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# EXPLORING AGGREGATION IN SPACE AND TIME

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## SUMMARY

Population and ecosystem processes are heterogeneous in both time and space, and every ecological study requires some level of aggregation or abstraction. Aggregating organism or environmental dynamics is challenging because the processes occur at a variety of spatial and temporal scales, and the scale-dependent effects of aggregation are not well understood. We used a spatially explicit individual-based simulation model of winter foraging and survival of free-ranging ungulates in northern Yellowstone National Park to explore effects of aggregation in space, in time, and of individual animals on model predictions. Aggregation in space was examined by (1) varying the heterogeneity represented in forage abundance across the landscape and (2) eliminating spatial heterogeneity in the accumulation of snow. Results suggest that any aggregation that averages the broad-scale patterns of forage biomass availability underestimates ungulate survival. Aggregation in time was examined by varying the temporal grain used to simulate snow accumulation through the winter. Ungulate survival was not sensitive to this temporal grain, probably because the response remained linear within the range explored. Aggregation





of individuals was done by varying the number of individuals contained within ungulate groups assumed to contain identical individuals. Aggregating across individuals was reasonable for small group sizes but led to substantial underestimates of survival for large group sizes. The effect of aggregation on an ecosystem or population parameter is a function of the question asked and a specified spatial and temporal scale. Even successful aggregation of processes will be reliable only if dynamic thresholds are not crossed, if keystone species are not eliminated, and if feedback loops remain intact.

## INTRODUCTION

Whenever ecologists study populations or ecosystems, phenomena of interest must be abstracted from the vast complexity of the world. For example, the study of a particular bird population requires decisions about what attributes of the vegetation (e.g., species, phenology, vertical or horizontal structure, age), other species with which it interacts (e.g., competitors, predators, or prey), and ecosystem-level processes (e.g., net primary production) are sufficiently important to warrant inclusion. Similarly, the study of ecosystem-level processes (e.g., production, decomposition) requires decisions about what species or species groupings must be included. Every ecological study, be it empirical or theoretical, requires some level of aggregation. To understand a population, what ecosystem phenomena must be disaggregated? To understand an ecosystem, what population phenomena must be aggregated?

Hierarchy theory (Allen and Starr, 1982; O'Neill et al., 1986) offers some guidance in determining what can be disaggregated: a study or model should include all the components and interactions that affect the process of interest and operate on the same spatial and temporal scales (but see Shachak and Jones, Ch. 27 for operation on multiple scales). O'Neill et al. (1986) suggest that processes that are three orders of magnitude larger or smaller than the process of interest can be safely aggregated. That is, those operating over much larger spatial or temporal scales act as constraints on the dynamics of a process, whereas those operating over much finer scales occur so rapidly that their dynamics are perceived as static. Although this rule-of-thumb provides some guidance, a lot of complexity still remains within that range of six orders of magnitude, and it is herein that ecologists come face to face with the problem of aggregation.

Examining aggregation effects and scale dependencies is complicated by the various ways in which processes can be aggregated. First, processes can be aggregated in scale, that is, with grain and/or extent in space and time. Grain refers to the finest level of spatial or temporal resolution used within a study, whereas extent refers to the size of the study area or the duration of the study (Turner et al., 1989a,c). Second, the spatial and temporal scales can remain constant, but groups of organisms, species, or similar processes might be ag-

gregated for particular functions (e.g., Gurney et al., Ch. 18; Schimel et al., Ch. 20). This type of aggregation can occur within or across biological levels of organization. Prior studies suggest that we can expect different results from these different types of aggregation (see next section); hence, it is difficult to develop a taxonomy of simple rules that can be applied to process aggregation.

Given the nature of ecological complexity, how then do we abstract what is important? What are the implications of particular choices of abstraction and aggregation? Are there any general rules that can guide the aggregation process? In this chapter, we first examine some results from previous studies of aggregation. Then, we use a spatially explicit simulation model of winter foraging by large ungulates to explore the implications of aggregation in space, in time, and of individuals on projected ungulate survival and habitat use. Aggregation in space is examined in two ways: (1) by varying the heterogeneity represented in forage abundance across the landscape and (2) by eliminating spatial heterogeneity in the accumulation of snow. Aggregation in time is examined by varying the temporal grain used to simulate snow accumulation through the winter. Aggregation of individuals within a feeding group is explored by varying the number of individuals from single animals to groups of 80. From these and other examples, we draw some general implications for process aggregation.

