

FORAGE ABUNDANCE AS THE IMPETUS FOR LARGE RUMINANT
AGGREGATION: A MODELING APPROACH

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ABSTRACT

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Two distinct explanations exist for the evolutionary origin of grouping in primary consumers: the reduction of individual predation risk and resource-mediated aggregation. Several studies have found little to no relationship between aggregation of a prey species and predation risk, while grazers may aggregate in response to a heterogeneous distribution of resources, suggesting that the second explanation may be more plausible. However, aggregated consumers will deplete resources more rapidly, thus resource mediated aggregation may not be stable. Using a modeling approach, I examine if forage preference alone can generate aggregation, and if so, what are the circumstances of its emergence and stability. The model is a spatially explicit consumer-resource model

using empirically derived parameters to simulate large ruminant foraging in a finite pasture. Model output indicates that grouping can arise in response to forage abundance and population density if grazers exhibit preference for forage of higher nutritional quality, usually associated with intermediate stages of forage growth. In this case, foragers can establish continuous areas of high quality forage wherein they aggregate. However, aggregation is temporary and occurs only within a narrow range of forage characteristics and population density. Findings indicate that resource mediated grouping may provide an alternative explanation for the evolution of sociality in gregarious ruminants during the Miocene epoch, when herbivore habitat transitioned from shrub-dense systems to the open grazing systems observed today. Because no modern analog to the developing Miocene grasslands exists, recent incidence of such grouping is unlikely. Moreover, transiency of grazer-maintained foraging areas occurred across all combinations of model parameters, indicating consumer behavior influenced frequent turnover of foraging areas. Preferential selection of nutritionally favorable (intermediate height) forage permits surrounding unforaged areas to mature while reducing growth rate within the maintained foraging area, suggesting that selection of nutritionally favorable forage may be ecologically unstable.

CHAPTER I

INTRODUCTION

Aggregation should reduce the predation risk of individuals while foraging for resources by group dilution of risk (Hamilton 1971, Alexander 1974, Inman & Krebs 1987, Delm 1990), group defense (Hoogland & Sherman 1976, Parrish & Edelstein-Keshet 1999), or increased vigilance (Elgar 1989, Delm 1990, Molvar & 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 (e.g., Elgar 1989, Quenette 1990, Lima 1995, Treves *et al.* 2001). Such inconsistencies indicate that other functional explanations should be considered to explain grouping behavior. In particular, foraging behaviors exhibited by grazing herbivores have been shown to vary in response to changes in group size and population density (e.g., Clutton-Brock *et al.* 1982, Weckerly 1998, Kie & Bowyer 1999, Weckerly *et al.* 2004). Although the local rate of resource depletion should increase with group size—a cost typically associated with aggregation—individuals within groups may effectively offset this cost by improving the quality of available forage (Fryxell 1991, Post & Klein 1996). If so, it is plausible that aggregation may provide heretofore undetermined benefits to individuals' foraging efforts.

Grazing herbivores can benefit from grouping by positively affecting the quality of subsequent available forage (Fryxell 1991, Van Soest 1994). The nutritional value of younger, pre-reproductive forage to ruminants is typically higher than that of mature forage (Parsons *et al.* 1983, Hofmann 1989, Van Soest 1994). As forage matures, biomass increases, and plant cell walls thicken to provide 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, Parsons *et al.* 1983, Hofmann 1989, Van Soest 1994, Jones & Hartley 1997, Van der Wal *et al.* 2000). Therefore, if consumers have a choice between forage in mature or intermediate (i.e., recently grazed) stages of development, individual grazers should prefer patches with intermediate levels of maturity (Crawley 1983, Fryxell 1991). This would imply that grazers return to recently grazed patches more often than would be expected by chance and could result in grouping.

Area-restricted searching typically results in improved foraging efficiency and intake (Tinbergen *et al.* 1967, Laca 2000, Ohashi & Thomson 2005), and is well-documented in ruminants (e.g., Underwood 1983, Post & Klein 1996, Turchin 1998, Fryxell *et al.* 2005, DeKnecht *et al.* 2007). Characterized by increasing foraging efforts closer to areas where high quality forage was recently found (Tinbergen *et al.* 1967), the resulting depletion in standing crop of forage in patches dictates that grazing ruminants constantly adjust to changes in forage abundance among patches. Once the standing crop of the patch has been reduced to less than that of the surrounding patches, the grazer may begin searching for other areas of high forage abundance, allowing time for the standing

crop in the initially grazed area to renew (Charnov 1976, Ohashi & Thomson 2005). Given that food resources of grazers are often widely dispersed and patches may vary in standing crops of mature and immature forage per unit area (Senft *et al.* 1987), area-restricted searching may retain an individual grazer closer to patches that it recently grazed, thus increasing the chances of return after the grazed patch recovered to an intermediate state of maturity. Individual grazers should therefore be able to produce a self-maintained foraging area, thus reducing search time and improving the nutritional value of their intake. In addition, localized foraging, given sufficient intervals between patch visitation, should in turn increase the abundance of immature standing crop with high forage value within the available foraging area (Fryxell 1991, Van Soest 1994, Van der Wal *et al.* 2000).

Area-restricted searching by individuals could lead to consumer aggregation. All that might be required is the chance driven overlap of two or more individual foraging areas. Since animals would not distinguish one high quality foraging area from another, such areas would be effectively shared, and two or more animals grouped, at the instance of overlap. If consumer aggregation were to occur as described, persistent grouping and the tendency for more if not all grazers in a forage area to aggregate in one large, shared area of high quality forage would require a tendency for consolidated foraging areas to persist once they were formed. However, consistent aggregation within a foraging area utilized by multiple consumers could increase the frequency of overgrazing (Schwinning & Parsons 1999). 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 begs the following critical questions:

1. Can consumer aggregation occur assuming no more than preference for forage of intermediate height and area-restricted searching?

2. If so, how is this phenomenon influenced by forage abundance relative to consumer abundance?

Below I describe a model to examine this scenario. Although other models of forage-mediated grouping exist (e.g., Gueron & Liron 1989, Wilson & Richards 2000a, 2000b), these did not attempt to simulate naturally occurring systems with empirically derived parameters. Furthermore, no studies to date have addressed the relationship between consumer density and total area within which forage is available, and its influence on forage mediated grouping in ungulates. Many ungulate species form temporary and long-term groups whose behavior are closely tied to forage abundance and quality (Hirth 1977, Clutton-Brock *et al.* 1982, Lewin 1985, Fryxell 1991, Molvar & Bowyer 1994, Weckerly 1998, Fryxell *et al.* 2005, DeKnecht *et al.* 2007), and their foraging behaviors and nutritional requirements have been extensively studied and quantified (e.g., Clutton-Brock *et al.* 1982, Spalinger & Hobbs 1992, Gross *et al.* 1993, Van Soest 1994, Barboza & Bowyer 2001, Illius *et al.* 2002, Fortin *et al.* 2004, Kuzyk & Hudson 2007), making them an ideal candidate for such a study. Therefore, I designed a spatially explicit model of large ruminant foraging behavior with continuous distribution of resources (forage), parameterized to simulate the foraging behavior of Roosevelt elk (*Cervus elaphus roosevelti*) in northern Californian meadows. Findings from such a model could provide further insight into the development of social bonding (consistent grouping of family units) within ungulate herds and improve our understanding of the

evolution of grazer aggregation when grasslands began to develop in the Miocene (Janis *et al.* 2002).

