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Modeling forage mediated aggregation in a gregarious ruminant

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Two explanations exist for the evolutionary origin of grouping in primary consumers: reduction of individual predation risk and resource-mediated aggregation. While several studies have assessed relationships between aggregation and predation risk, few studies have examined the circumstances under which resource-mediated aggregation can lead to stable group formation. Using a model, we examined if forage preference alone can generate stable aggregation, and what were the circumstances of its emergence and stability. The model was a spatially explicit grazing model using empirically derived parameters to simulate large ruminant foraging in a meadow. Simulation results indicated that aggregation can spontaneously arise if grazers exhibit preference for forage of higher nutritional quality, usually associated with intermediate stages of forage growth. In this case, foragers could establish and maintain 'islands' of high quality forage as a result of revisiting continuous paths of previously grazed patches. However, aggregation was an intermittent phenomenon and occurred only within a narrow range of parameters. If grazer density was low compared to the amount of forage, the grazers' foraging paths intersected too rarely to form contiguous islands of high forage quality; if their density was too high, the entire available area was uniformly utilized and foraging movements resembled unbounded random walks. We conclude that it is difficult to conceive of the evolution of grouping without the involvement of predators, since the relationship between grazer and forage abundance is ultimately co-regulated by predator abundance, and because in modern grazers, predator avoidance and foraging behavior seem to be functionally inseparable. Future research should consider the reinforcing effects of predator avoidance as well as foraging behavior on consumer aggregation.

Aggregation should reduce the predation risk of foragers by dilution of risk (Hamilton 1971, Alexander 1974, Inman and Krebs 1987), group defense (Berger 1979), or increased vigilance (Elgar 1989, Molvar and Bowyer 1994). Attempts to correlate anti-predation effects with group size have proven inconsistent, often producing unexpected results or simply failing to establish any relationship (Elgar 1989, Quenette 1990, Lima 1995). Such inconsistencies indicate that additional functional explanations, as well as potentially complex interactions between predator avoidance and foraging behavior, may be required to explain grouping behavior satisfactorily. For example, foraging behaviors exhibited by grazing herbivores have been shown to vary in response to changes in group size and population density (Clutton-Brock et al. 1982, Kie and Bowyer 1999, Weckerly et al. 2004), which may in turn be controlled by predation pressure. Although the local rate of resource depletion may increase with group size – a cost typically associated with aggregation – this may be offset by improvements in the quality and growth rate of the forage (Fryxell 1991, Post and Klein 1996). If so, it is also plausible that foragers may aggregate in the absence of predators simply for the nutritional benefit.

The nutritional value of younger, pre-reproductive forage to grazing ruminants is typically higher than that of mature forage (Van Soest 1994). As forage grows taller and matures, cell walls thicken to provide greater structural support to growing plants. Chiefly composed of cellulose and hemi-celluloses, cell wall materials must be retained in the fermentation chambers for longer periods of time to be digested, resulting in increased processing time and higher energetic costs to the individual (Crawley 1983, Van Soest 1994). Therefore, if consumers have a choice between forage in mature or intermediate (i.e. recently grazed) stages of development, they should prefer patches of intermediate maturity (Crawley 1983, Fryxell 1991). This implies that grazers should return to recently grazed patches more often than would be expected by chance, and this behavior could conceivably result in area-restricted searching and aggregation.

A benefit of area-restricted searching is improved foraging efficiency and intake (Ohashi and Thomson 2005), which is well-documented in ruminants (Underwood 1983, Post and Klein 1996, Fryxell et al. 2005). Ruminants tend to focus foraging efforts close to areas where high quality forage was recently found, until the standing crop drops below some acceptable level, at which point they move on, allowing time for crop renewal (Ohashi and Thomson 2005). Meanwhile, area-restricted searching may retain an individual grazer close to recently abandoned patches, thus increasing the chances of a timely return to harvest the patch again as it enters the preferred state of intermediate maturity. Individual grazers should therefore be able to produce and maintain an 'island' of improved forage quality, which simultaneously reduces search time and improves nutrition.

Area-restricted searching by individuals could lead to consumer aggregation, requiring only chance driven overlap of two or more individual foraging paths. Provided that animals were indifferent to which individual last visited a patch, such areas would be effectively shared at the instance of overlap. More individuals could join in the same way, exhibiting what amounts to grouping behavior. However, consistent aggregation within a foraging area utilized by multiple consumers could increase the frequency of overgrazing (Schwinning and Parsons 1999), and it is not clear how persistent such groups would be, since the random events that formed the group could also, in time, pull individual foraging paths apart. This suggests that, if such resource mediated grouping were to occur, it would depend on a delicate balance between consumer density and forage abundance. This raises the following questions:

1. Can consumer aggregation occur as a result of preference for forage of intermediate height and area-restricted searching?
2. If so, how is this phenomenon regulated by forage-consumer abundance dynamics?
3. How robust is this mechanism of aggregation, and how stable are the groups that result from it?