## APPROACHES TO AGGREGATION

Problems with aggregating dynamic components of a complex system have long been discussed by ecologists (O'Neill, 1973, 1979; Cale and Odell, 1979, 1980) and economists (Chipman, 1975, 1976). Most of the work has been done on mathematical models (Zeigler, 1976; Iwasa et al., 1987, 1989) but the principles can be applied to the abstractions necessary for any ecological study (Rastetter et al., 1992a; Rastetter and Shaver, Ch. 21).

If one is dealing with "near normal" conditions (i.e., equilibrium) and simple responses to environmental change (i.e., linear dynamics), then reasonable criteria exist for aggregation. One can, for example, aggregate "functionally redundant" species [i.e., parallel configurations and similar turnover rates (O'Neill and Rust, 1979; Gardner et al., 1982)]. The aggregated model is not exact, but the errors are bounded and acceptably small relative to other sources of error.

It may also be possible to isolate one part of the system [i.e., decomposable matrix (Simon and Ando, 1961)] and consider it as a simple component. Almost all ecologists have performed this type of implicit abstraction when they lumped several thousand species (not to mention phyla and kingdoms) in a little box labelled "decomposition" and assumed it would "do its thing" stably during the course of an experiment.



These types of aggregation are reliable as long as radical changes do not occur in the behavior of the aggregated components. Clearly, if one crosses dynamic thresholds, eliminates keystone species, or breaks feedback loops, the assumptions are violated and the aggregations can lead to serious error (Cale et al., 1983).

The situation becomes significantly more difficult if a study requires aggregating food webs [i.e., series configurations (Gardner et al., 1982)] or lumping complex nonlinear responses. Nevertheless, some progress has been made in approximating global responses to $CO_2$ and temperature increases, while retaining fine-scale understanding of the processes (Sinclair et al., 1976). Approaches include explicit integration of fine-scale models across measured spatial and temporal heterogeneity (King et al., 1989). In simple cases, an analytical solution can be obtained directly. In other cases, the fine-scale model can be considered to be stochastic in space and time. Solutions of the model for larger scales can be approximated by expanding the moments of the stochastic model (Rastetter et al., 1992a). For very complex models, Monte Carlo simulation provides a solution (King et al., 1991).

For limited, well-defined research objectives it is sometimes feasible to use a calibration approach (Rastetter et al., 1992a). Monte Carlo runs of the fine-scale model are made over the required range of conditions. The output is regressed against the environmental conditions of interest (e.g., temperature and rainfall). The regression model is then used to calculate large-scale responses, with known uncertainty. This approach is strictly limited to the range of conditions considered in the regression analysis.

Research on model aggregation has clearly demonstrated the dependency of any abstraction on scale and research objectives. The aggregation may be adequate at one scale (e.g., annual dynamics on a landscape) and false at another (e.g., daily dyamics on a 1-ha plot). The annual/daily difference may be obvious but other changes of scale are not (Cale and O'Neill, 1988). The abstraction is necessarily specific to the immediate objectives and even subtle changes in objective can invalidate an abstraction (Bartell et al., 1988). A water quality model may aggregate fish species as functionally redundant. This aggregate may well be valid, but the model is now invalid for studying the impact of pollutants on a specific game fish.

## OVERVIEW OF THE NORTHERN YELLOWSTONE PARK MODEL

The Northern Yellowstone Park (NOYELP) model simulates the search, movement, and foraging activities of individuals or small groups of elk (*Cervus elaphus*) and bison (*Bison bison*) (Turner et al., 1994). The model was developed

to explore the effects of fire scale and pattern on the winter foraging dynamics and survival of these free-ranging ungulates in northern Yellowstone National Park, Wyoming, U.S.A. The 77,020-ha landscape is represented as a gridded irregular polygon with a spatial resolution of 1 ha. Grasslands cover most of the northern range and are dominated by big sagebrush (*Artemisia tridentata*), bluebunch wheatgrass (*Agropyron spicatum*), and Idaho fescue (*Festuca idahoensis*).