CHAPTER II

MATERIALS AND METHODS

Characteristics of Simulated 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 and typically aggregate in herds of 5 to greater than 200 individuals (Weckerly 1999) and inhabit a landscape matrix consisting of forage-rich grazing meadows surrounded by forage-deficient forest habitat. Roosevelt elk preferentially forage within meadows (Weckerly 2005) and may actively forage up to a maximum of 18 hours per day (Clutton-Brock *et al.* 1982). Fortin *et al.* (2004) illustrated that comparable species of grazing ruminants consume approximately 25% of the standing crop within a foraging patch, and elk exhibit similar tendencies (Weckerly, unpublished data).

The forest habitat consists of dense canopy in which coastal redwood (*Sequoia sempervirens*), Douglas fir (*Pseudotsuga menziesii*), and western hemlock (*Tsuga heterophylla*) are ubiquitous. The understory is typically dense and shrubby and contains flora that is not utilized by Roosevelt elk such as bracken fern (*Pteridium* spp.), sword

fern (*Polystichum* spp.), and *Rhododendron* spp. In contrast, the meadow habitats are large open areas (10-1000 hectares) consisting primarily of a continuous distribution 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 2005).

Model Structure

The model was built using a well-established set of equations describing ruminant foraging at the patch scale (Spalinger & Hobbs 1992, Illius *et al.* 2002), spatially extended to the scale of the entire foraging area (e.g., Schwinning & Parsons 1999), and applied to Roosevelt elk using empirically derived model parameters pertinent to the study system (Table 1; Jones 1963, Harper *et al.* 1967, Clutton-Brock *et al.* 1982, Gross *et al.* 1993, Fortin *et al.* 2004, Kuzyk & Hudson 2007). The foraging area was represented by a variably sized two-dimensional array of contiguous, homogeneous 1 x 1 m cells, approximating the foraging area taken up by Roosevelt elk individuals (Clutton-Brock *et al.* 1982). Henceforth, the entire foraging area will be referred to as the meadow, and cells as patches.

Patch quality was represented by biomass density and was permitted to vary independently according to grazing and growth rate. Ten identical grazers were distributed randomly throughout the meadow and permitted to move between adjacent patches, selecting patches on the basis of comparing their biomass densities. Upon selecting a patch for exploitation, grazers moved into the patch and uniformly depleted

the available forage by a fixed predetermined percentage, then move on. Grazers continued to forage until either their daily intake requirements were met or the maximum time allotted to foraging was utilized (i.e., at "night"). Forage growth occurred only after all grazers had achieved one of these two predetermined states.

Forage Growth

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

$$b_{forage}(t+1) = b_{forage}(t) + b_{forage}(t) * r * (1 - b_{forage} / k), \quad \text{equation 1}$$

where b_{forage} is biomass density of forage available for consumption (g DM/m²), r is the relative rate of forage growth (d⁻¹), and k is a carrying capacity (g DM/m², Verhulst 1838). Density-dependent growth was selected to model forage growth for its prevalence in studies of plant growth (Thornley & Johnson 2000), describing well the asymptotic behavior as forage biomass matures (Verhulst 1838).

Foraging decisions are presumed to be made on the basis of forage quality, which was not modeled explicitly. Instead, it was assumed that forage quality is maximized at $0.5*k$, representing forage in an intermediate state of growth, consistent with observation (Crawley 1983, Fryxell 1991, Van Soest 1994).

Foraging Decisions

The rules for general grazing behavior and movement were modeled to simulate observed patterns of Roosevelt elk foraging behavior (e.g., Weckerly 1999, Weckerly *et al.* 2001, Weckerly *et al.* 2004). An individual simulated grazer follows a stepwise decision-making process:

1. Patch selection: The grazer assesses the quantity/quality of forage contained in the eight patches immediately adjacent to the patch it occupies and determines which patch has the smallest absolute difference from the "ideal" patch state, b_{pref} (g DM/m²), assumed to be equal to $0.5*k$. However, some patches are immediately excluded from this assessment if a) patch biomass is below the ungrazable horizon, $b_{ungraze}$ (g DM/m²), b) it lies outside the meadow boundary, or c) it is occupied by another grazer. Ruminants decrease their foraging efforts in areas of low forage abundance (e.g., Underwood 1983, Post & Klein 1996, Fryxell *et al.* 2005), and Roosevelt elk become increasingly aggressive within one body length of conspecifics (Weckerly 1999, Weckerly 2001). If multiple patches are of identical quality, the grazer selects randomly from those patches. If none of the adjacent patches are acceptable according to the above criteria, the grazer assesses the next adjacent sixteen patches applying the same rules for selection. If still no patches are viable, then 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: Once a target patch has been selected, the grazer moves into the target patch. It is assumed that movement to an adjacent or next to adjacent cell has a

Table 1. Variables and parameters of the foraging model.

Parameter Description	Symbol	Value and Unit	Citation
Number of Grazers	N_{grazer}	10 grazers	--
Meadow Size	--	600 m * 600 m	--
Carrying Capacity	k	495 g DM/m ²	Jones 1963
Rate of Growth (% standing crop)	r	0.05* b_{forage} g DM	--
Forage Biomass	b_{forage}	Variable, g DM	--
Preferred Forage Biomass	b_{pref}	0.5* k g DM	Crawley 1983
Ungrazable Horizon	$b_{ungraze}$	0.01* k g DM/m ²	--
Offtake (% standing crop)	o	0.25* b_{forage} g DM	Fortin <i>et al.</i> 2004
Body Size	w	272154 g	Harper <i>et al.</i> 1967
Maximum Gut Content	b_{gut}	0.01* w g DM	Kuzyk & Hudson 2007
Patch Area	A_{patch}	1 m ²	--
Bite Area	A_{bite}	0.01 m ²	Harper <i>et al.</i> 1967
Number of Bites to Defoliate Patch	N_{bites}	A_{patch}/A_{bite} bites	--
Crop Time	h	0.012 min	Gross <i>et al.</i> 1993
Bite Size	S	$o*b_{forage}*A_{bite}$ g DM	--
Maximum Processing Rate	R_{max}	52.95 g DM/min	Gross <i>et al.</i> 1993
Time to Defoliate Patch	T_{defol}	Variable, min	--
Maximum Foraging Time	T_{max}	1080 min	Clutton-Brock <i>et al.</i> 1982

negligible or 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 time cost of one minute for movement. Although not necessarily realistic, this avoids an artifact of unlimited foraging movement in a uniformly overgrazed meadow, but otherwise 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 defoliating its patch, even if the patch it is leaving is of higher quality than the target patch. This encourages constant movement while foraging (Clutton-Brock *et al.* 1982) and allows the grazer to constantly assess the quality of surrounding forage based on the principles of area-restricted searching (Tinbergen *et al.* 1967, Ohashi & Thomson 2005).

3. Intake: The grazer uniformly defoliates the forage contained in the target patch. Specific rules for the consumption of forage are discussed below. If the target patch was selected at random and none of the patches surrounding the originally occupied cell were grazable according to step 1, the grazer does not defoliate the patch and proceeds with patch selection (step 1) without delay.

This sequence of individual foraging decisions continues until the grazer has either consumed the maximum amount of forage permitted by its body weight, b_{gut} (g), or the maximum daily time allotted to foraging, T_{max} (1080 min), has elapsed (see Table 1).