We developed a spatially explicit grazing model with parameters that were derived from the foraging behavior of Roosevelt elk *Cervus canadensis roosevelti* in northern Californian meadows. Although other models of forage-mediated grouping do exist (Gueron and Liron 1989, Wilson and Richards 2000), these did not attempt to simulate natural systems with empirically derived parameters, nor did they examine the role of forage abundance and quality in group formation. We chose an ungulate as a model species because their foraging behaviors and nutritional requirements have been extensively studied and quantified, and they are known to exhibit the forage preference conducive to producing forage-mediated aggregation (Clutton-Brock et al. 1982, Spalinger and Hobbs 1992, Gross et al. 1993, Van Soest 1994, Barboza and Bowyer 2001, Illius et al. 2002, Fortin et al. 2004, Kuzyk and Hudson 2007). In addition, we know that their grouping behavior is variable and closely tied to forage abundance and quality (Hirth 1977, Clutton-Brock et al. 1982, Lewin 1985, Fryxell 1991, Molvar and Bowyer 1994, Fryxell et al. 2005). This presents an opportunity to compare the output of our model with known patterns of ungulate aggregation and foraging behavior.

Material and methods

Characteristics of the model system

The model was designed to simulate the grazing behavior of Roosevelt elk, a subspecies of large grazing ruminant inhabiting the Pacific northwest of the United States and Canada. They are gregarious, typically aggregate in herds of 5 to greater than 200 individuals, and inhabit a landscape matrix consisting of forage-rich meadows surrounded by forage-deficient forest habitat (Weckerly 1999). Roosevelt elk preferentially forage in meadows (Weckerly 2005) for up to 18 h per day (Clutton-Brock et al. 1982). Fortin et al. (2004) illustrated that North American elk *Cervus canadensis* consume approximately 25% of the standing crop within a foraging patch, and the Roosevelt subspecies exhibits similar tendencies.

Meadows are large open areas (10–1000 ha) consisting primarily of perennial and annual grasses and forbs. Each meadow is distinctly bounded by the surrounding redwood-conifer forest, clearly delineating forage and non-forage habitat (Weckerly 1999, 2005).

Model structure

The model was composed of a well-established set of equations describing ruminant foraging at the patch scale (Spalinger and Hobbs 1992, Illius et al. 2002), spatially extended to the scale of the entire foraging area (Schwinning and Parsons 1999), and parameterized to apply to Roosevelt elk (Table 1; Jones 1963, Harper et al. 1967, Clutton-Brock et al. 1982, Gross et al. 1993, Fortin et al. 2004, Kuzyk and Hudson 2007). A single meadow was represented by a two-dimensional array of contiguous, homogeneous 1×1 m^2 cells (patches). The cell size was chosen on the basis of the approximate size of a patch utilized by a stationary elk (Clutton-Brock et al. 1982).

Patch quality was represented by biomass density and varied according to offtake and growth. Meadows were occupied by identical grazers that moved from patch to patch, selecting the next patch based on which nearby patch best fit their preference. Grazers uniformly depleted each chosen patch to a fixed percentage of its previous biomass. Daily intake was limited either by a daily maximum intake or a daily maximal foraging time. Forage growth occurred after all grazers had ceased grazing (i.e. at 'night'). See supplementary material Appendix A1 for a complete list of model assumptions.

Forage growth

Growth of forage biomass was governed by a discrete form of the logistic growth equation,

$$b_{forage}(\mathrm{t} + \partial) = b_{forage}(\mathrm{t}) + \partial \times r \times b_{forage}(\mathrm{t}) \times (1 - b_{forage}/k) \quad (1)$$

where b_{forage} is density of forage biomass in grams of dry matter available for consumption (g DM m^{-2}), ∂ is time (1 day), r is the relative rate of forage growth (day^{-1}), and k is a carrying capacity (g DM m^{-2}; Thornley and Johnson 2000). Density-dependent growth was selected to model forage growth due to observed sigmoidal growth behavior as forage biomass matures under heavy grazing conditions (Schwinning and Parsons 1999, Thornley and Johnson 2000). In lieu of a more complex representation to distinguish forage quantity from quality, we simply assumed that forage quality is maximized at $0.5k$, as has been observed in multiple grazing systems (Crawley 1983, Fryxell 1991,

Table 1. Variables and parameters of the foraging model.

Parameter description	Symbol	Default value and unit	Citation
Number of grazers	N_{grazer}	10 grazers	–
Meadow size	–	600 × 600 m	–
Carrying capacity	k	495 g DM m^{-2}	Jones 1963
Rate of growth (% standing crop)	r	0.05 day^{-1}	–
Delta time	∂	1 day	–
Forage biomass	b_{forage}	variable, g DM m^{-2}	–
Preferred forage biomass	b_{pref}	$0.5k$ g DM	Crawley 1983
Ungrazable horizon	$b_{ungraze}$	$0.01k$ g DM*m^{-2}	–
Offtake (% standing crop)	o	$0.25b_{forage}$ g DM	Fortin et al. 2004
Body size	w	272 154 g	Harper et al. 1967
Maximum gut content	b_{gut}	$0.01w$ g DM	Kuzyk and Hudson 2007
Patch area	A_{patch}	1 m^2	–
Bite area	A_{bite}	0.01 m^2	Harper et al. 1967
Number of bites to defoliate patch	N_{bites}	A_{patch}/A_{bite} bites	–
Crop time	h	0.012 min	Gross et al. 1993
Bite size	S	$o \times b_{forage} \times A_{bite}$ g DM	–
Maximum processing rate	R_{max}	52.95 g DM min^{-1}	Gross et al. 1993
Time to defoliate patch	T_{defol}	variable, min	–
Maximum foraging time	T_{max}	1080 min	Clutton-Brock et al. 1982

Van Soest 1994). Thus, the patch state most preferred by grazers, b_{pref}, was set equal to $0.5k$.