The model simulates daily forage intake as a function of an animal's initial body weight, the absolute amount of forage available on a site, and the depth and density of snow. Energy balances are computed daily, with energy gain a function of forage intake and energy cost a function of baseline metabolic costs and travel costs. When the energy expenditures of an animal exceed the energy gained during a day, the animal's endogenous reserves are reduced to offset the deficits. Simulations are conducted with a 1-day time step for a duration of 180 days, approximately November 1 through April 30. The model has been used to examine the effects on ungulate survival and habitat use of fire size, fire pattern, winter weather conditions, and initial ungulate numbers (Turner et al., 1994).

## EXPLORING AGGREGATION IN SPACE AND TIME: EXAMPLES USING THE NOYELP MODEL

The NOYELP model was used to explore the effects of several different types of aggregation on simulated elk survival and habitat use. Because we focus only on aggregation effects, several parameters were held constant across all simulations. We simulated the winter of 1988–1989, the first winter following the extensive fires that affected Yellowstone National Park and a winter of average severity. These fires affected 22% of the northern range study area, and no forage was present in burned areas during this first post-fire winter. All simulations use the actual snow accumulations observed in, 1988–1989 and begin with 19,270 elk and 600 bison. Observed winter mortality of elk was between 38 and 43% (Singer et al., 1989), and the baseline prediction of the model results in 40% mortality (Turner et al., 1994). The total abundance of forage across the landscape was also held constant in the simulations, although its spatial heterogeneity was varied.

### Aggregation Across Space I: Forage and Habitat Heterogeneity

Biomass abundance varies spatially across a landscape. When lines are drawn on a map to delineate different habitat types, assumptions are often made about the characteristics of the vegetation within those habitats. The NOYELP model includes six different vegetation types (dry, mesic, moist, and



wet grasslands; canopy forest; aspen stands) whose spatial distribution was obtained from the Park's geographical information system. The abundance of prewinter forage in each of these six habitats was quantified during the fall of 1990 (Wallace et al., 1994) by field sampling. The model uses the mean and 95% confidence interval obtained from these data to distribute forage to each grid cell such that the mean forage abundance within each habitat type matches the mean obtained from the data, but any given grid cell within a habitat type has a forage value assigned from the distribution.

To explore the effects of aggregating across this spatial heterogeneity, a series of three successive aggregations was conducted. First, the burn pattern and the spatial distribution of the six unburned habitats was maintained, but the within-habitat heterogeneity in forage abundance was removed by assigning to each grid cell the mean forage abundance for its habitat type (Tab. 19-1, "no within-habitat heterogeneity"). Second, the burn pattern was preserved, but the between-habitat heterogeneity in the unburned area was removed (Tab. 19-1, "no between-habitat heterogeneity"). The forage biomass assigned to each grid cell was obtained by dividing the total biomass on the landscape by the number of unburned grid cells and assigning this mean value to each unburned grid cell. Finally, all heterogeneity in forage abundance was removed by completely eliminating the burn pattern (Tab. 19-1, "no heterogeneity"). Each grid cell in the landscape was assigned the same forage value, obtained by dividing the total landscape biomass by the number of grid cells.

**Table 19-1.** Levels of forage biomass assigned by habitat in the baseline model and each of three successive aggregations.

| Aggregation | Habitat Type | Forage Biomass (kg/ha) | |
|---|---|---|---|
| | | Mean | SEM |
| Baseline | Burned | 0 | — |
| | Dry | 520 | 59 |
| | Mesic | 631 | 139 |
| | Moist | 1122 | 166 |
| | Wet | 2259 | 266 |
| | Forest | 333 | 85 |
| | Aspen | 659 | 101 |
| No within-habitat heterogeneity | Burned | 0 | — |
| | Dry | 520 | 0 |
| | Mesic | 631 | 0 |
| | Moist | 1122 | 0 |
| | Wet | 2259 | 0 |
| | Forest | 333 | 0 |
| | Aspen | 659 | 0 |
| No between-habitat heterogeneity | Burned | 0 | 0 |
| | Unburned | 729 | 0 |
| No heterogeneity | All | 568 | 0 |

