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IMPLICATIONS OF BODY MASS PATTERNS: LINKING ECOLOGICAL STRUCTURE AND PROCESS TO WILDLIFE CONSERVATION AND MANAGEMENT

Jan P. Sendzimir

Craig R. Allen

Lance Gunderson

Craig Stow

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1.1   The Challenge of Structure and Process at Multiple Scales

The unprecedented scale of problems affecting wildlife ecology today overwhelms many managers. Challenges are no longer local in origin, but rather a tangle of local, regional and even global externalities often interacting in unpredictable ways. Previously isolated ecosystems have become increasingly connected at global, hemispheric and regional levels, eroding their integrity. Endocrine-disrupting compounds applied in Mexico have changed avian sexual development in the Great Lakes (Colborn et al. 1996). Chamois (*Rupicapra rupicapra*) reproduction in the Carpathian mountains falters when the color of newborns is no longer cryptic because climate change prematurely melts snow cover (K. Perzanowski, Polish Academy of Sciences, pers. comm.). Climate change predictions (Houghton et al. 2001) now project sea-level rise up to 5 meters within the next few centuries, which will displace more than a billion people and inundate coastal plains. The populations of many species have dwindled and disappeared as they have been displaced by invasive and introduced species and as habitat removal and fragmentation change migration patterns and the carrying capacity of landscapes.

These large-scale crises surprise us and force us to look beyond local issues to consider regional influences. This is not the first time that our worldviews have been challenged to expand. More than a half-century ago, collapsing fish and forestry industries forced resource managers to consider regional context when assessing local problems. These reassessments of causes at larger scales provoked a variety of theoretical advances in ecology (see Walters 1986, for forestry and fisheries examples). Theories of catastrophe (Casti 1982), complexity (Kauffman 1993, Kay 2000), and hierarchy (Allen and Starr 1982, O'Neill et al. 1986) marked new insights into the structure, function and dynamics of ecosystems, especially at larger scales. The resulting synthesis of all these initiatives is summed in the descriptive term for ecosystems as "complex, adaptive systems" (Holling 1992, Levin 1992, Levin 1998, Kay 2000). However, while these theories increased our understanding of the interactions underlying these resource crises, the science of putting these new insights into practice is in its infancy. What tools do these theories put in the hands of a manager with on-the-ground responsibility to manage and conserve wildlife?

A central question in ecology has been: is there meaningful, repeatable pattern in ecosystems or do all apparent patterns and structures arise continuously from chance interactions that are *contingent* (Lawton 1999) on local conditions of species abundance, environment and the web of species interactions? In the former case, our understanding of ecosystem pattern and structure resulting from the study of one ecosystem can be applied to other systems. On the other hand, if systems are

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assembled randomly, then each event is unique, and we must learn anew in each ecosystem. Holling (1986, 1992) addressed these questions by asking whether random events could produce the regularity observed in disturbance periodicities (fire, flood, pest outbreaks). Does the regular return (around eight to twelve years in the absence of intervention) of fire to Florida sand pine forests indicate some deeper, underlying structure that persists despite random variations? Similar clustering of time series data is evident for such processes such as insect outbreaks (Clark et al., 1979, McNamee et al. 1981, Holling 1988, 1992), fires (Clark 1990), and floods (Fiering 1983), which all cluster into small sets of repetitive cycles. Holling (1992) proposed that ecosystems have structure that emerges from the effects of relatively few processes that operate over distinct scales in space and time. This chapter describes efforts to test how such regularities of pattern in time and space consistently influence (entrain) characteristics of animals, such as body size. In brief, Holling predicted that animal species will cluster in size (lumps) as they interact with the clustering in time (periodicities) and space (landscape structure) of their environment, and that those animal size clusters will correspond with the key scales of structure available in a given system.

We first review the findings in support of this proposition, and then discuss its management applications for vertebrates in terrestrial ecosystems. In particular we address four questions directed at wildlife management. What evidence is there that ecosystems operate as Complex Adaptive Systems (CAS)? Are there predictable natural patterns ("is the world lumpy?"), and does this influence animal behavior,

survival, and evolution? How do animals interact with a lumpy world and what are the consequences for their conservation and management? And finally, does a lumpy framework of analysis help us address at what scales animals respond to pattern in the environment?