Foraging

Foraging consisted of repeating the following sequence of decisions and events:

1. Patch selection
The grazer determines which one or more of the adjacent patches have the smallest absolute difference from the 'ideal' patch state, b_{pref} (g DM m^{-2}). The maximal number of adjacent patches is eight, but this number could decrease due to the exclusion of patches that have biomass densities below the ungrazable horizon, $b_{ungraze}$ (g DM m^{-2}); are occupied by another grazer; or represent the meadow boundary. If multiple patches are equally desirable, the grazer selects one of them at random. If none of the adjacent patches are acceptable, the grazer assesses the next adjacent sixteen patches, applying the same selection rules. If still no patches are viable, the grazer randomly selects an unoccupied patch that is no more than two meters away, permitting it to escape the immediate neighborhood of poor quality patches.

2. Movement
The grazer moves into the selected target patch. It is assumed that movement to an adjacent or next to adjacent cell has no time cost, as grazers can walk and chew at the same time (Fortin et al. 2004). However, if an individual is forced to randomly select a patch because none of the surrounding patches within two meters are viable, the grazer incurs a fixed time cost of one minute for movement. Although this is not a precise estimate, it avoids the artifact of unlimited foraging movement in a uniformly overgrazed meadow. Otherwise, the assumption has no significant impact on the simulation.

Unless the grazer has run out of foraging time, or has been satiated for the day, the grazer always moves after grazing the patch once, even if the patch it is leaving has more biomass than the next target patch. This behavior is considered realistic, as it encourages constant movement (Clutton-Brock et al. 1982) and allows the grazer to combine consumption with forage assessment in the context of area-restricted searching (Ohashi and Thomson 2005).

3. Intake
When the grazer has arrived at a grazable patch, it uniformly defoliates it by a fixed percentage of the standing biomass, but not in excess of $b_{ungraze}$. Grazing adds foraging time and gut content in proportion to the biomass taken off. A grazer who moved to a patch randomly as an escape from a local area of poor quality patches (see step 1) does not take part in this step, as they have already incurred a time cost from movement to the random patch.

This sequence of individual foraging decisions and events (1–3) repeats until the grazer has either consumed the maximum amount of forage permitted by its body weight, b_{gut} (g DM), or has used the maximum time allotted to foraging, T_{max} (1080 min; Table 1). On the following day, the grazer resumes foraging in the patch last visited.

Temporal resolution

Under natural grazing, grazer movement is not synchronized; that is, one grazer may be moving while another is stationary, or one grazer may harvest a patch more quickly than another in a different patch. We resolved the problem of asynchrony by simulating grazing in one minute intervals, keeping track of the fractions of a minute needed to complete a task that was started in an earlier minute interval. Movement, in most instances, was assumed to be instantaneous, and was executed at the end of the one minute intervals (but see Foraging step 2 above). Thus patch selection was done while a given animal was at rest.

Grazing constraints

The time cost of grazing has two components (Spalinger and Hobbs 1992, Illius et al. 2002): a fixed time required for apprehending a bite (h, min), and a variable time required for chewing the bite, proportional to bite size (S, g DM),

$$T_{bite} = h + S/R_{max} \quad (2)$$

where R_{max} (g DM min^{-1}) is the maximum rate at which food may be processed. With a bite area of A_{bite} (m^2) and a patch of area A_{patch} (m^2), the grazer must take a number of bites (N_{bites}) equal to A_{patch}/A_{bite} to deplete the patch uniformly. Thus, the total time required to defoliate a patch is

$$T_{defol} = N_{bites} \times (h + S/R_{max}) \quad (3)$$

Grazers remove a fixed percentage o of standing biomass b_{forage}, which in turn determines the bite size (g DM),

$$S = o \times b_{forage} \times A_{bite} \quad (4)$$

Substituting S into Eq. 3 provides the time in minutes required to uniformly graze a patch based on percent offtake and bite area and expressed as a linear function of the amount of biomass consumed:

$$T_{defol} = N_{bites} \times (h + o \times b_{forage} \times A_{bite}/R_{max}) \quad (5)$$

Indicators of grouping

Grouping in a biological sense is traditionally recognized as a reduction in interpersonal distance in relation to the total available space. Statistically, it has been identified by measures of spatial autocorrelation or ‘clustering’ and is indicated by positive or negative correlation between the states of nearby locals (Vinatier et al. 2011). For example, if a patch in the vicinity of an occupied patch has a greater than random chance of also being occupied, we would take this as an indication of clustering, or positive autocorrelation. This approach to identifying spatial aggregation focuses on space itself, whereas we aimed to quantify aggregation through an intuitively more appealing method that focuses on quantifying the distances between individuals, independent of their absolute position in the grid, which, after all, continuously changes. We therefore chose to quantify grouping using the nearest neighbor criterion (Clark and Evans 1954), which prohibits distinguishing between the presence of one group versus multiple groups in a simulation but is commonly used to assess patterns of aggregation in small populations at the individual level (Vinatier et al. 2011).