The removal of within-habitat heterogeneity had little effect on elk survival (Fig. 19-1a). However, aggregating habitats such that between-habitat heterogeneity was eliminated underestimated survival of elk cows and bulls by 30% (Fig. 19-1a). Removal of all spatial heterogeneity in forage abundance further underestimates elk survival by approximately another 20%. The decreases in survival with the loss of between-habitat heterogeneity are due, in part, to energy costs associated with increased daily movement. The mean distance travelled in a day for elk cows increases sooner (in February rather than in March) when there is no between-habitat heterogeneity (Fig. 19-1b). Animals are forced to move more when they are not obtaining sufficient forage to meet their daily requirements, and hence expend more energy. If we examine the proportion of animals present at the end of each month (Fig. 19-1c), we note that mortality begins during February for all scenarios but is much more rapid when the between-habitat heterogeneity in forage abundance is reduced.

These results illustrate for wintering ungulates the importance of maintaining coarse-scale variability in forage biomass when conducting a study/simulation at this spatial and temporal scale. Assuming animals respond to the mean landscape biomass would be misleading; the distribution across the landscape of areas of high and low biomass enhances ungulate survival.

## Aggregation Across Space II: Snow Conditions and Topography

The depth and density of snow also varies spatially across the landscape. In the baseline simulations, the depth and density of snow on each grid cell are assigned by modifying a projection that assumes a flat site by the slope and aspect of the cell. A set of coefficients was obtained by sampling snow depth and density across a wide range of topographic positions in northern Yellowstone (Turner et al., 1994). To eliminate heterogeneity in snow, simulations were conducted in which each baseline projection was applied to each grid cell; that is, snow conditions were applied homogeneously across the landscape.

The homogeneous snow conditions resulted in substantial underestimates of ungulate survival (Fig. 19-2a). The proportion of elk cows surviving, for example, declined from ~70% to ~20%. The mean distances travelled per day by elk cows increased dramatically in January in the absence of snow heterogeneity and remained elevated as compared to the baseline simulation for the rest of the winter (Fig. 19-2b). Some changes in the frequency of use of different habitats occurred (Fig. 19-3a), with dry habitats receiving more use and moist habitats less use. Because fewer animals survived and foraging was more difficult in general, the end-of-winter biomass present within each habitat generally increased with homogeneous snow (Fig. 19-3b).

These results illustrate that the spatial heterogeneity of snow conditions, especially the maintenance of snow-free or low-snow areas, is important for