1.2   The Spoor Of Complex Adaptive Systems: Patterns Of Ecological Processes, Landscape Structure, And Body Size

Ecological processes such as succession, nutrient cycling and seed dispersal can sustain and sometimes transform ecosystems over time (Peterson et al. 1998). We can describe an ecosystem as a Complex Adaptive Systems (CAS) if complex behavior emerges unpredictably (non-linearity) without the influence of central control but as a result of adaptive behavior by its component, interacting agents (Holland 1995). Such agents can 'self-organize' (change their rules of interaction as experience accumulates) and act in anticipation, such that, under stress, the system coheres or completely changes its composition. If ecosystems operate as a CAS then we predict that they persist or change depending on the functioning of feedback interactions between ecological processes, landscape structure, and biota (Allen and Hoekstra 1992, Levin 1998, Peterson et al. 1998). We emphasize that complex systems, particularly ecosystems, are organized hierarchically, because separation into semi-autonomous levels is a prerequisite for evolutionary advances to take hold (Simon 1962). Evolution is unlikely in a world without hierarchical levels to isolate organisms from the inordinate distraction possible if all organisms in a system could

interact with equal intensity (Allen and Hoekstra 1992). The first test, therefore, is to see if we detect discontinuities in landscape patterns that suggest hierarchical structure. The second test looks for discontinuities in animal sizes that suggest a hierarchical organization of biota that reflects the discontinuities in the landscape pattern. We describe evidence from these two tests and then consider what interactions might cause them. First, we examine hierarchical landscape pattern more closely.

We refer to landscape structure here as the distribution in space and time of opportunities for animals to eat, compete for mates or territory, find shelter, and nest. Holling (1992) proposed that these opportunities are not spread smoothly across the landscape like continuous gradients running from dry to wet or high to low. Rather, opportunities tend to cluster discontinuously, because different sets of opportunities are evident depending on the interaction between discontinuous scales of perception and scales of landscape structure. We use two factors, window (or extent) and grain (resolution), to describe how perception scales with body size. A vole will see very different sets of opportunities than a moose. Both are mutually oblivious to or ignore key landscape features of the other. Grass runway corridors for voles are invisible to or ignored as noise by a moose, and the sizes and distances between alder thickets for moose are ignored as background by voles. How can landscape ecologists begin to imagine the separate perceptive scales of different animals? The book Powers of Ten (Morrison and Morrison 1994) illustrates vividly the jerky or discontinuous way that different landscape features jump out at one as one changes perspective by zooming in

or out from any point in space. Starting from a beach blanket in Miami and stepping back in stages that differ by an order of magnitude (1 meter, 10 meters, 100 meters, a kilometer, and so forth) different patterns of attributes are apparent at different ranges of distance from the origin. After several steps one pattern suddenly disappears, to be replaced by another set, previously not evident.

Such jumps between evident sets of pattern are referred to as 'scale breaks' (Allen et al. 1999), which separate the scales at which we can delineate one spatial domain from another. Scale breaks do not necessarily coincide with any measure, such as order of magnitude shifts in distance, and the quantification of scale breaks remains a key future avenue of inquiry. The theories underlying CAS propose that such discontinuous pattern is fundamental to ecosystems and results when different sets of processes operate over distinct ranges of scale, organizing the landscape into different spatial and temporal domains. If animals perceive and respond to this discontinuous structure (Holling 1992) we may gain insight into the assembly and structure of animal communities. If animals respond to discontinuous scales of landscape structure, the species in an assemblage of animals will cluster at discreet size ranges because specific size ranges will optimally compete for resources in each of these spatio-temporal domains. Briefly, lumpy landscape pattern should be mirrored by lumpy body size patterns, as interactions link animals with the lumpy geometries of structure and the time/space clustering of ecological processes.

The groups of objects that constitute the predominant structure of each level in the landscape hierarchy are intuitive. The fine-scale structure of herbaceous vegetation, the medium-scale mosaic of forest patches, the grand geological sweep of the landscape, have an appealing cohesiveness and fit, nested like Russian dolls or a Chinese puzzle. But is there real pattern giving rise to this appealing sense of symmetry, or are these notions just another imposition of human values and scales on the world? And if there is real, discontinuous landscape pattern, what significance does it really have for animals? We discuss efforts to apply objective measures of landscape pattern and then examine evidence of similar patterns in animal assemblages.