We calculated the average distance between each grazer and their nearest neighbor (average minimal distance, AMD) and evaluated it against the average nearest neighbor distance of an equal number of randomly placed grazers in a meadow of equal size, estimated as the average of 100 independent simulations of a random distribution of as many grazers (AMD$_o$). We defined a Grouping index (I) as AMD/AMD$_o$ such that $I < 1$ indicated aggregation, $I = 1$ random distribution and $I > 1$ hyperdispersion. This statistic was calculated every ten minutes of simulated time and daily averages were reported once every 10 days.

At the end of each day, grazers stopped their foraging bouts at slightly different times, thus some distances were calculated between individuals which were still moving while others stood still. However, these samples composed a small fraction of the daily subsamples, and were not fundamentally at odds with our intent to measure the distances between foraging individuals.

All simulations were started at forage carrying capacity for the entire meadow and with a random distribution of 10 grazers. We allowed a generous run-up time to remove the potentially confounding effect of initial conditions.

Parameter ranges

To examine the influence of forage:consumer abundance on aggregation, we varied the number of available patches (meadow size), forage carrying capacity (k), and the low-density (maximal) growth rate of the forage (r), while leaving the number of foragers constant at 10. Simulated meadow sizes ranged from 100×100 m^2 to 600×600 m^2, or 1 to 36 hectares. Although this did not reflect the full range of meadow sizes available to Roosevelt elk in California, it captures more than an order of magnitude of variation in meadow size, thus providing a meaningful, if not comprehensive basis for comparison. The carrying capacity k was varied to encompass all naturally occurring values, as reported by Jones (1963). No estimates for low-density growth rate r could be obtained, however, and so we tested across an intentionally wide range from 1% to 20% daily relative growth. In the Supplementary material Appendix A2, we also explored the effect of changing forage preference (b_{pref}) for each combination of model parameters on observed patterns of aggregation and meadow usage.

Model validation

We verified that the model produced behavior similar to that observed in the target system. Simulated grazers moved less frequently, and in shorter distances, in scenarios of high forage biomass. In instances of low forage biomass, consumers were observed to move farther and with greater frequency. This general behavior coincides with foraging behavior observed in free ranging Roosevelt elk (Franklin et al. 1975, Jenkins and Starkey 1982) and suggests that our model assumptions produce simulated behavior sufficiently similar to our target system.

Results

Effect of forage abundance on grouping

Grouping, as indicated by $0 < I < 1$, was observed only for higher forage growth rates and meadows above a minimal size (Fig. 1). As meadow size increased, the smallest rate of forage growth required to produce grouping declined. Increasing meadow size also promoted increased variation in I at higher forage growth rates. However, with the exception of the largest meadow size (600×600 m^2), all mean values of I were well below 1. Similar results were obtained by varying carrying capacity from 165–495 g DM m^{-2} per Jones (1963) while maintaining growth rate at a value that previously promoted grouping ($r \approx 0.16$).