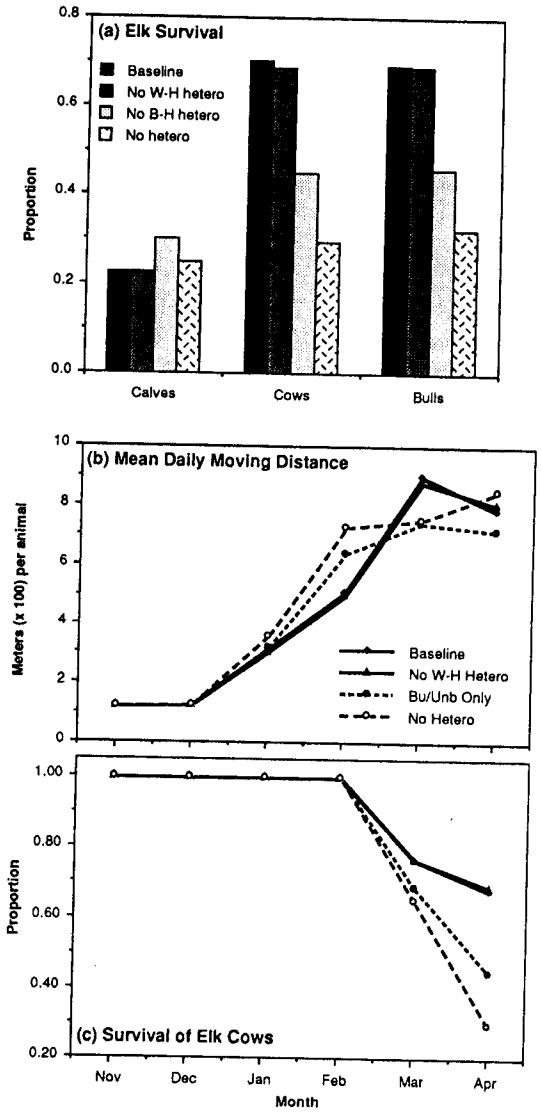



**Figure 19-1.** Simulated responses to the three levels of aggregation of forage heterogeneity across the landscape. (a) Overall survival of elk cows, calves, and bulls. (b) Mean distance moved per day for elk cows at the end of each month. (c) Survival of elk cows through time (legend as in *b*). "Baseline" indicates no aggregation; "No W-H hetero" indicates no heterogeneity within each habitat; "No B-H hetero" indicates no heterogeneity between habitats, but the burned vs. unburned pattern remains; and "No hetero" indicates no heterogeneity among grid cells (see Tab. 19-1).

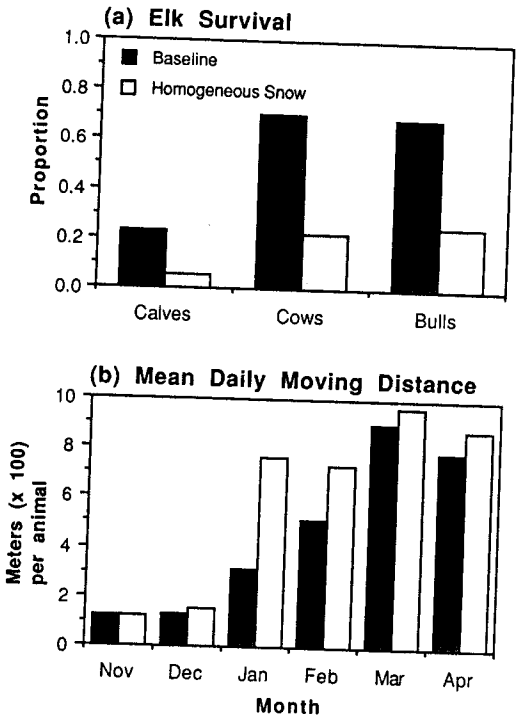



**Figure 19-2.** Simulated responses with and without spatial heterogeneity of snow depth and density. (a) Elk survival. (b) Mean distance moved per day for elk cows at the end of each month (legend as in *a*).

estimating winter ungulate survival. Although the mean snow accumulation across the landscape will certainly be an index of the overall winter severity, homogeneity across space cannot be assumed in a study at this spatial and temporal scale. Of course, this does not negate the use of mean snow accumulation in some other analyses, for example, statistical models of ungulate mortality across many years as a function of mean snow conditions.

## Aggregation in Time: Interval Used for Snow Conditions

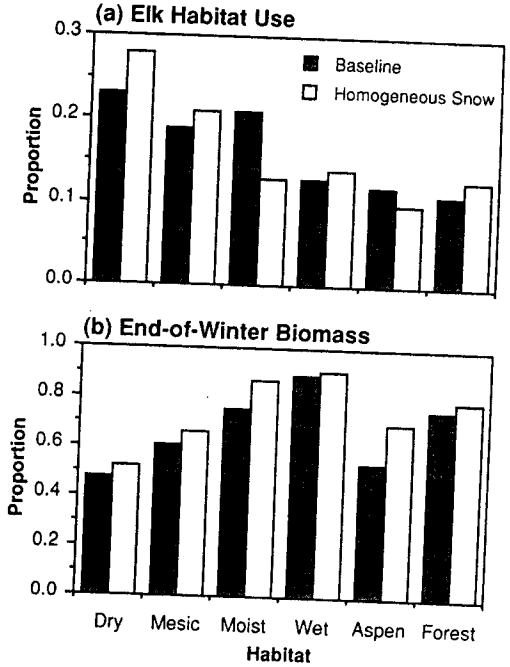
Snow varies not only across space but also through time. Snow accumulation data are available on a monthly basis from a snow course sampled on approximately the first of each month through the winter. However, snow conditions are actually changing at a finer temporal scale. In the baseline runs of the model, a snow interval of 3 days is used. The snow conditions for two sequential months are compared, change between them is assumed to be linear,



and the changes are then parcelled out in 10 equal 3-day increments. To examine the effect of aggregating across the changes in snow conditions within each month, we varied the interval from 1 day, giving a linear increase in snow, to 30 days, which is a step function. Note we are varying the temporal grain of the snow simulation, but the temporal extent and underlying temporal pattern of snow through the winter are maintained.

