive foraging options, forage quality, density dependent feedbacks on animal performance, management complexity, and overhead costs. The relationships among variables are based on data reported in the literature (see discussions in text for details).

it when most needed if moved too frequently or managed at high densities, whereas the resource may be absent from small paddocks.[49,50] Thus, we hypothesize that the length of time an animal has to forage in a paddock before being moved to a new paddock has a positive monotonic relationship with adaptive foraging options (Fig. 3D).

Simulating general foraging ecology principles to achieve optimal cattle production on commercial ranches

Seasonal adaptive foraging movements of large herbivores

Large herbivore seasonal adaptive foraging movements must account for 1) seasonal variation in forage quantity and quality, and 2) seasonal variation in the energy, protein, and mineral requirements of reproductive females. As a consequence of maximum resource demands for reproductive females and growing calves during the growing season, wild herbivores globally deliberately focus their efforts on finding short, immature forage of the highest quality during the growing season, which may include tracking new growth after snow melt on altitudinal and aspect gradients in mountain ranges in the northern hemisphere[18,19] or after removal of mature forage by fire, grazing, or mowing in savannas and grasslands.[5,7,21-23,30,39] In addition, herbivores will seek out short, high-quality forage in short grasslands on shallow soils on the crests of catenas[24,25] or will migrate to short grasslands in saline regions for the growing season.[19,20,36] Taller grass grazers such as African buffalo seek out high-quality leafy grasses in woodland habitats during the growing season.[52] These high-quality growing season ranges are either rendered unavailable by heavy snow layers and cold in the northern hemisphere severe winters or dry out and are depleted during dry seasons of African savannas or during the winters of prairies forcing herbivores to more productive regions with longer growing seasons, warmer winters, and permanent water supplies (dormant season habitats). Typical dormant season habitats include lowlands at the base of mountain ranges in the northern hemisphere,[18,19] valley bottomlands at the base of catenas,[24,25] and high-rainfall regions, wet meadows/dambos, or floodplains.[19,20,36]

The key point to take note of with regards to designing grazing management strategies on commercial cattle ranches is that these global-scale foraging strategies can be summarized in a general foraging ecology concept of moving seasonally on grassland structural gradients from short, high-quality grassland during the growing season to a more reliable reserve of taller, adequate-quality grassland during the dormant season. The fact that such a foraging strategy is a global phenomenon and has been shown to result in more productive and stable herbivore populations[26-30] suggests it has a lot of potential for incorporation into cattle management strategies on commercial cattle ranches to optimize cattle production.

Violation of foraging ecology principles in the design of several grazing management strategies on commercial cattle ranches and the economic consequences

The importance of the forage maturation-quality principle and its impact on intake of energy and nutrients by herbivores has been strongly recognized in herbivore ecology[19,22,37,39,41] but has been ignored in the design of several past and present popular livestock grazing management strategies. For example, in traditional rangeland management practices grassland structural heterogeneity (patch structural heterogeneity) is considered as undesirable.[5,53] An important approach of short-duration grazing (SDG) was to provide paddocks with several months' rest period before being grazed, achieved through management with high cattle densities and herds rotated sequentially among many paddocks.[54] Having evolved from SDG, holistic planned grazing, also promotes several months of rest before grazing, high cattle densities, and frequent movement.[2] Other similar approaches are ultra-high density grazing and mob grazing.[55] While there are several potential advantages to these approaches for rangeland sustainability, such as concentrated animal hoof impact on litter and soils, minimizing of regrazing of grasses and providing long recovery periods after grazing, the approaches violate several foraging ecology principles, which may have negative consequences for reproduction and animal weight gain. For example, resting paddocks for several months allows grasses to mature well past the optimal height and biomass where intake rates of energy and nutrients are maximized (Fig. 1), so livestock are forced to forage in paddock after paddock containing mature, sub-optimal quality forage. Under these conditions, forage quality, not quantity, limits intake (Figs. 1 and 3A). For this reason, wild herbivores avoid foraging in long-rested patches of mature forage, selecting rather immature forage.[18-25,27,28]

In addition to the problems of forage maturation under grazing systems that allow several months' recovery period before grazing, grazing cattle at high densities increases competition for high-quality forage and reduces intake of energy and nutrients (Fig. 3B),[43-45] whereas small paddocks may restrict access to functional resource heterogeneity (balanced nutrition) and magnify stocking rate effects on animal performance (Fig. 3C).[49-51] Finally, rapid movements between paddocks (short period of occupation of paddocks) may reduce adaptive foraging options (Fig. 3D).