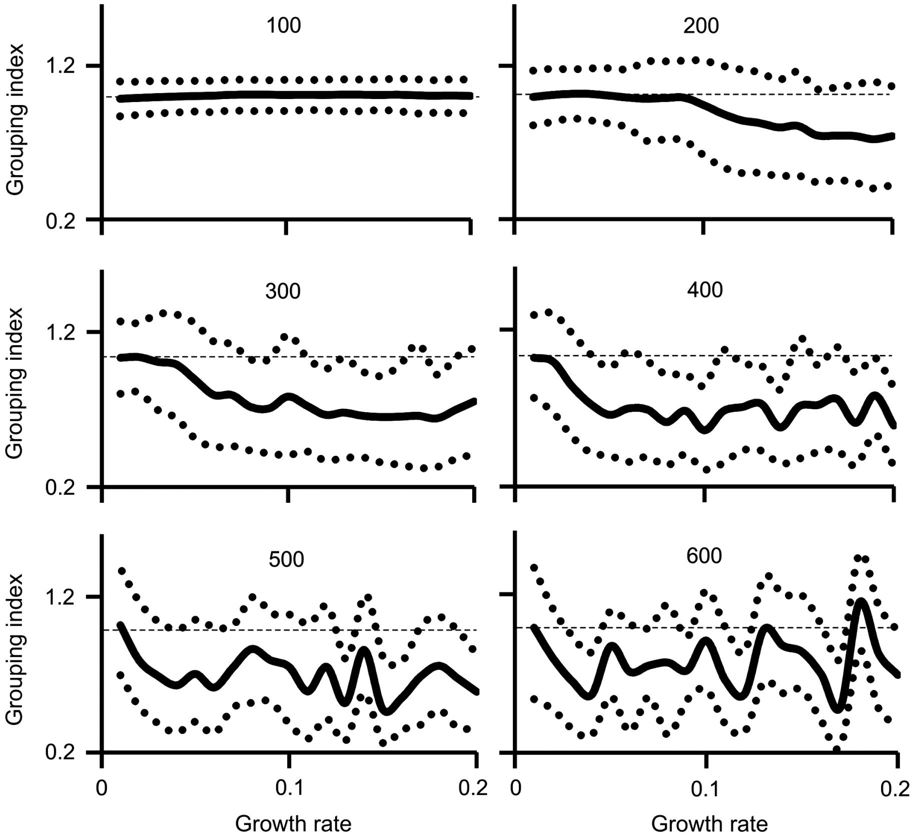

Figure 1. Changes in Grouping index (*I*) as a function of forage growth rate (*r*). The title for each panel describes the size of the meadow (e.g. 100×100 m^2). The dotted lines represent the upper and lower 95% CIs for the estimate of *I*. The value of *k* was kept constant across all panels at the default of 495 g DM m^{-2}. Significant decreases in *I* are observed with increasing *r* across all but the smallest meadow size, with increasing variation in *I* as meadow size increases.

Thus, increases in forage abundance by three different means (meadow size, forage growth rate and carrying capacity) had overall similar effects on grouping. They never produced a consistent pattern of hyperdispersion ($I > 1$), but did produce grouping ($I < 1$) with the most consistent indication of grouping found at intermediate levels of forage abundance. This behavior was also observed, and was more pronounced, under grazer preferences for lower forage biomass (Supplementary material Appendix A2). However, decreasing preference toward lower biomass resulted in more pronounced aggregation with reduced variation in estimates of the Grouping index, and increasing preference produced less aggregation (Supplementary material Appendix A2). This suggests that forage abundance coupled to consumer preference, more so than any specific model parameter, mediates the occurrence of grouping.

Meadow states

Incidents of strong grouping ($I << 1$) coincided with the existence of large, continuous areas of low forage abundance relative to the surrounding ungrazed patches (Fig. 2). The size of such frequently grazed 'islands' decreased with increasing forage abundance and ultimately demonstrated a tendency to disintegrate into multiple smaller islands, each one tended by one or two grazers. Recently disintegrated islands still produced low values of *I* if they were initially more clustered than would be expected by chance (Fig. 2b). However, in time they would also drift apart and become more randomly dispersed. This random consolidation and dispersion of frequently grazed islands tended by individual foragers at least in part explains the high degree of variation in *I* under conditions conducive to island formation (Fig. 1).

Incidents of weak grouping ($I \approx 1$) under conditions of low forage abundance were typically associated with a more uniformly depleted meadow (Fig. 3). The island sizes tended by one grazer were substantially larger when resources were less abundant, indicating that grazers covered more ground in a day when forage per patch was scarce. Thus, the merging of just a few individual islands could amount to spanning the entire meadow, and at that stage, the tendency to aggregate was lost. A further decrease in forage abundance resulted in uniform overexploitation of the entire meadow.

Overgrazing and variation in grouping estimates

The large confidence intervals observed in the estimates of the Grouping index is indicative of large variation in the state of aggregation even under conditions that favor aggregation on average. Since we determined that grazer aggregation occurs when the frequently grazed islands tended by single grazers converge, we hypothesized that the dissolution of jointly grazed islands was facilitated by overgrazing from within. In particular, overgrazing would accelerate grazer