Offtake and Grazing Constraints

Each patch is uniformly defoliated by 25% of the standing biomass or to a minimum at the ungrazable horizon. Grazing incurs a time cost, described by equations introduced by Spalinger & Hobbs (1992) and rearranged by Illius *et al.* (2002). This cost has two components: the fixed time required for apprehending a bite, and the time required for chewing the apprehended biomass (which is proportional to the bite size):

$$T_{bite} = h + S/R_{max}, \quad \text{equation 2}$$

where h is the time required to crop a bite (min), S is the size of the bite (g DM), and R_{max} is the maximum rate at which food may be processed (g DM/min). To estimate a realistic foraging time for a 1 x 1 m patch, we must also determine how many bites are taken to defoliate the patch uniformly. Assuming the grazer has a bite area of A_{bite} (m²) and forages from a patch of area A_{patch} , the number of bites required to uniformly defoliate the forage contained in the patch is $N_{bites} = A_{patch}/A_{bite}$, thus the total time required to defoliate the patch becomes,

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

Further, grazers defoliate the available forage by a set percentage, o (g DM).

Given the bite area A_{bite} , one may determine the bite size as,

$$S = o * b_{forage} * A_{bite}. \quad \text{equation 4}$$

Substituting this value into equation 3 provides the time in minutes required to uniformly defoliate a patch based on percent offtake and bite area,

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

Indicators of Grouping

Grouping in a biological sense is traditionally recognized as a reduction in interpersonal distance in relation to total available space. Such aggregation of consumers suggests the use of spatial autocorrelation statistics to determine the degree of clustering (Moran 1950, Geary 1954, Premo 2004). However, estimates of spatial autocorrelation measure the likelihood with which an event will occur (i.e., presence/absence of a consumer) given its occurrence in a nearby area and suggests long-term predictability in spatial patterns. This distinction is unnecessary for the quantification of grouping as defined above. Consumer aggregation, both realistically and within the model, may be temporary and can be easily quantified as a decline in average interpersonal distance in relation to time and space.

Herein, grouping was defined as a reduction in the average minimal distance between all grazers (AMD) relative to the average minimal distance of the randomly placed grazers (AMD_0) in a meadow of identical size. To calculate this statistic, for each grazer the distance to the next nearest neighbor was calculated and averaged across all grazers. To minimize the influence of temporal autocorrelation on this measure and promote independence of individual estimates, this statistic was recorded every ten minutes of simulated time and averaged at the end of each foraging day to obtain an estimate of AMD across a single day. AMD_0 was derived by running 100 simulations wherein the grazers were distributed randomly within the meadow and calculating the mean AMD of all simulations. A grouping index (I) was then calculated as AMD/AMD_0 such that $I < 1$ indicates aggregation relative to a random distribution and $I > 1$ indicates hyperdispersion relative to random distribution.

All simulations were started at uniform carrying capacity for the meadow and a random distribution of 10 grazers. Even though the exact time to steady state was generally difficult to determine, because the grouping index often continued to fluctuate, we selected a conservative value of 30,000 simulation days, after which we sampled AMD once every ten simulated days to determine the grouping index I (see Appendix for detail).

Parameters of Interest

Model parameters that most influence forage mediated grouping were determined to be those directly influencing forage abundance, namely number of available patches (meadow size), carrying capacity of forage per patch (k), and forage growth rate per patch (r). Simulated meadow sizes ranged from 100 x 100 m² to 600 x 600 m² in increments of 100 m length and width, or 1 to 36 hectares. Although this does not reflect the full range of meadow sizes available to *Roosevelt elk*, it varies the number of potential foraging patches by more than an order of magnitude, thus capturing some of the variation in meadow sizes and permitting a comparison between "small" and "large" meadows.

Parameters of forage growth (r and k) were varied to encompass all naturally occurring values. Jones (1963) described the maximum harvestable yield across seasons for grasslands in a county adjacent to that wherein *Roosevelt elk* foraging behavior was studied, Mendocino county, California. Forage carrying capacity was thus varied to reflect the values found in Jones (1963). Because no estimates for growth rate in

California grasslands could be obtained, forage was permitted to grow at a rate of 1% to 20% of forage biomass within a patch on a per day basis in increments of 1%.

CHAPTER III

RESULTS

Effect of Forage Abundance on Grouping

Because forage mediated grouping can only occur when there is sufficient forage to support a population of grazers, simulations began with the highest possible carrying capacity (495 g DM/m²), and growth rate was varied from 0.01-0.2. 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 x 600 m²), all mean values of I were well below one.

Similar results were obtained by varying carrying capacity from 165-495 g DM/m² instead of forage growth rates (Fig. 2). For this simulation, we chose an intermediate value of r (0.16) that produced grouping in the previous set of simulations. Again, grouping occurred in all but the smallest meadow sizes and tended to increase with carrying capacity up to a point. The smallest carrying capacity required to produce grouping declined as meadow size increased. Variation in I again increased with meadow