As predicted by the forage maturation-quality principle (Figs. 1 and 2A), sheep[56,57] and cattle[41] gain weight faster if forage is kept in an immature, shorter phase by fire or grazing. Long rest periods, which allow forage to mature, have been observed to negatively affect diet quality for sheep.[58] It is important to note here that keeping forage in a short immature phase by grazing does not mean being maintained in an immature state by long-term heavy continuous grazing, which would be unsustainable. Rather, selected paddocks can be prioritized to be kept in a short immature state by season-long grazing over the growing season followed by season-long recovery in the following year to allow perennial grass recovery from the previous year's grazing. This approach will be explained in greater detail in a later section.

Grazing systems with a paddock recovering for a month or longer (e.g., SDG) before grazing the paddock have been observed to result in cattle having lower intake of forage and protein than those under continuous grazing.[46] As expected, therefore, weight gain of cattle has been observed to be poor in SDG systems.[54,59] However, on planted pastures where forage quality may not decline as rapidly with maturation due to fertilization and selection for leafy digestible grasses, and where the rest period between grazing events is only 2 to 3 weeks, time available for forage maturation beyond the optimal height and biomass (Fig. 1) is small and animal performance may be similar between SDG and continuous grazing.[60]

Data also suggest that high animal densities in SDG systems are responsible for depressed animal performance, and it is difficult to disentangle the relative contributions of recovery effects on forage quality versus herd density effects on access to forage. A recent long-term grazing experiment in Colorado demonstrated, with stocking rate held constant, weight gains of cattle were 14% lower in treatments with higher cattle densities.[47] Unpublished GPS movement tracking data from cattle in this experiment showed that cattle in the higher density treatments walked in straighter lines (less lateral deviation) than cattle in lower density treatments (David Augustine, personal communication by Zoom meeting 3rd February 2021), suggesting reduced freedom to forage adaptively (Fig 3B), which likely contributed to lower weight gains in those treatments.[47]

Where studies have investigated how SDG and continuous grazing affected conception rates of cattle herds, greatly depressed conception rates have been observed for SDG relative to continuous grazing (59% vs. 80%; Table 1), but as

Table 1
Data from pregnancy diagnosis (PD%) tests on cattle in Zimbabwe on short-duration grazing ranches and ranches on which cattle forage continuously

	High rainfall sourveld			Low rainfall sweetveld		
Grazing management	No. cows	No. ranches	PD %	No. cows	No. ranches	PD %
Short duration grazing	2882	8	59	3979	1	71
Continuous grazing	9293	4	80	660	1	75

Note. Data from Jackson.[61]

discussed in the concepts underlying the grassland productivity-grazing facilitation principle (Fig. 2), the effect was dependent upon rainfall and grassland productivity.[61] In lower rainfall semiarid "sweetveld" regions, where quality does not decline as severely with maturity, the pregnancy diagnosis percent was 71% and 75%, for an SDG and a continuous grazed ranch, respectively (Table 1).[61] Similarly, ultra-high density (mob) grazing has also been noted to result in reduced conception rates for cattle herds.[55]

In summary, the poor weight gains and poor conception rates observed for cattle managed under SDG and ultra-high density grazing strategies[47,54,55,59,61] are predicted through the foraging ecology principles developed here (Figs. 1 and 3). The mechanisms underlying these effects are likely a combination of grazing at high density and rapid rotations between many small paddocks, in which forage has matured during the recovery period before grazing. Thus, animals managed in this way experience increased competition for forage, have reduced adaptive foraging options, and have poor access to immature, high-quality forage. Considering that high rates of reproduction and calf survival are needed to maintain the economic viability of ranches based on cow-calf operations,[1,8] there are expected to be negative economic consequences for commercial cattle ranches experiencing poor weight gains of cattle and reduced conception rates.