Elk survival was not very sensitive to variation in the interval used to modify snow conditions. Survival declined somewhat when snow was simulated as a monthly step function (Fig. 19-4a), possibly in response to increased daily moving distances in April (Fig. 19-4b). These results illustrate that the temporal grain of snow within the range of 1 to 30 days was not particularly important. This may occur because there is a linear response to snow conditions within that time scale and no qualitatively different response occurs. However, some deviations from the baseline simulation did occur at a 30-day grain size, suggesting that larger aggregations would not be appropriate.

**Figure 19-3.** Frequency of habitat use by elk (a) and remaining end-of-winter biomass by habitat (b) with and without spatial heterogeneity of snow depth and density (legend as in *a*).



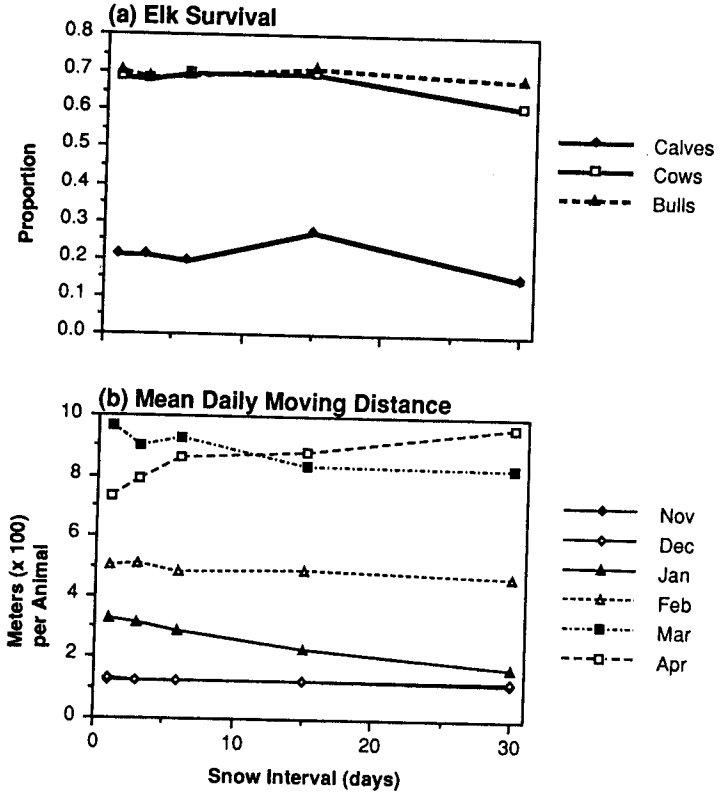



**Figure 19-4.** Simulated ungulate responses to changing the temporal grain of the snow simulation from 1 to 30 days. (a) Overall elk survival. (b) Mean daily moving distance of elk cows at the end of each month.

## Aggregation of Individuals

The final aggregation experiment we conducted was to vary the size of groups that are simulated together from single individuals to groups of 80. When a group is simulated, the group size is used as a multiplier for all foraging and energetic relationships. For example, if the maximum daily foraging rate for an individual elk cow is 5 kg per day, then the same rate for a group of 10 elk cows is 50 kg. Of course, if the forage intake required is greater than the forage present at a site, the group obtains less than its daily requirement and must move to another site to meet its needs.

Elk survival was sensitive to group size. Survival of elk calves began to decline at a group size of four animals and reached zero for a group size of eight (Fig. 19-5a). Survival of adults, however, declined rapidly between group sizes of 20 and 40. This decline in survival corresponds to a substantial increase in the mean daily moving distances (Fig. 19-5b). Above group sizes of 10, moving distances increase even in early winter, resulting in increased energetic costs. Both simulated habitat use (Fig. 19-5c) and end-of-winter biomass (Fig. 19-5d) remaining in each habitat show fluctuation with group size.



The results from varying ungulate group sizes illustrate effects of aggregating across a level of biological organization. Although sex and age differences were maintained in this aggregration, individuals were lumped under the assumption that all were identical and that simply multiplying the dynamic processes by the number of individuals would maintain the biological relationships intact. This assumption was acceptable with small groups of individuals (≤4 for calves, ≤10 for cows and bulls) but not with large groups. At the spatial and temporal scale of the model, aggregating across individuals led to serious error.