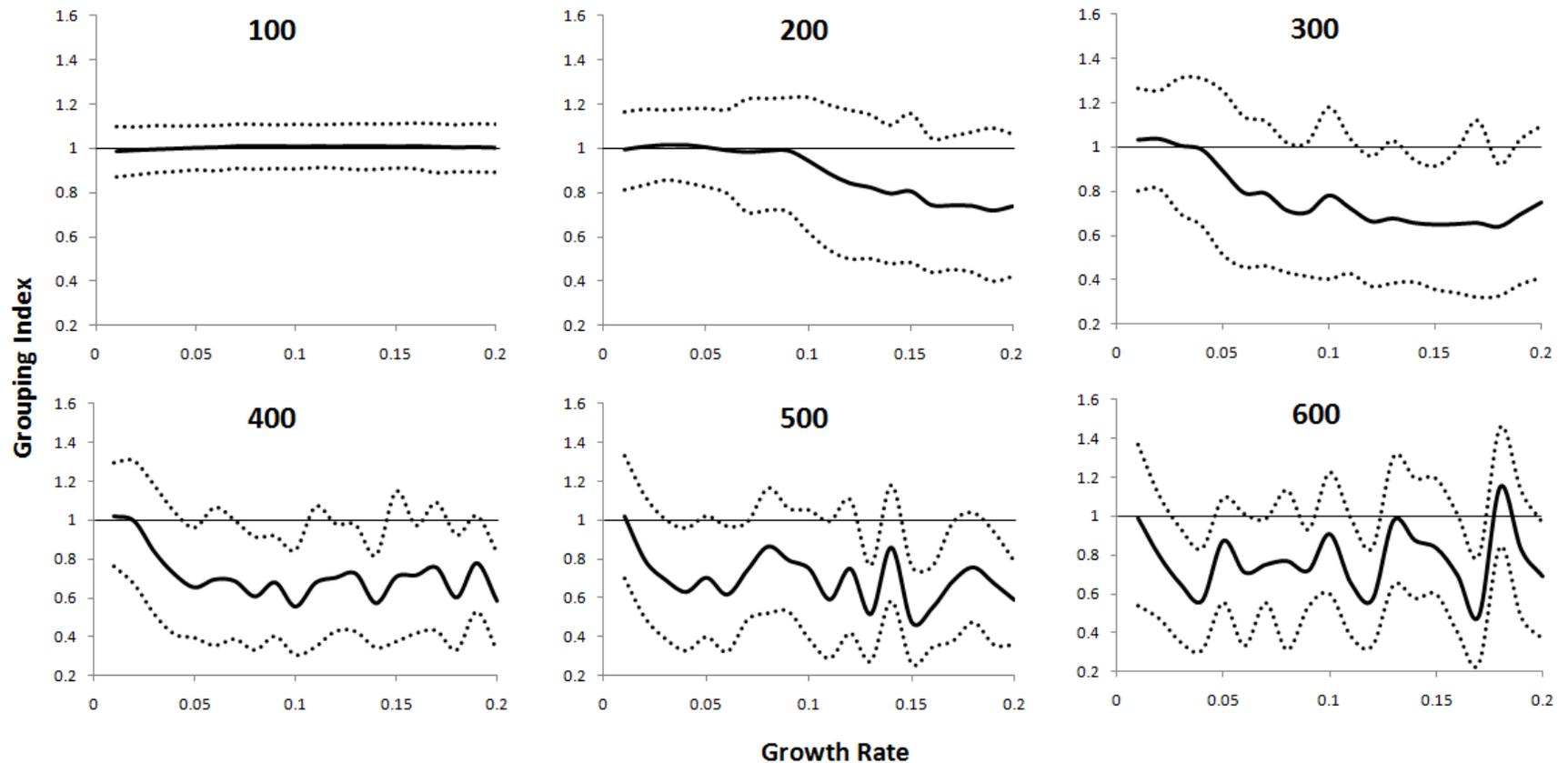


Figure 1. Changes in Grouping Index (I) as a function of forage growth rate (r). The title for each panel describes the size of the meadow (e.g., 100 x 100 m²). The dotted lines represent the upper and lower 95% CIs for the estimate of I . The value of k was kept constant across all panels at the default of 495 g DM/m². 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.

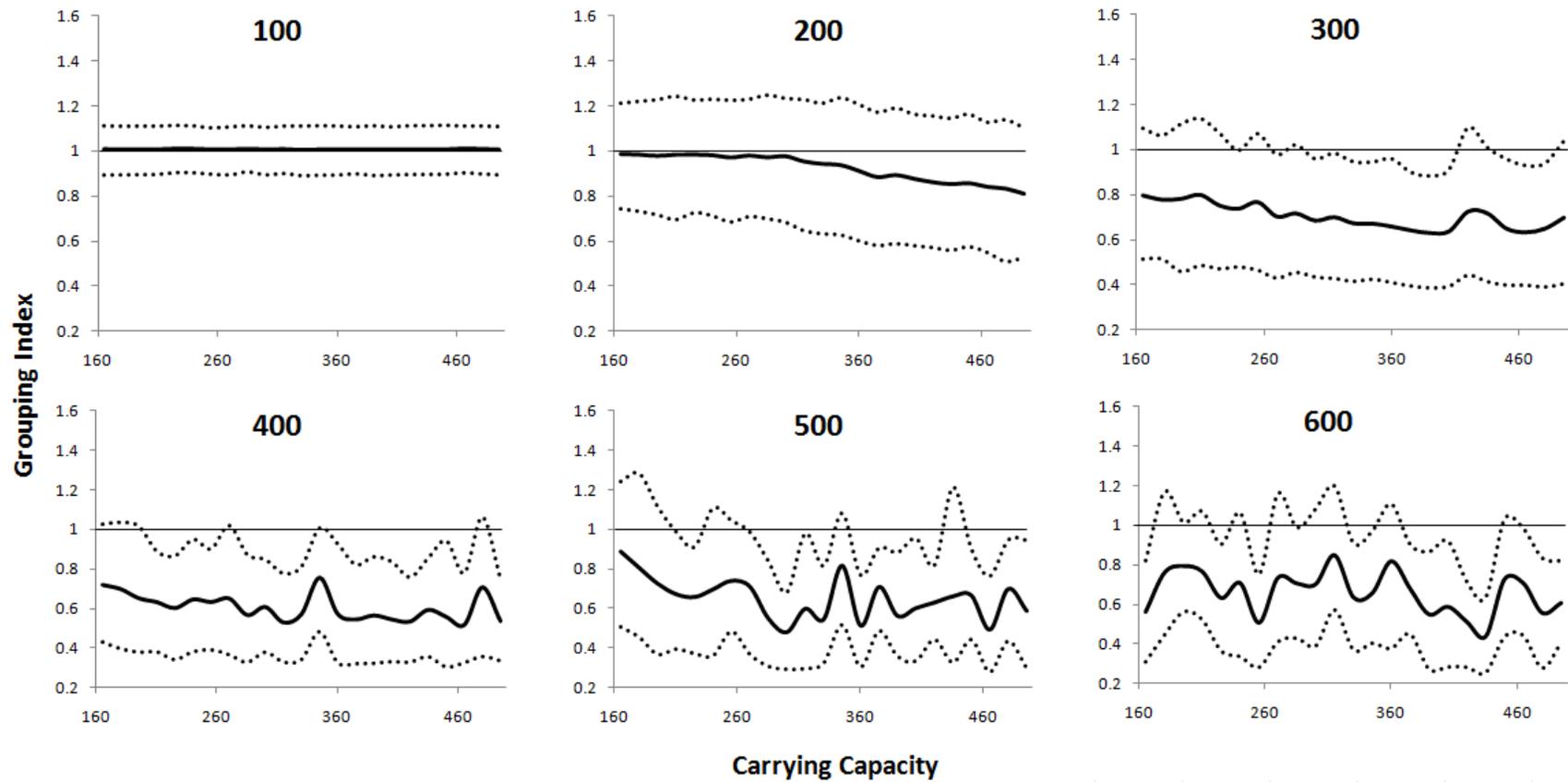


Figure 2. Changes in Grouping Index (I) as a function of patch carrying capacity (k). The title for each panel describes the size of the meadow (e.g., 100 x 100 m²). The dotted lines represent the upper and lower 95% CIs for the estimate of I . The value of r was kept constant across all panels at 0.16, which promoted grouping across all meadow sizes wherein grouping occurred. Significant decreases in I are observed with increasing k across all but the smallest meadow size, with increasing variation in I as meadow size increases.

size and carrying capacity, although the amplitude of this variation was not as large as that observed with changing rate of growth (Fig. 1).

Thus, increases in forage abundance by three different methods (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 suggests that meadow state, more so than any specific model parameter, mediates the occurrence of grouping.

Meadow States

For this analysis, spatial patterns of meadow state associated with changing values of I were examined. Incidents of strong grouping ($I < 1$) were typically observed in conjunction with the existence of large, continuous areas of low forage abundance relative to the surrounding ungrazed patches (Fig. 3 & 4). The size of such areas decreased with increasing forage abundance and ultimately demonstrated a tendency to disintegrate into multiple smaller foraging areas, each one tended by one or two grazers. Disintegrated areas could still produce low values of I in the largest meadow sizes if maintained foraging areas were more clustered than would be expected by chance (Fig. 3b & 4b). However, they could also be dispersed randomly. This explains in part the high degree of variation in I at high forage abundances (Fig. 1 & 2).