For example, in Botswana cattle need to grow at 800 to 1,000 g/d (1.7-2.2 pounds per day) to achieve optimal carcass mass and quality gradings at the abattoir (Kevin Grant, personal communication by email on the 8th December 2021). A 250 kg (551.2 lb) prime carcass can fetch 10,000 Pula ($850) at the Botswana Meat Commission abattoir in Lobatse compared with a lighter carcass at 8,500 Pula ($723) (Kevin Grant, personal commmunication). Using these data in a simple economic analysis that combines the effect of poor nutrition on conception rates and carcass weight/quality mediated sales (see methods in Table 2), it can be seen for a breeding herd of 500 cows that if poor nutrition results in a decline in conception rates from 85% to 70%, there is a 30% decline in income (assuming all calves are sold at maturity) amounting to a loss of $109,650 (Table 2). These are realistic effects of grazing management on conception rates, where in Zimbabwe, SDG grazing systems have been observed to result in conception rates as low as 59% (Table 1). These statistics highlight the severe economic consequences of rangeland management strategies that result in poor nutrition for cattle, undermining the economic sustainability of cattle ranches.

Table 2

Economic analysis* of how cattle management effects on the nutritional status of cattle may influence the economic viability of commercial cattle ranches

Cows	Nutrition	Conception	Calves	Price ($)	Income ($)	Loss ($)	Decline (%)
500	Poor	70	350	731	255,850	109,650	30
500	Good	85	425	860	365,500	0	0

Note. Nutrition is the major factor influencing the conception rates of cattle breeding herds[8,55,61] as well as the price attained per carcass at the abattoir, which results in multiplicative negative effects on income from yearly cattle sales (financial losses).

* The analysis assumes from published data[8,55,61] that poor nutrition results in depressed conception rates of breeding herds 85% to 70% (our use of 70% conception rates was conservative).[61] The number of calves produced was calculated from 500 cows in the breeding herd multiplied by the conception rate (0.7 or 0.85). Income on the ranch was calculated as the product of price attained per carcass at the abattoir and number of calves produced (which are sold at 2 years of age). Price attained per carcass at the abattoir is actual data from a local cattle rancher in Botswana.

Incorporating foraging ecology principles into the design of grazing management strategies on commercial cattle ranches

The foraging ecology principles developed here, and the observed consequences of violating them for cattle production and ranch income, highlight the importance of designing grazing management strategies that better meet cattle production objectives for economic viability, while also attending to ecological sustainability objectives. In this regard, we have highlighted the importance of ensuring that reproductive female cattle and their calves have access to the highest possible forage quality (provided forage quantity is sufficient to maintain optimal intake rates) during the growing season period of growth, lactation, and calving. In addition, it is important to ensure that cattle have access to a reserve of adequate quality forage during the dormant season to maintain fetus development and body stores.

A grazing strategy that facilitates optimal intake of energy, protein, and minerals in the long term must ensure that a high cover of desirable perennial grasses is attained. Tufted perennial grasses cannot survive repeated defoliation in the long term without sufficient recovery periods to recover lost nutrients and photosynthetic material.[62,63] Consequently a recent meta-analysis demonstrated that incorporating periods of rest after grazing (periods of absence from paddocks) can have positive effects on grassland biomass and cover.[4] While desired grass composition can be maintained at conservative stocking rates without formal recovery periods in continuously grazed ranches,[3] although this may depend on soil fertility and species composition, rotational grazing systems concentrate cattle in paddocks resulting in higher defoliation intensity within an occupied paddock, which is not sustainable without long enough recovery periods between grazing events.[62,63] To ensure grasses do not mature and lose quality excessively, ranchers could use short recovery periods of less than a month between grazing events. It is questionable, however, how effective short recovery periods are for rangeland sustainability because they can miss key pulses of rainfall for recovery of photosynthetic material and associated pulses of nutrient mineralization for plants to recover nutrients lost in grazed material.[62] Short recovery periods may also not adequately enable root development during the period of maximum root development at the end of the growing season.[62] For example, on a ranch in Colorado it was found that desirable grasses, such as western wheat grass (*Pascopyrum smithii*), would not recruit until at least 100 days (>3 months) of recovery were applied.[63] A study in Botswana found that a full growing season recovery was optimal for recovery of the vigor of high-quality grasses,[64] which was also the conclusion for high-rainfall sourveld regions of South Africa.[65] It appears, therefore, that, especially in productive regions where grass growth is rapid, effective recovery periods (>3 months) give more than enough time for grasses to mature well past the optimum biomass for yielding sufficient intake of energy and nutrients to support satisfactory levels of growth and reproduction in cattle (Fig. 1).