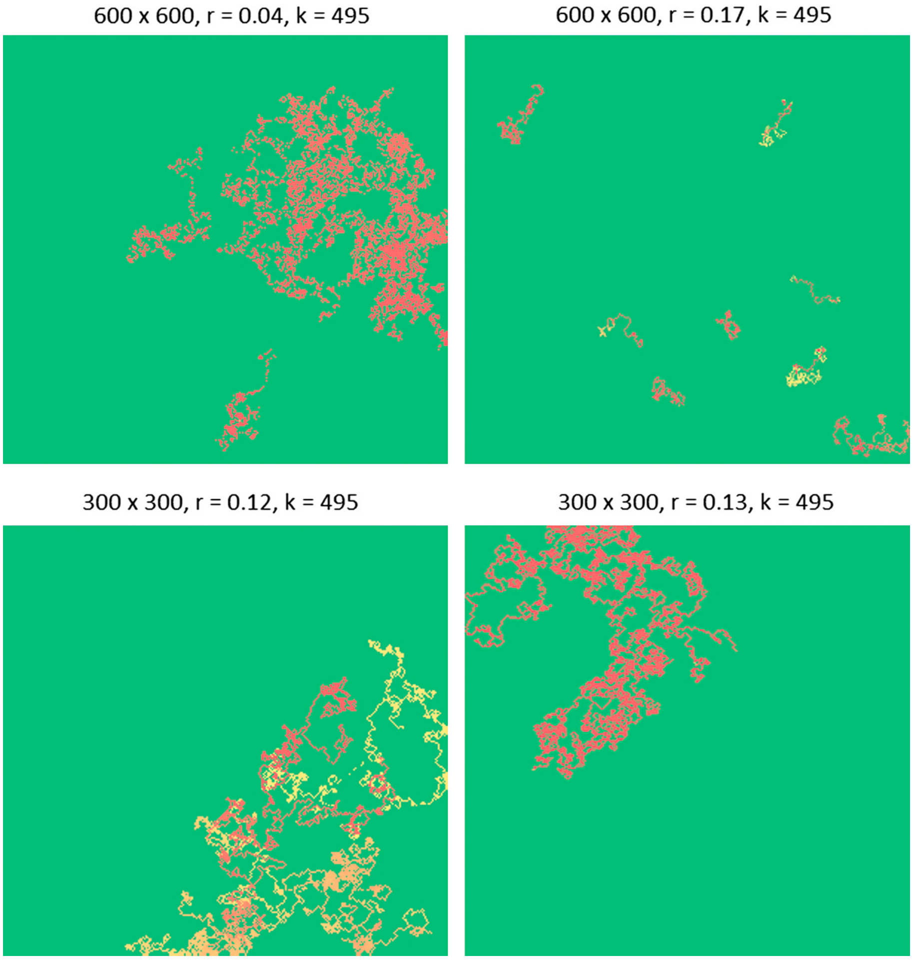

Figure 2. Snapshot of meadow-wide forage abundance when Grouping index (*I*) equals that in Fig. 1 at the rate of growth (*r*) and meadow size specified by the panel title. Within patch forage biomass increases from red to green. Small values of *I* are typically associated with the presence of grazing lawns utilized by multiple grazers. In large meadow sizes with high *r*, individual grazing lawns may not coalesce, but small values of *I* may occur due to spatial clustering of individual lawns.

movement and eventually drive grazers to accept a patch at carrying capacity, which equates to breaking out of the jointly grazed island. This behavior imparts a certain mutability to the maintained foraging areas, causing them to shift over time as new foraging areas are established following overgrazing and permitting groups to add newly encountered individuals to their unit or remove those that lag behind.

We tested this hypothesis in a single simulation over a 200-day period, using a combination of model parameters that promoted aggregation (300×300 m^2 meadow, $k = 300$ g DM m^{-2}, $r = 0.1$ day^{-1}). Fluctuations in the Grouping index showed clear evidence of quasi-periodicity with return times between 30–60 days (Fig. 4), indicating that highly aggregated states were predictably unstable, but randomly dispersed grazers had a tendency to cluster eventually. A correlated periodicity was found in the number of ungrazable patches. Periods of peak aggregation were associated with a rapid increase in the number of ungrazable patches, while periods of reduced aggregation led to their rapid decline. Thus, aggregation in this model was a fundamentally dynamic state, bounded by the inevitability of overgrazing in a phase of high aggregation, and by the tendency of individually tended frequently grazed islands to merge in a phase of low aggregation. Additionally, this lends credence to our use of nearest neighbor to estimate grouping, as the mutable size and distribution of the maintained foraging areas render many spatial estimates unnecessary or uninformative.

Discussion

Mechanism of forage mediated grouping in grazers

The purpose of this research was to determine if consumer aggregation would arise spontaneously as a consequence of optimal foraging (area restricted foraging and patch selection), using realistic, empirically-derived model parameters and equations. Results from the model support this hypothesis, in general, as indicated by negative *I*-values produced in many simulations. However, they also showed that the emergence of grouping depends critically on forage abundance relative to consumer density. In particular, when forage abundance was very low, grazers were randomly distributed; when forage abundance was intermediate, animals tended to aggregate; and when forage abundance was high, grazers did not consistently aggregate. Furthermore,