Incidents of weak grouping ($I \approx 1$) under conditions of low forage abundance were typically associated with a more uniformly depleted meadow (Fig. 5 & 6). Low

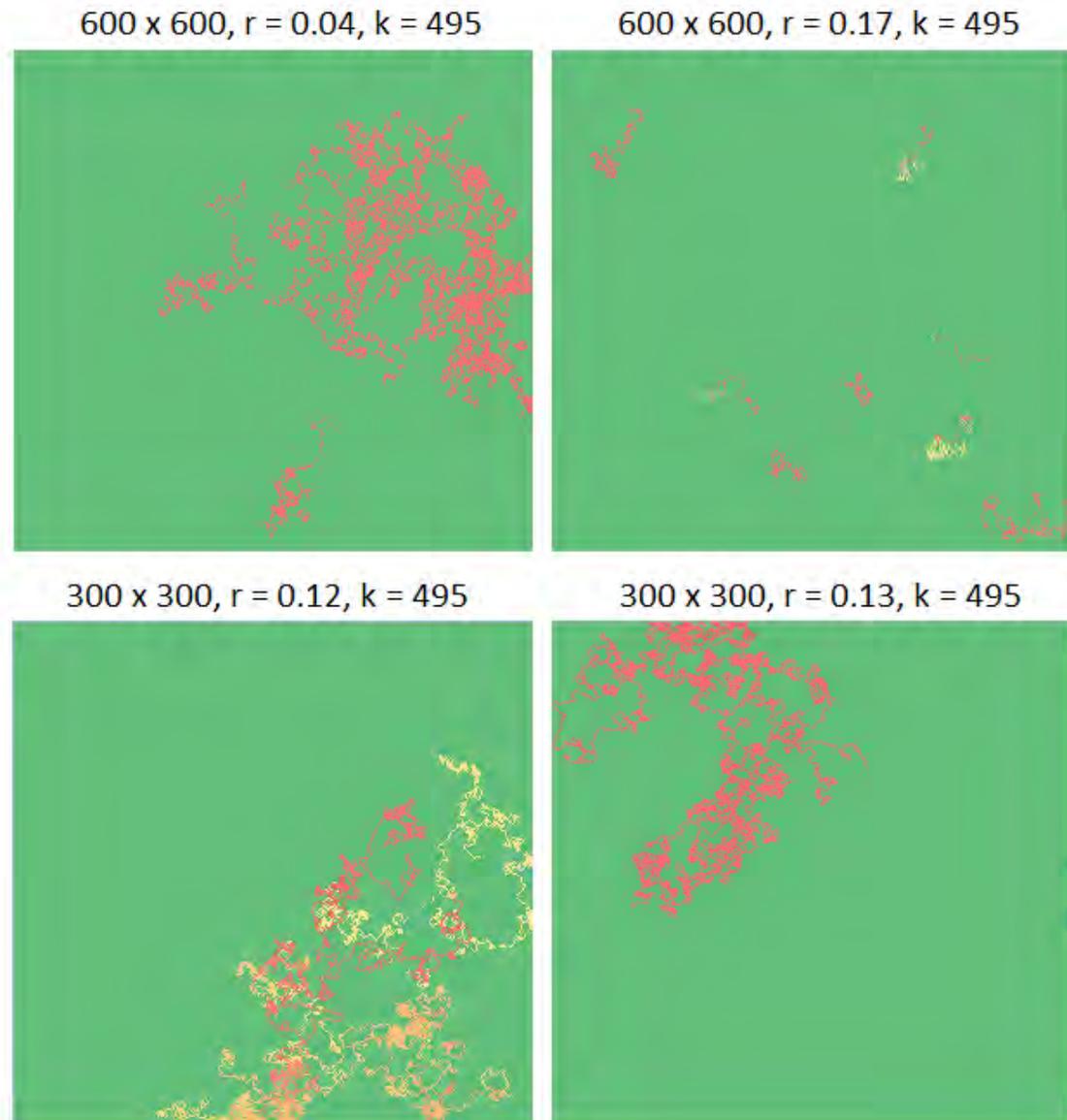


Figure 3. Snapshot of meadow-wide forage abundance when Grouping Index (I) equals that in Fig. 2 at the rate of growth (r) and meadow size specified by the panel title. Within patch forage biomass increases from red to green. Small values of I are typically associated with the presence of grazing lawns 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.

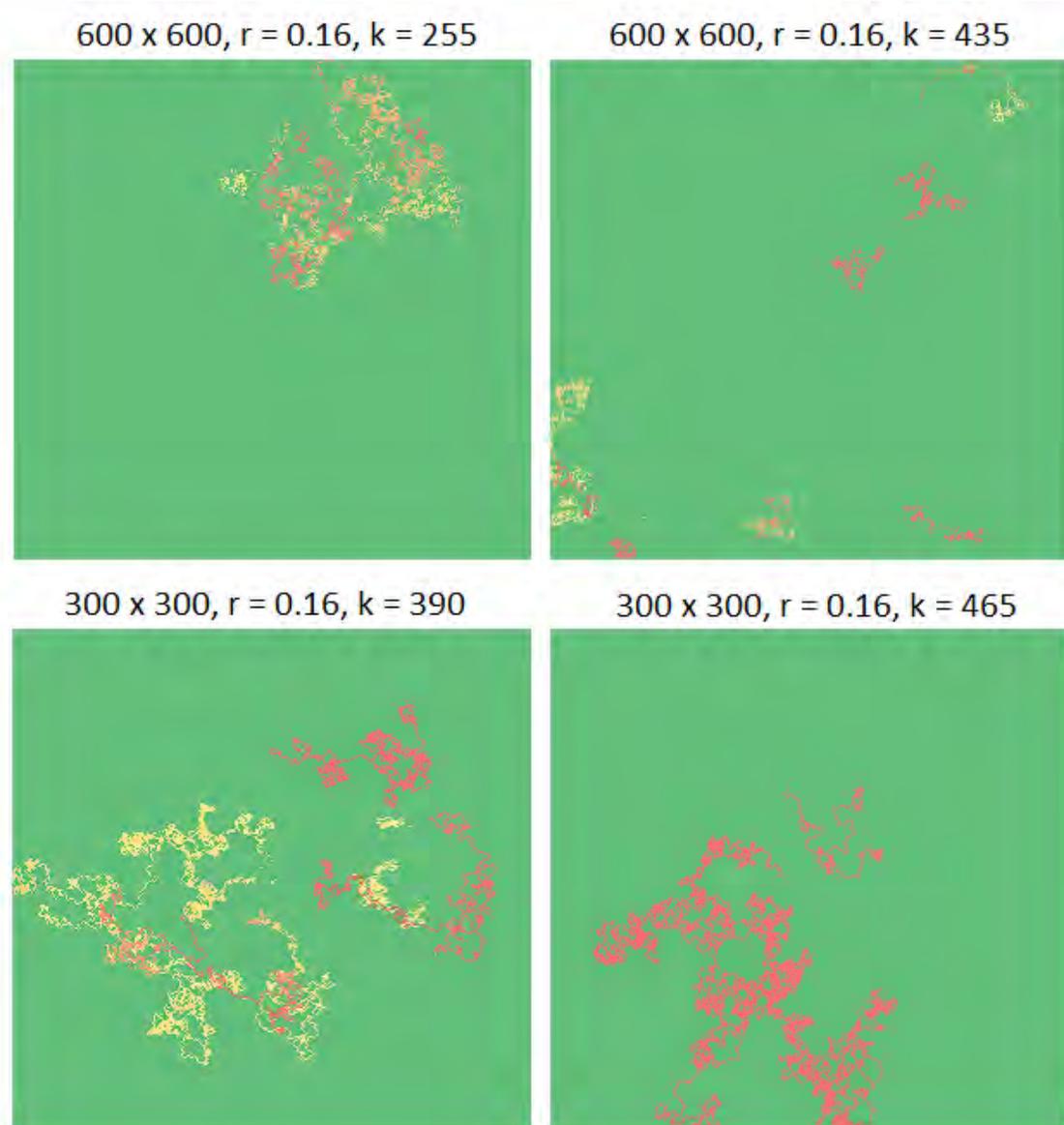


Figure 4. Snapshot of meadow-wide forage abundance when Grouping Index (I) equals that in Fig. 3 at the carrying capacity (k) and meadow size specified by the panel title. Small values of I are typically associated with the presence of grazing lawns utilized by multiple grazers. In large meadow sizes with high k , individual grazing lawns may not coalesce, but small values of I may occur due to spatial clustering of individual lawns.