Taking the above points into account it appears that a management dilemma arises for ranchers—recovery periods over several months or longer are required for ecological sustainability but only short recovery periods (2-3 weeks) will optimize energy and protein intake by cattle to promote cattle production and economic sustainability (Fig. 3A). This dilemma is, however, only severe in regions where grass production potential exceeds several hundred grams per square meter of standing biomass (i.e., in intermediate and especially high rainfall regions; Fig. 2). Thus, grazing management strategies for ranches in intermediate and high rainfall regions need to maintain grazed paddocks in an immature, higher quality state by season-long grazing (i.e., dealing with the forage maturation-quality principle: Fig. 3A), while also ensuring that cattle graze at low density in large heterogeneous paddocks that provide optimal adaptive foraging options and low competition for high-quality forage (dealing with the herd size/density - nutrition principle; Fig 3B-D). Moreover, to ensure a reserve of adequate-quality forage over the dry season a sufficient proportion of the paddocks on the ranch (up to half) must be left ungrazed over the entire growing season (season-long recovery), which also ensures perennial grass recovery[62] and seed set,[63] and thereby ecological sustainability. Thus, the solution to the rangeland managers' dilemma is to separate grazing and recovery activities into different years through season-long grazing of a paddock in the 1st year and season-long recovery in the following year. This was also the conclusion reached by Kirkman and Moore in the high rainfall sourveld regions of South Africa.[65]

Venter and Drewes[66] designed a grazing system for the high-rainfall sourveld regions of South Africa to prevent forage maturation and loss of forage quality. The strategy uses priority grazed paddocks for the growing season, which are burned at the start of the growing season to remove old low-quality material and are then kept in a short, high-quality state all growing season by focusing grazing on the priority paddocks to prevent grass exceeding a predetermined height (Fig. 4A). Keeping both palatable and less palatable grasses in a short, immature state means less palatable grasses remain acceptable to cattle resulting in grazing of both palatable and unpalatable grasses, which favors the palatable grasses. Other paddocks are used as reserves of forage and only grazed when the priority paddocks run short on grazing while others are completely rested all year. Thus, cattle have access to high-quality forage as well as reserves of forage should high-quality forage run short. In the following season priority paddocks become reserve paddocks and reserve paddocks become rested paddocks. Clive Bunting on Strathearn ranch in the high-rainfall grasslands near Dundee, KwaZulu-Natal used the Venter-Drewes system and achieved among the best cover of desirable grasses seen on any ranch in the region, leading to the Grassland Society of Southern Africa awarding him the Peter Edwards award in 1998 for best conservation rancher.

Kirkman and Moore[65] for sheep in the high-rainfall grasslands of Mpumalanga province, South Africa and Riaan Dames[67] for cattle in the semi-arid savanna regions of North West province, South Africa independently developed very similar grazing management strategies that aimed to provide season-long recovery periods to facilitate 1) recovery of vigor of desired perennial grasses and 2) the development of a reserve of forage for the dormant season (Fig. 4B). Season-long grazing of other paddocks was employed to ensure maintenance of grassland in an immature high-quality state for the growing season. In both approaches, half the available paddocks on the ranch are rested while the other half are grazed continuously over the growing season and early dormant season. Animals are moved from the grazed paddocks to the paddocks under recovery in the early to mid-dormant season (determined by forage remaining in the grazed paddocks), where they remain until the next dormant season before being moved to the paddocks having received a full growing season recovery. The effects of a full growing season of grazing on grasses are compensated by providing a full growing season recovery period, which facilitates recovery of root systems, cover, and productivity.[4,62-65] A key component of all of these grazing approaches[65-67] is that they create a gradient of grassland structural states from short high-quality grassland for optimal intake of energy and nutrients by livestock during the growing season to taller adequate-quality grassland as a reserve of forage for the dormant season. Selection of short high-quality grassland over the growing season and a taller reserve of forage during the dormant season (and dry periods within the growing season) is typically observed with wild herbivore populations[18-20,23-25] and results in more productive and stable populations.[26-30]