1.2.1   *Landscape Structure: Multi-Level Patterns*

Many concepts about hierarchical structure and non-linear dynamics in ecosystems that suggest a discontinuous or lumpy world were presented decades ago in systems science (Simon 1962, von Bertalanffy 1968, Odum 1982). Opportunities to detect pattern and test these ideas at larger scales awaited the advent of satellite sensors and relatively cheap, high-speed computers in the early 1980s. Since then attempts to develop objective means to detect pattern without human bias have created a diversity of indices for landscape structure, such as fractal breaks (Mandlebrot 1982, Morse et al. 1985, Milne 1997), and fractal dimensions based on perimeter-area and on mass (Hargis et al. 1997).

If key ecological processes each interact at characteristic space and time scales to produce discontinuous structures, then data from systems should reflect such a pattern. That is, cross-scale analyses of key spatial variables should reveal discreet changes in pattern as scale changes, and analyses of time series should produce a few dominant frequencies that reflect a clustering of temporal processes. Below we present results that show how such analyses identify key structures and processes from a large freshwater wetland ecosystem, the Everglades in Florida, USA, and are indicative of a general pattern for all ecosystem types.

1.2.1.1   Spatial Attributes Of Natural Landscapes

Spatial and temporal data that are thought to represent key variables in the Everglades ecosystem were analyzed for breaks and clusters. Fourier techniques were used to detect dominant frequencies in time series data including rainfall, water depth, water flow, evaporation, and fire sizes. Spatial data of vegetation and topographic profiles were analyzed using fractal techniques to test for breaks in scaling dimensions.

Three dominant frequencies appear in the time series data. Surface water levels fluctuate on daily, annual, and decadal cycles. The daily and annual fluctuations in stage levels are related to processes that produce convective thunderstorms. The dominant frequencies for water flow, evaporation and fire frequencies occur at approximately decadal intervals (Gunderson 1992). The longer-term fluctuations appear to coincide with variation patterns in two processes: evapo-transpiration rates

and, to a less evident degree, decadal fluctuations in rainfall related to the periodicities of El Niño events.

Spatial patterns exhibit scales of self-similarity separated by distinct breaks. The soil surface topography appears to vary at two distinct spatial scales. The broad scale is apparently a result of geologic features and the small scale appears related to the processes of organic soil accretion and removal. The vegetation patterns exhibit breaks between regions of self-similarity related to the interaction among water levels, water flow, and fire patterns (Gunderson 1992).

Figure 1 shows cross-scale ecosystem structure and processes in the Everglades mapped in the form of a Stommel diagram. The primary axes are logarithmic scales over space (abscissa) and time (ordinant) that cover about six orders of magnitude and are matched with their non-log equivalents. Entities within the diagram are defined by grain and extent. Grain is the smallest resolution required to identify an entity, as indicated by the lowest margin (time) and the left edge (space) of a polygon in Figure 1. These correspond to the minimum time step in sampling to detect an object and the pixel size on a screen at which an object is recognizable. By the same token, the window is the extent of that object, as indicated by the highest margin (time) and the right edge (space) of a polygon in Figure 1. These correspond to the life span and the window size that can frame the entire object of interest. Breaks in the fractal dimension of spatial patterns can be used to define breaks between entities in the

spatial dimension. Similarly, dominant frequencies appear to differentiate temporal entities or levels.

The analysis of the Everglades ecosystem supports the hypothesis that spatial patterns exhibit breaks and that temporal patterns cluster around a few cycles. Spatial patterns exhibit scales of self-similarity separated by distinct breaks. The soil surface topography appears to vary at two distinct spatial scales. Breaks in fire size may be related to the approximately decadal time period between large burns. The vegetation patterns exhibit breaks between regions of self-similarity, although the reasons are unclear. Temporal patterns in water stage and flow reflect dominant frequencies in the interplay between the faster dynamics of the atmosphere, the intermediate speeds of the surface water (stage and flow) and the longer-term variations in vegetation, climate and sea level.

Scale breaks in the time behavior of processes and the spatial distribution of landscape pattern confirm in the Everglades what has seemed apparent in a range of landscapes: the environment is clustered into a small number of groups of objects of relatively similar size. Were variation in object sizes unlimited, then no clustering would be evident. However, size variation is bounded for different types of objects from the smallest to largest scales: vegetation, patches, eco-tones, and topography. The conservation implications of hierarchical patterns in landscapes increase if animals respond to it in predictable ways. We discuss evidence for this below.

1.2.2. Macroecology: Size Attributes Of Animal Assemblages

Even if distinctive patterns appear to divide a landscape into separate ranges of scale, is there compelling evidence that animals interact with such discontinuous pattern in ecologically meaningful ways? We now consider evidence from animal assemblages, for example, all the animals of one taxon that feed and reproduce on a landscape. A typical example of such an assemblage might be all mammals in the Everglades ecosystem.