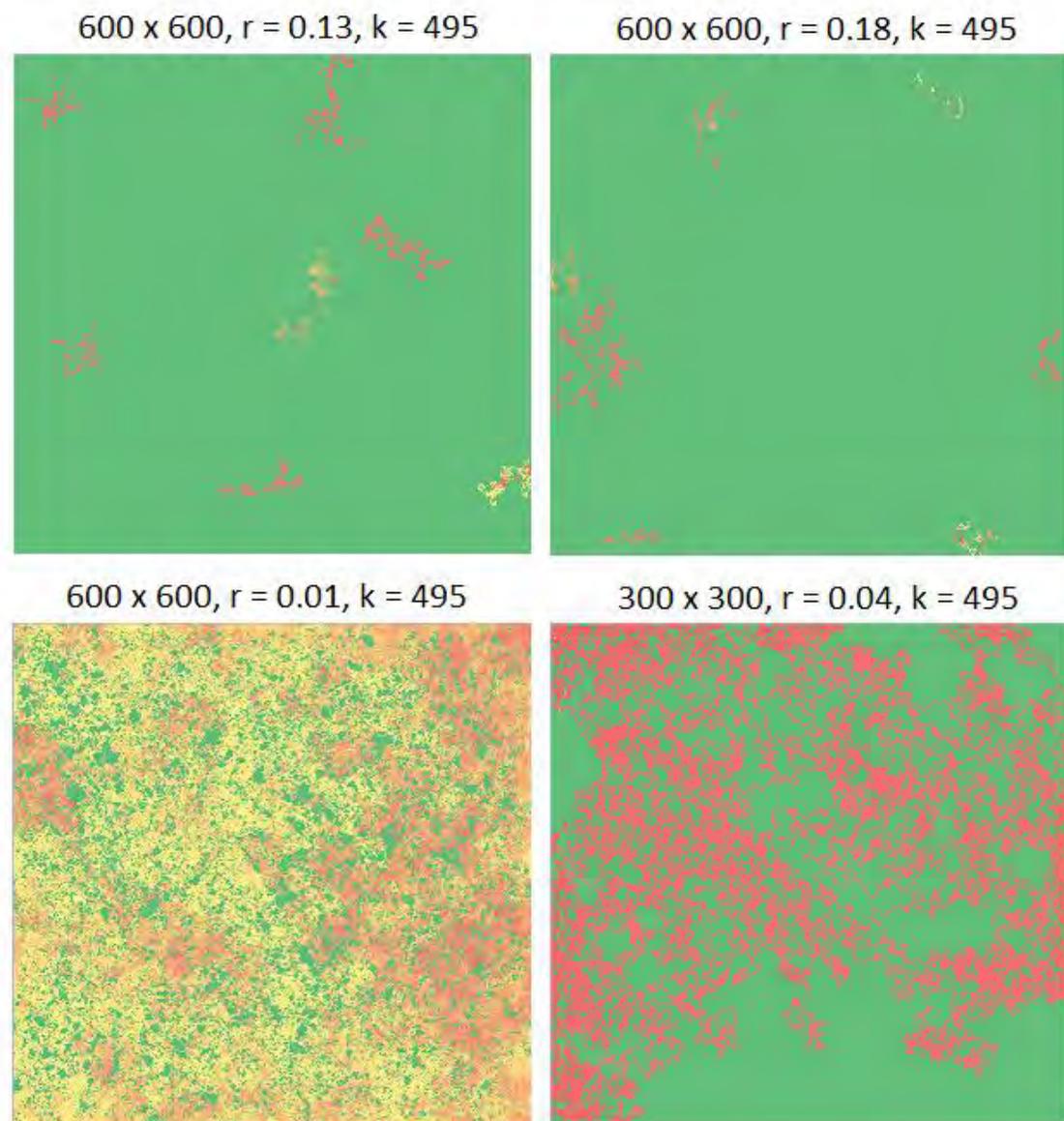


Figure 5. Snapshot of meadow-wide forage abundance when Grouping Index (I) equals that in Fig. 2 at the rate of growth (r) and meadow size specified by the panel title. At low r , large values of I are associated with grazing lawns that span the entire meadow at large meadow sizes or overexploitation 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.