A key component of the Riaan Dames grazing strategy (also known as the split-ranch grazing strategy)[67] is to have fewer and much larger paddocks (i.e., several hundred hectares or larger), to maximize incorporation of functional heterogeneity within paddocks and lower cattle densities for improved adaptive foraging options and reduced negative density-dependent feedbacks on cattle production (Fig. 3B, C).[49-51] Importantly, having fewer and larger paddocks also minimizes the significant costs of construction and maintenance of an extensive fencing infrastructure, which can significantly reduce profits and economic viability (Fig. 3C).[2,9]

For ultimate simplicity of management and optimal access to functional heterogeneity across the ranch, an alternative approach to what we have presented here[65-67] is to simply have one perimeter fence on the ranch combined with several interior moveable paddocks (using electrical fencing) from which livestock are excluded during the planned recovery period, thereby minimizing the costs of fencing infrastructure. A manager can plan the size and location of the property to be

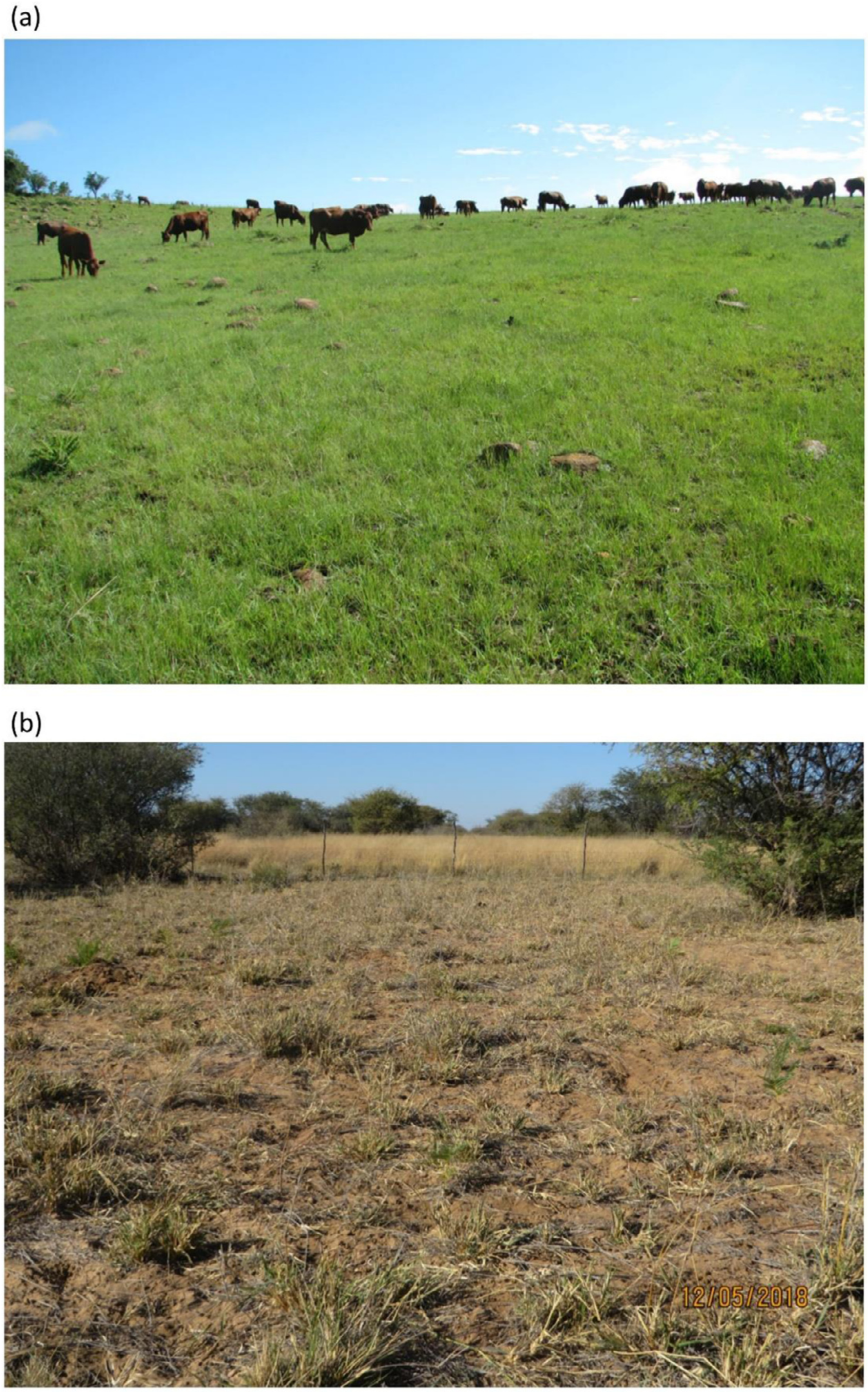

Figure 4. A, Cattle grazing on short high-quality grass in a priority graze paddock on Mr. Clive Bunting's Strathearn Farm in high rainfall sourveld, near Dundee, KwaZulu-Natal, South Africa (Photo courtesy of Richard Fynn). B. A fenceline contrast between a season-long grazed paddock (foreground) and a season-long rested paddock (background) in the early dormant season on Tiisa Kalahari Ranch, Botswana, where the manager Mr. Kevin Grant uses the split-ranch grazing strategy (Photo courtesy of Richard Fynn).[67] Note how season-long grazing has facilitated maintenance of a short sward while season-long recovery has facilitated the development of a significant reserve of forage for the dormant season.

under recovery each growing season, while affording the cattle maximal opportunity to forage adaptively at low densities in large landscapes (Fig. 3B, C). Here, the manager is rotating the pasture under recovery without rotating the livestock. In the season-long grazed pastures the manager can promote heterogeneity in forage maturity and quality by implementing patch burns over parts of the grazed area, which promotes adaptive foraging options between the shorter burned patches and the taller unburned patches.[30,53] Whatever the approach used, all require the setting of conservative stocking rates to allow uninterrupted season-long recovery. The duration of recovery periods is inextricably interlinked with stocking rate—