Brown (1995) proposed "macroecology" to explore overarching patterns at larger scales (biome to global scales in space and decadal to millennial in time) to bridge gaps in understanding of processes defined at smaller scales by population and community ecologists. By forging synthetic links between ecology, biogeography, paleobiology and macro-evolution, macroecology aims to establish an informed context for smaller scale questions of abundance, distribution and diversity of species as affected by interactions between species and their environment. The shapes and bounds of statistical distributions of animal size indices are patterns which reflect either "intrinsic, evolutionary or extrinsic, environmental constraints on variation" (Brown 1995). In brief, the echoes of large-scale processes are sought in the size distributions of animal assemblages over wide areas (landscape level and higher). Some general trends do relate animal morphometric patterns to large-scale evolutionary, ecological and climatic patterns. Mammal body size correlates strongly with seasonality, the amplitude of seasonal climatic variation (Lindstedt and Boyce

1984). For evolutionary lineages, the general trend for body size to increase within a phylogenetic group (Cope's Law) now appears to apply only to the upper size range, since many species shrink in size over evolutionary time (LaBarbera 1989).

Macroecology (Brown 1995, Maurer 1999) expands the arena in which we can test ideas about ecological processes from the local to the regional and even continental. However, are these the only scales at which ecological processes operate? Holling (1992) proposed a far wider variety of scales of operation for the ecological processes structuring the Boreal forest, dissecting it more finely into eight separate scale ranges. Clearly, the science of defining the scales of operation for ecological processes is in its infancy (Peterson et al. 1998, Peterson 2000). For example, the tension emerging from arbitrary applications of a wide variety of different scales to the term 'ecosystem' (Noss and Cooperrider 1994) sparked the struggle to define its 'true' dimensions or abandon it altogether. Examining landscape pattern simultaneously *across scales* will provide a more unifying framework for defining ecologically meaningful scale domains than trying to synthesize analyses done individually at different scales (e.g. mycologists, mammalogists, and forest ecologists)

1.2.2.1 Lumpy Size Patterns in Animal Assemblages

Intuitive and even objective indications that landscapes are hierarchies do not prove any link with animal behavior or community assembly. Scale breaks are distinct to human eyes, but it is premature to assume what animals perceive (Ims 1995). Even if

evidence existed that animals perceive scale breaks, is there evidence that animals respond to scale breaks and clusters of objects within a domain of scale? To test this, Holling (1992) proposed that discontinuities in the landscape would be translated into gaps in the size distributions of the animal assemblages. If a mouse's scale of perception only fits a certain window and reveals only certain objects clearly, then its choices to feed or flee will depend on those perceptions. And if the scale of perception is proportional to body size, then for each scale only a certain range of body sizes perceive resources within that scale range. Therefore, animal species should cluster in certain size ranges that compete best over specific scale ranges. Animals would not be competitive if their size fell in the range that perceives resources best within scale breaks, the ranges of scale over which resources were not apparent (or poorly so), or were hyper-variable (Allen et al. 1999). In summary, 'lumps' of similarly sized animals will be adapted to 'lumps' of apparent resources in the landscape.

The methods for finding gaps or discontinuities that separate 'lumps' (modes, aggregations or clusters) in size distributions are relatively new and non-trivial. We can profile the size distribution of any animal assemblage by lining up, by mean adult body size, all the animals that live in a landscape from the smallest to the largest species. Viewing across the profile we may notice that sections have continuous outlines where the species are quite similar in size. These smooth sections stand out further because they are bounded on either end by relative jumps in size from one species to the next. This jump in size between two species is the simplest notion of a size gap between the clusters of animals of similar size. We use a cumulative

distribution function to illustrate the locations of lumps and gaps in the size

distribution of a mammal assemblage (Figure 2).

<div align="right">Figure Two</div>

While a debate continues (Manly 1994, Siemann and Brown 1999) regarding the

methods and conceptual justification for identifying lumps, Gap Pattern (GaP)

analysis (Restrepo et al. 1997) has shown credible consistency in providing assistance

to visual inference regarding the body mass distributions of a variety of taxa around

the world. Discontinuous body mass distributions have been shown for the bird and

mammal assemblies of the Canadian boreal forest and prairie (Holling 1992), birds in

Colombian montane forests (Restrepo et al. 1997), birds, mammals and herpetofauna

in the South Florida ecoregion (Allen et al. 1999), birds and mammals of

Mediterranean-climate Australia (Allen et al. 1999), Mexican cave bats (Allen et al.