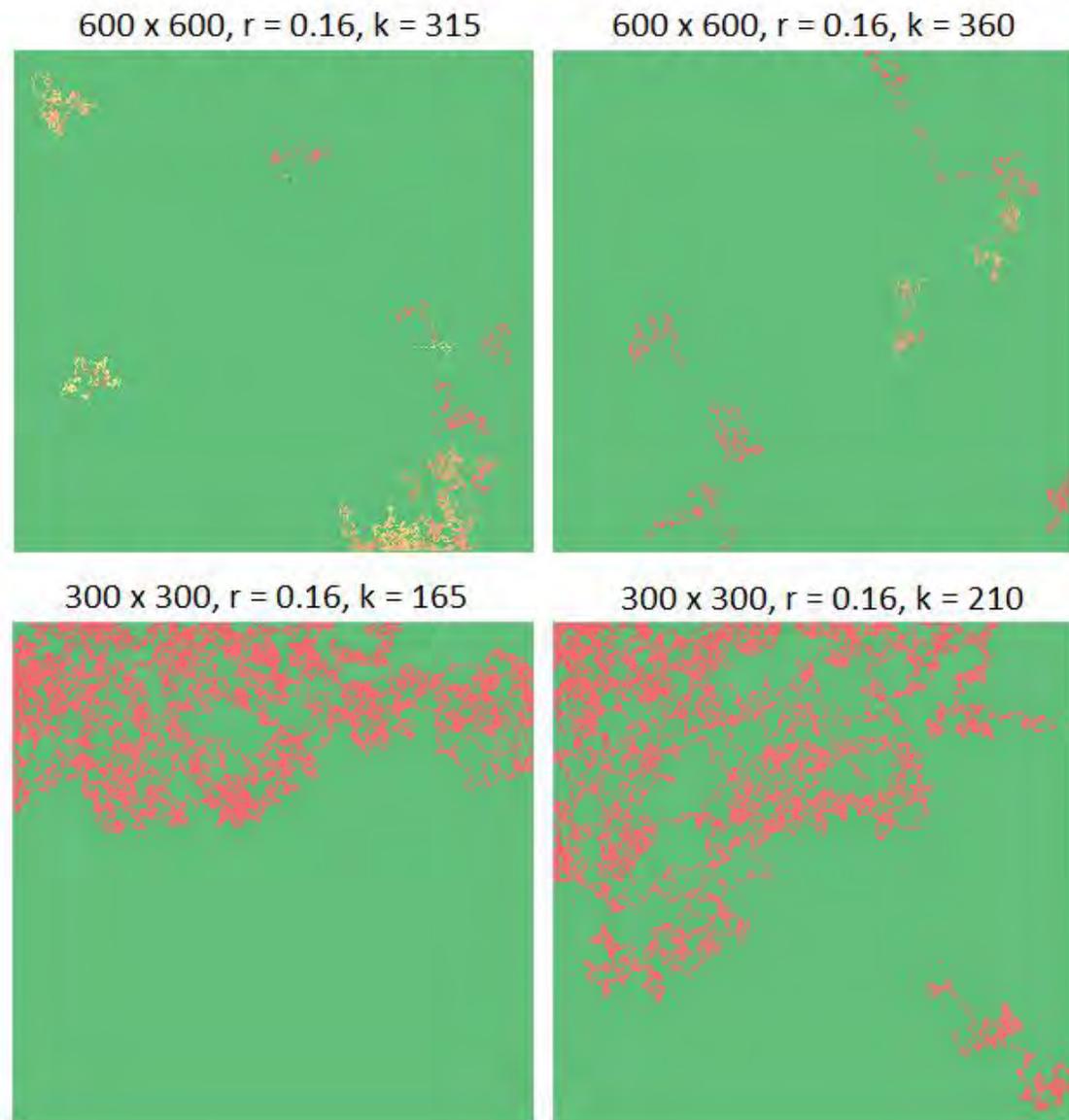


Figure 6. Snapshot of meadow-wide forage abundance when Grouping Index (I) equals that in Fig. 3 at the carrying capacity (k) and meadow size specified by the panel title. Large values of I at low k are associated with grazing lawns that span a large proportion of the available meadow. At high k , large I values are typically associated with random distributions or hyperdispersion of individual grazing lawns.

biomass foraging areas were substantially larger and contained more patches when resources were less abundant, often resulting in areas spanning 50-100% of the foraging habitat. Particularly low forage abundance resulted in uniform overexploitation of the entire meadow. As before, with increasing forage abundance, consumer-maintained foraging areas contracted, spanning an increasingly smaller proportion of the entire meadow area, with the result of reducing observed grouping.

CHAPTER IV

DISCUSSION

Mechanism of Forage Mediated Grouping in Grazers

The purpose of this research was to determine if consumer aggregation would arise as a consequence of assumptions of optimal foraging (area restricted foraging and patch selection) using realistic, empirically-derived model parameters and equations. The model supports this hypothesis, as indicated by the declining value of I produced in many simulations. However, the model 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 had the largest propensity to group consistently; and when forage abundance was high, grazers could group but did not do so consistently.

Further, these distribution patterns were associated with the sizes of grazer-maintained foraging areas created under the variable conditions of forage abundance. Under the highest levels of forage limitation, there was only one large area that encompassed the entire meadow. Within that area, patch states are relatively uniform, resulting in foraging paths that are more nearly random, thus dispersing animals

randomly throughout the meadow. As forage abundance increases, the area required to obtain resources adequate to meet an individual's nutritional demands decreases (McNaughton 1984). This eventually leads to the contraction of the foraging area, becoming smaller than the entire available meadow. At that point, patch choices made by the consumers become relevant and will tend to retain grazers within the confines of the maintained foraging areas, as forage outside such areas is of lesser quality. This is the condition under which we see the most consistent patterns of grouping, as grazers self-confine to a fraction of the meadow. The model output clearly indicates that predictable, consistent grouping in grazing ruminants requires high population density and limited yet readily obtainable resources. This finding is consistent with other related studies (e.g., McNaughton 1984, Coughenour 1985, Lewin 1985, Huntly 1991, Lewis 1994, Wilson & Richards 2000b, Dwyer & Morris 2006).

As forage abundance further increases, individual daily foraging paths taken by the grazers shorten, as grazers spend more time exploiting individual patches. This contracts the consumer maintained foraging areas to such an extent that animals can become cut off from each other by "barriers" of mature forage. At this stage, each grazer becomes associated with a distinct, self-maintained foraging area, which drifts independently from other foraging areas across the meadow. Thus, grazers can become randomly distributed once again. However, this distribution is not entirely random as attested by the on average low, but highly oscillatory, value of I (Fig. 1 & 2). This condition is characterized by the intermittent emergence of coalesced foraging areas involving any number of grazers and their eventual drifting apart. The oscillations seen in Figures 1 and 2 indicate a high degree of temporal autocorrelation. Thus, highly

dispersed foraging areas tend to remain separate for long periods of time and coalesced areas tend to remain coalesced for long times as well.

Despite obtaining overall evidence for forage mediated grouping, the conditions under which consistent grouping was obtained were surprisingly narrow and restricted to intermediate forage abundance, where forage was abundant relative to population density, but not excessively so. Selecting realistic values for r and k , our model suggests that grouping should be seen among large grazing ruminants for population densities between 1.1 and 2.5 grazers ha^{-1} . Consumer densities below this range likely result in overexploitation of resources, and densities above this range can produce a random distribution of consumers. Increasing or decreasing forage abundance will similarly shift the associated range of consumer densities that can promote grouping. Our model held consumer density constant within meadow sizes, but the relationship between forage and consumer abundance is clearly not independent.

Evolution of Group Living

These results have implications for the evolution of sociality in grazing ruminants. As previously noted, studies have provided inconsistent results when attempting to correlate group living and predation (e.g., Elgar 1989, Quenette 1990, Uetz & Hieber 1994, Lima 1995, Treves *et al.* 2001). Forage mediated grouping may provide an explanation for these inconsistencies. 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, Janis *et al.* 2004). During this period ecosystems widely converted

from C₃ dominated shrublands to the open C₄-dominated grasslands observed today (Janis *et al.* 2002, Janis *et al.* 2004). Concurrently, C₃ browsing species began to steadily decline ~18 million years ago and were replaced by C₄ 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, Janis *et al.* 2004). 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 optimal foraging behavior according to the mechanism identified in this model.

As a caveat to this conclusion, the developing grassland ecosystems of the latter Miocene epoch have no modern analog (Janis *et al.* 2000, Janis *et al.* 2004). Given the close interaction between consumer density and forage abundance, it seems unlikely that forage mediated grouping could serve as an alternative explanation for the evolution of grouping behavior in more recently social ungulate species. For example, Molvar and Bowyer (1994) examined the effects of group living in *Alces alces gigas* (Alaskan moose) 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 in highly social grazers (e.g., Weckerly 1999, Weckerly *et al.* 2001) indicates that further research into forage mediated grouping is needed to determine if it is behaviorally viable in previously non-social species.