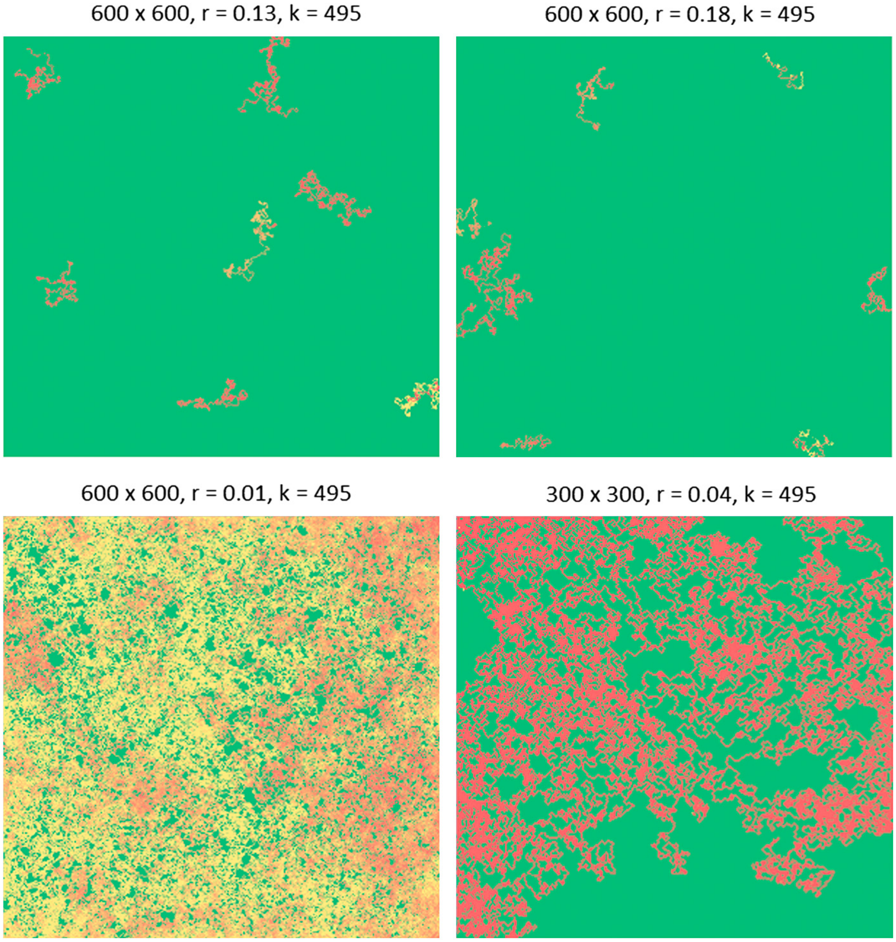

Figure 3. Snapshot of meadow-wide forage abundance when Grouping index (*I*) equals that in Fig. 1 at the rate of growth (*r*) and meadow size specified by the panel title. At low *r*, large values of *I* are associated with grazing lawns that span the entire meadow at large meadow sizes or overexploitation of all available resources at smaller meadow sizes. Large values of *I* at higher *r* are typically associated with random distributions or hyperdispersion of individual grazing lawns.

the simulations showed that aggregation was a transient phenomenon, limited by the rapid development of overgrazed patches in shared, frequently grazed islands, which drove consumers to disperse out into previously ungrazed patches.

Key to understanding both the dynamic limitations of aggregation, and its dependence on forage:grazer abundance, is the effect of patch state on the time spent grazing a patch, and the effect of the overall meadow state on the daily distance traversed by grazers. When forage availability was low, grazers took small bites and moved on quickly, thus visiting more patches in a single day. This also meant that the frequently grazed islands they produced individually (through exhibiting preference) were relatively large. Under the highest levels of forage limitation, the entire meadow became frequently-grazed, and grazers moved fast and took many bites in a single day. This increased meadow uniformity and in turn made the foraging paths more random. Thus, the ability to aggregate was lost when there was a forage deficit to grazers.

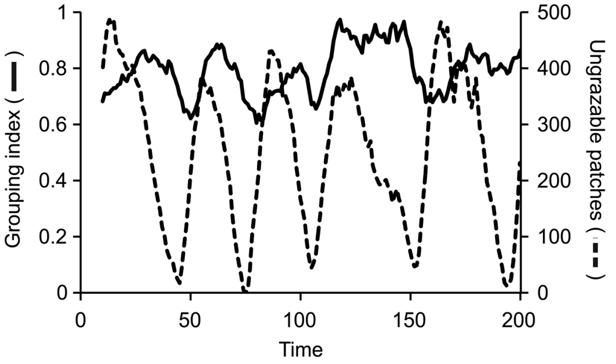

Figure 4. Changes in Grouping index (*I*) and number of ungrazable patches over time. Greater aggregation, indicated by low values of *I* (solid line), are concurrent with few ungrazable patches (dashed line).

As forage abundance increases, the area required to obtain resources adequate to meet an individual's nutritional demands decreases (McNaughton 1984). For the highest levels of forage abundance, the frequently grazed islands of individual grazers were of minimal size. Accordingly, the probability of their chance overlap was also low. Thus, grazers were also randomly distributed.

For more balanced ratios of forage:grazer abundances, the frequently grazed areas tended by individual grazers were smaller, comprising only a fraction of the total meadow. Grazers essentially self-confined to a fraction of the meadow for the presumed benefit of higher quality forage. In this state it was possible for frequently grazed areas to merge after chance overlap, resulting in grazer aggregation. However, all ten grazers did not necessarily consolidate into one grazed area. This again was related to forage limitations and the sizes of individually tended grazed areas. As those areas became smaller, fewer animals tended to share a grazed area.

While the merging of grazed areas happened at random – and thus could occur in a shorter or longer time, and involve more or less animals – the eventual break-up of jointly grazed areas was a predictable event, brought on by an excess of grazing. However, this was not a consequence of aggregation per se. Single grazers also abandoned frequently-grazed areas when they became overgrazed. Thus, grouping had neither positive nor negative effects on intake or foraging efficiency. Grouping was simply a by-product of the preference-driven self-confinement of individual grazers (to improve forage quality) and the random drift of frequently grazed areas, which allowed occasional overlap.