## DISCUSSION

The effect of aggregation on an ecosystem or population parameter clearly is a function of the spatial and temporal scales at which the parameter is being studied and of the question being asked. Describing the effects of aggregation cannot be done in the absence of a question of interest. For example, aggregating the spatial heterogeneity of forage biomass between habitats had a substantial effect on simulated survival of wintering ungulates studied over a single season and using a daily time step. Within-habitat heterogeneity was not important, and we aggregated the multitude of species into a single "biomass" component. However, aggregating in this way would not be suitable for a study of wintering ungulates over a short time span (e.g., days) and within a single habitat because critical interactions would be missing.

The aggregations or abstractions made in ecological studies or models are often represented as unstated assumptions. For example, in the model presented here, we assume that species-by-species differences in forage quantity and quality can be aggregated, but sex and age differences of the two ungulate species cannot. We aggregate when we expect, either by hypothesis or through empirical data, that the aggregated entities do not differ qualitatively for the process of interest. Here, we assumed that the individual grasses and forbs could simply be summed, without changing the fundamental effect on ungulates. However, summing all elk and bison could not be done because the energetic demands differ substantially among males and females and between juvenile and mature animals. The important point is this: for ALL ecological

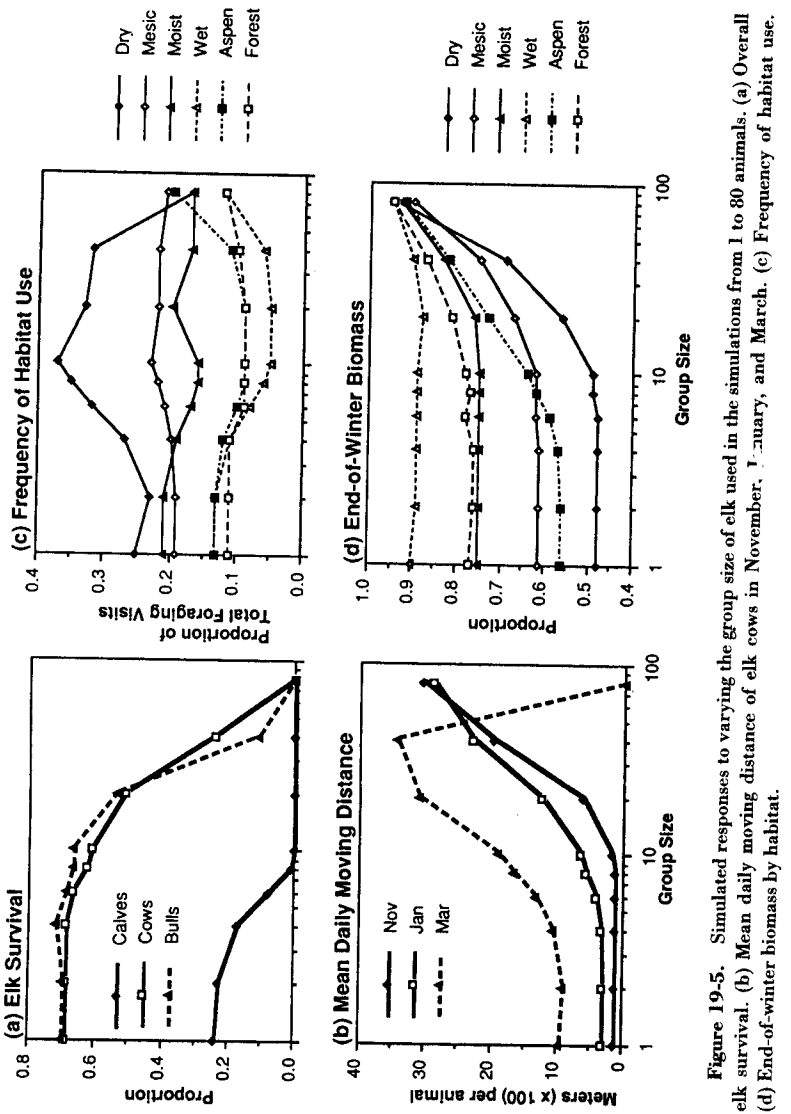



**Figure 19-5.** Simulated responses to varying the group size of elk used in the simulations from 1 to 80 animals. (a) Overall elk survival. (b) Mean daily moving distance of elk cows in November, January, and March. (c) Frequency of habitat use. (d) End-of-winter biomass by habitat.





studies or models, a tremendous amount of aggregation has occurred, even though it may not be stated as such.