Grazing Lawns and Absence of Predation

Another mechanism typically associated with the aggregation of grazing herbivores is the development of grazing lawns, areas of low, dense forage containing a high concentration of nutrients (McNaughton 1984, McNaughton 1986). Such lawns arise due to consistent grazing pressure over extended periods of time, which promotes the evolution of morphological and phenological traits favoring plant survivorship in response to grazing, and numerous grazing species have been shown to exhibit this behavior across a wide variety of foraging habitats (e.g., McNaughton 1984, Lewin 1985, Coughenour 1985, Milchunas & Lauenroth 1989, Semmartin & Oesterheld 1996, Werger *et al.* 2002, Archibald *et al.* 2005). McNaughton (1984) proposed that the development of grazing lawns required predation pressure in order to force grazers to aggregate, after which their combined foraging efforts would sufficiently defoliate the grazing area and produce a grazing lawn. The improved foraging efficiency achieved by utilizing the lawn then promoted the evolution of sociality.

Grazing lawns should not develop in systems where predation pressure is minimal or nonexistent. This model, however, indicates that predation is not necessary for the formation of grazing lawns. Model output indicated that preferential selection of forage can produce a large area of low forage biomass that is utilized by multiple grazers (Fig. 3 & 4). This grazing pressure is the fundamental environmental condition required for the evolution of grazing lawns (McNaughton 1984, McNaughton 1986) and occurs in the absence of predation pressure given the appropriate forage characteristics (limited forage abundance and limited patches relative to population density). Given this, it may be

asserted, at least theoretically, that the development of grazing lawns may arise in grazing systems with little to no predation.

Transiency of Maintained Foraging Area

Although not shown here, real-time graphic output indicated that maintained foraging areas were not stable over time. Grazers would develop and utilize an area until the average within patch biomass was at or below the ungrazable horizon, at which point they would abandon it and develop a new foraging area elsewhere. McNaughton (1986) noted that overexploitation of resources could occur in closed foraging areas such as that utilized in this model and suggested this behavior was associated with population density. Conversely, given that overexploitation was observed across all meadow sizes, it is more likely that consumer behavior is responsible for grazing lawn transiency.

In particular, preferential selection of forage seems a likely driver of foraging area turnover. Conventional wisdom holds that low to intermediate biomass is nutritionally favorable for grazing ruminants (Parsons *et al.* 1983, Van Soest 1994); however, 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 & 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, particularly in closed or bounded grazing systems. Further investigation of

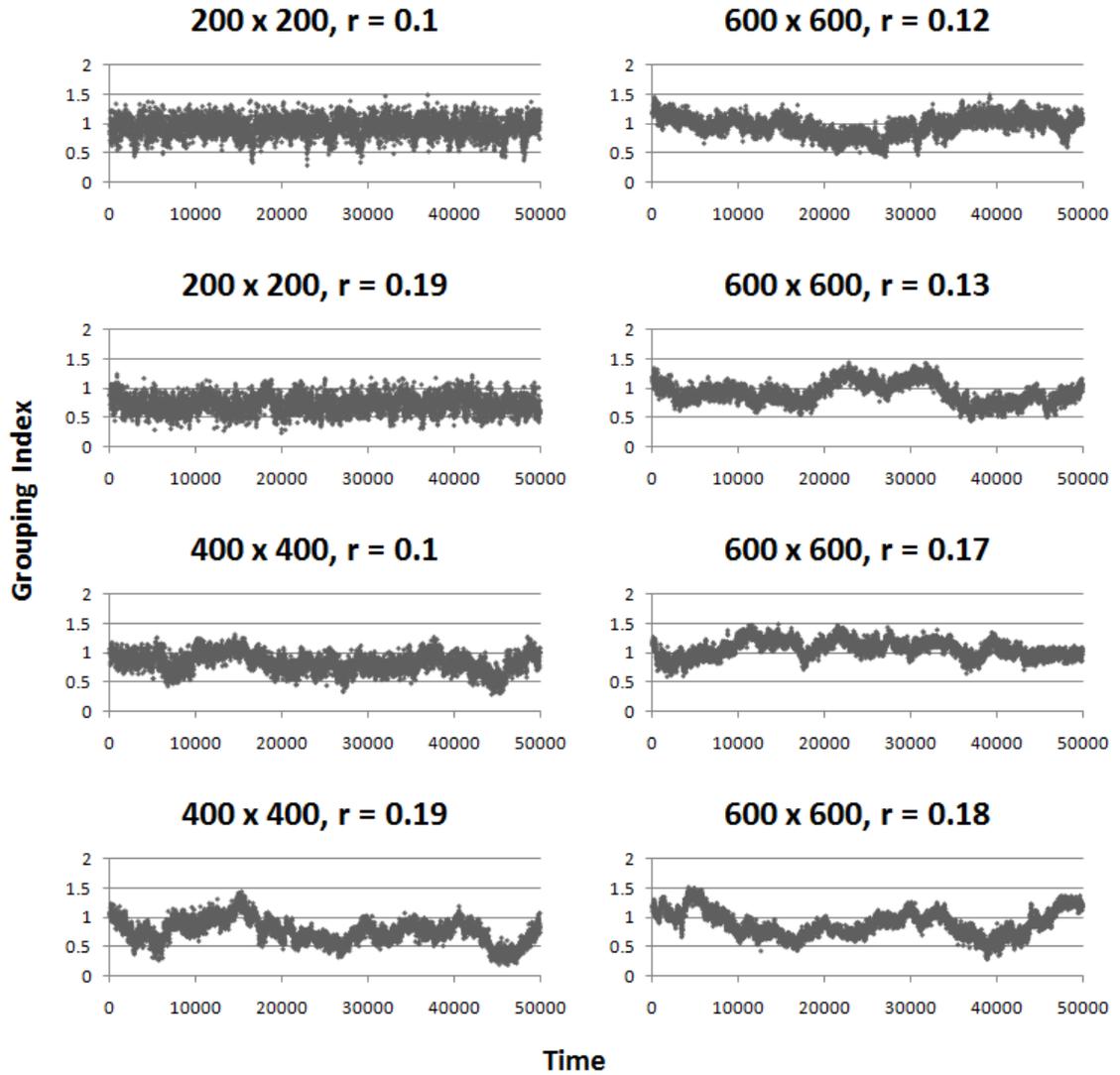
forage selection, specifically in terms of meadow- or patch-scale grazing stability (Noy-Meir 1975, Schwinning & Parsons 1999), may yield new insight into this phenomenon.

APPENDIX

DETERMINATION OF MODEL EQUILIBRIUM

Determination of the equilibrium state of a mathematical model is a nontrivial task. Model output may be unreliable if one does not account for the influence of initial conditions such as abnormal consumer distribution or resource homogeneity, particularly in complex systems (Thornley & Johnson 2000). The stochastic nature of this model resulted in highly variable values of I within a single simulation and across all combinations of model parameters (Fig. 7), complicating the determination of the equilibrium state. Furthermore, the maintain-breakout cycle of grazing lawn transience (see Discussion) makes identification of a traditional equilibrium state impossible in this model.

Regardless of initial parameter values, unforaged patches were observed to obtain k within 100-200 days, and grazers had established grazing lawns. However, because I continued to decline and had not begun to vary at that point, it was decided to permit the system to run for several thousand days in order to observe the developing variation in I . The system was observed to begin variation by $t = 15000$ at the latest, thus the approximated time to achieve equilibrium was doubled to $t = 30000$. The remaining 20000 simulated days were used to obtain estimates of I (Fig. 1 & 2) and meadow state images (Fig. 3-6).



Changes in Grouping Index (I) over simulated days within a single model run. Extreme variation in I is obtained across all combinations of model parameters wherein deviation from the null model ($I = 1$) occurs

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