the higher the stocking rate, the faster the rate of forage depletion and, therefore, less time available for recovery periods in paddocks set aside for season-long recovery. Thus, stocking rate is critical for ecological sustainability, irrespective of grazing system.[3]

These days promoting grassland structural heterogeneity on ranches is becoming an important concept, not just for animal performance, but also for maintaining biodiversity.[5] For example, evidence from studies worldwide indicate different bird species have habitat requirements for different stages of grassland height/maturity,[68-70] which is also true for ungulates.[6,23] Effective and sustainable ranch management and biodiversity conservation are not mutually exclusive but can be complementary when ranches are managed strategically according to the theory and concepts discussed here on developing grassland structural/maturity heterogeneity. Grassland structural heterogeneity, therefore, promotes adaptive foraging options to seasonal variation in 1) herbivore resource intake requirements and 2) forage quantity and quality, while also increasing habitat diversity for different birds and ungulates.

Conclusions

There is growing evidence that management for grassland structural heterogeneity and functional resource/habitat heterogeneity provide robust principles for the co-development of rangeland management and biodiversity conservation strategies. Foraging on grassland structural gradients over the annual cycle is optimal for stable and productive animal production, while also providing habitat heterogeneity for biodiversity. An emergent property of ranch management underlain by this grassland structural heterogeneity framework is economic sustainability through improved animal production (access to functional resource heterogeneity) and reduced costs of production (less fencing and management costs).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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