The most important conclusion to be drawn from the studies of aggregation can be summarized in the principle of the "Title Translator." By this principle, one takes the title of a paper, such as, "An Analysis of X," and translates the title into: "One specific analysis of X, over very limited time/space scales, using a set of limiting assumptions, mostly unstated, for a specific research objective, and not precluding other, completely different ways of looking at X."

We cannot offer a simple conclusion on process aggregation, but we suggest an approach toward determining what can and cannot be aggregated in an ecological study:

1. Ask the question. Whenever the question is changed, then both the spatial/temporal scale and the level of abstraction also change.
2. Specify the spatial and temporal scales of interest, both in terms of grain and extent. Again, the level of aggregation or abstraction will vary as the scale of the question is changed.
3. Aggregate the processes that occur much more slowly than the processes of interest and consider these to be constraints on the process of interest.
4. Aggregate the processes that occur much more quickly than the processes of interest and consider these to be "noise" to the process of interest.
5. Identify the interacting factors that influence the process of interest. To determine whether any more aggregation can be done at this scale, address the following:
   a. Is there functional redundancy among some components or processes? In our example, there was functional redundancy among forage species, but not among different habitat types or different age/sex classes of ungulates.
   b. Are there feedbacks at the particular spatial and temporal scale of interest? If not, then the processes may be aggregated or ignored. In our model, for example, the temporal extent is 180 days, a single winter. Therefore, processes such as reproduction, nutrient feedbacks, and decomposition were not addressed, but these would likely be unacceptable omissions from a mulityear consideration.
   c. Are there nonlinearities, or threshold dynamics? If so, it may be possible to aggregate below and above a threshold, but not across it. Spatially, for example, there may be thresholds in connectivity for a particular organism or process (e.g., Gardner et al., 1987; Turner et al., 1989b; Gardner and O'Neill, 1991). Above the threshold, the abundance of the organism might be proportional to the abundance of habitat because the organism can access all the habitat. Below the threshold, however, the abundance of the organism might be related to the probability of success of long-distance dispersal, a qualtitatively different relationship.

Even successful aggregation of processes will be reliable only if dynamic thresholds are not crossed, if keystone species are not eliminated, and if feedback loops remain intact. If any of these occur, either through aggregation or

through fundamental changes in the system, then the aggregation will lead to serious error (Cale et al., 1983).

This approach does not presume to be a cookbook recipe for aggregation nor does it presume to be exhaustive. Rather, the steps listed above illustrate the critical dependence of aggregation effects on both the question and scale of interest in a study. We suggest that thoughtful consideration of each of these steps will help answer questions about what processes can and cannot be aggregated in studies linking populations and ecosystems.

## ACKNOWLEDGMENTS

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# AGGREGATION OF SPECIES PROPERTIES FOR BIOGEOCHEMICAL MODELING: EMPIRICAL RESULTS

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## SUMMARY

In many biogeochemical models, plant species are aggregated such that only one generic plant type is represented. If multiple species are present, each "species" or functional type is represented as a collection of physiological traits. We recently have been exploring the physiological responses of co-occurring plant species of a variety of growth forms to determine how many separate physiological types are needed in order to capture the dynamics of net primary production, decomposition, carbon (C) storage and nitrogen (N) availability. We measured species-level photosynthetic responses, canopy light extinction, leaf N and lignin, and soil nutrient processes. In both the prairie and the shrub-savanna we found that photosynthetic responses scale with light within the plant canopy such that for calculation of C gain, the canopy can be modeled as a single unit, regardless of the vertical distribution of species. Nutrient cycling and C storage are, however, very different in herbaceous areas compared to wooded areas, such that shrub-dominated areas have different soil C levels and N mineralization rates from grassland areas. In Texas, shrub-dominated areas have higher soil C and N mineralization. The dominant woody