Despite obtaining overall evidence for forage mediated grouping, the conditions under which consistent grouping was obtained were relatively narrow, involving a high density of grazers and spatially limited yet readily obtainable resources. This finding is consistent with related empirical studies (McNaughton 1984, Coughenour 1985, Lewin 1985, Lewis 1994).

Grazing lawns and preference for forage quality

Consistent aggregation of grazing herbivores is associated with the development of grazing lawns, areas of low, dense forage containing a high concentration of nutrients (McNaughton 1984). Such lawns arise due to grazing pressure over evolutionary time, which promotes morphological and phenological traits that convey resilience to heavy grazing, and have been observed in numerous grazing systems (McNaughton 1984, Coughenour 1985, Lewin 1985, Semmartin and Oesterheld 1996, Archibald et al. 2005). McNaughton (1984) proposed that the evolution of grazing lawn vegetation required predation pressure in order to force grazers to aggregate and exert local but severe grazing pressure. In this scenario, the evolution of grazing lawn vegetation enabled group living.

The present model showed that frequently grazed areas can also arise spontaneously through grazer preference for vegetation in a state of recovery from recent grazing. Whether or not this can be considered an alternative explanation for the evolution of grazing lawns depends on whether the ancestral forage species also had higher nutritional value after having been recently grazed. Perhaps not, since rapid recovery from defoliation, through the growth of nutrient-rich and fiber-poor new leaves, is a quintessential element of grazing resilience in herbaceous species. Thus, the forage preference observed today may have evolved after the evolution of grazing lawn vegetation.

Moreover, selecting forage biomass closest to the intermediate value permits the surrounding unforaged patches to grow to carrying capacity and increases grazing pressure within the maintained foraging area while reducing growth rate (Schwinning and Parsons 1999). This effect should be intensified in systems wherein aggregation of grazers occurs, resulting in quick overexploitation of available forage. This suggests that although lower biomass is nutritionally favorable for ruminants, its preferential selection may be ecologically unstable, encouraging overexploitation and intraspecific competition, particularly in closed or bounded grazing systems.

Implications for group living

Modern ungulates likely evolved in the mid- to late-Miocene, when climatic conditions began to favor C_4 over C_3 photosynthetic flora (Janis et al. 2000). During this period ecosystems widely converted from C_3-dominated shrublands to the open C_4-dominated grasslands observed today (Janis et al. 2002). Concurrently, C_3-browsing species began to steadily decline ~18 million years ago and were replaced by C_4-grazers (Janis et al. 2000). The loss of browsing ungulate species and increase in the abundance of grazable flora during this period indicates a gradual change in herbivore habitat from widely distributed, shrub-dense ecosystems to the more open grazing systems observed today (Janis et al. 2002). As areas containing grazable forage began to develop and expand, it is likely that such grazing 'islands' were still bounded by shrub-dense systems that were less valuable to grazers. This spatial restriction would increase the likelihood of range overlap among individual grazers and may have provided a necessary condition for the evolution of sociality in gregarious ruminants, perhaps further encouraged by foraging behavior according to the mechanism identified in this model.

However, the present model highlights the relative weakness of exclusively forage-mediated grouping, underscoring the necessity of additional foraging constraints. At a minimum, there is a requirement for the coordination of foraging movements, so that when grazers abandon a jointly grazed area, they do not depart in random directions. This would require, first, awareness of other grazers and, second, an avoidance of letting the distances to other grazers become too large. Mechanisms that delay or avoid overgrazing may also help to stabilize spatial aggregation, which could involve a greater degree of acceptance for high mass, low quality forage, perhaps in the context of avoiding being too close to another animal. Such new rules would supersede the rules of optimal foraging, and are therefore likely to result in decreased foraging efficiencies that should be offset by some other benefit.

It seems unlikely therefore that forage mediated grouping could serve as a stand-alone alternative explanation for the evolution of grouping behavior in social ungulate species. For example, Molvar and Bowyer (1994) examined the effects of group living in Alaskan moose *Alces alces gigas* and found that decreasing predation risk was a better explanation for sociality than improved foraging efficiency due to increased rates of aggression while in close proximity of conspecifics. Similar behavior is observed even in gregarious grazers (Weckerly 1999, Weckerly et al. 2001).

Ultimately, foraging and predator avoidance behaviors are inseparable, as predation pressures co-determine forage:grazer abundance and the likelihood of grouping, while predator avoidance affects foraging efficiencies. Both processes thus co-evolve, and an explanation involving just one process would be incomplete and unsatisfactory. Future studies examining prey species aggregation and the evolution of sociality should consider the reinforcing benefits of selective foraging as consumers aggregate to reduce individual predation risk, particularly in organisms capable of dramatically affecting the distribution and abundance of resources through consistent foraging pressure.

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Supplementary material (available as Appendix O20974 at <www.oikosoffice.lu.se/appendix>). Appendix A1–A2.