1999), Pleistocene mammals in savanna-forests (Lambert and Holling 1998), and

birds in North American suburban landscapes and Neo- and Paleo-Boreal Forests

(Hostetler 1997). Sendzimir (1998) tested for and confirmed lumpiness in 150

mammal data sets in 18 different biomes from four continents. Lumpy size patterns

for animal communities are revealed by size gaps as well as the regularity of size

distributions *within clusters*. Allen and Sendzimir (*unpublished data*) found that

within the clusters the animal sizes are more evenly spaced than expected by chance

The consistency with which lumpy size distributions are found in terrestrial

ecosystems make them compelling. What process(es) might cause such ubiquitous

lumpiness? Sendzimir (1998) found no evidence that membership in a lump is

<div align="right">14</div>

correlated with membership in a trophic class or a taxonomic order. Gaps between lumps are not explained by size differences because of trophic relations, and lumps are not explained because of limited adaptive radiation from a common ancestor (Holling 1992). The remaining explanation, that animal lumps arise from animal interactions with a lumpy landscape, becomes more compelling when we examine the regularities of lump pattern. If body size distributions reflect animal interactions with landscape structure, then certain lumpy body size patterns should be consistently associated with particular landscape structures. In fact, lumps and gaps in different animal assemblages tend to line up at the same places along the size axis, but only if the two assemblages inhabit relatively similar landscapes, such as in the same biome (Sendzimir, *unpublished data*). Taxonomic overlap does exist to various extents between such assemblages, but it does not explain these pattern regularities. When comparing different animal assemblages, indices of lump pattern regularity had only a random relationship with indices of species similarity (Sendzimir 1998). Finally, these regularities of lump pattern gained a further degree of credibility when computer simulation showed that their degree of regularity was not the product of chance.

1.3 Implications For Conservation And Management

1.3.1 Animal Interactions With Landscapes

Animals are not merely passive responders to ecological patterns in space and time. They interact by utilizing ecological pattern at certain scales and, in some cases, by reinforcing processes that structure the landscape. Conversely, structure is not simply

the end product of processes mediated by animals or abiotic factors. Landscape patterns interact with processes (and therefore animals), often in mutually reinforcing ways that sustain the pathways, cycles and species of a landscape as a complex, adaptive system.

1.3.1.1 Exploitation Of Ecological Pattern And Architecture

Evidence links certain body sizes to certain landscape features evident within one or a few ranges of scale. Groups of similarly sized animals show regular associations with certain sets of landscape features at different scales. At micro-scales, arthropod body sizes have been related to various vegetation architectures (Morse et al. 1988, Shorrocks et al. 1991). In the Boreal forest, guilds of small birds, such as foliage gleaners, forage for insects among the micro-architecture of tree needles and leaves (Holling 1992). Between micro- and meso-scales, artiodactyl size correlates with the structure of the undergrowth so as to minimize resistance from vegetation (Dubost 1979) and small rodents use overgrown fence-lines and hedgerows as corridors (Fahrig and Merriam 1985, 1994). At meso-scales, medium to large size animals, such as raccoons and white-tailed deer (*Odocoileus virginianus*) interact with larger structures, such as patchy edges and ecotones. Mega-fauna discriminate and respond to specific macro- scale structures. For example, moose (*Alces alces*) interact with large-scale landscape patterns, such as the distribution of marshes within a landscape. Grizzly bears (*Ursus ursus* horribilis) seldom use habitat within 100 meters of a highway, whether the road is in use or not (Turner 1989), and European bison (*Bison*

bonsasus) often will not cross a road even in total absence of vehicles or people (K. Perzanowski, pers. comm.). The link between body size and landscape structure was dramatically demonstrated in Cameroon by Smith et al. (1997) where sub-populations of the same bird species, the little greenbul (*Andropadus virens*), have significantly different body size and wing size morphometrics that correlate with differences with landscape structure, but are not attributable to genetic drift. As Holling predicted, birds in more open habitats (the forest/savanna ecotone) have larger body and wing sizes than birds in the more enclosed habitat (interior forest).

Measuring landscape structure is far easier than quantifying links between structure and animal behavior. From the wider perspective *across* all scales in a landscape, work on quantifying and describing landscape structure (Gardner and Turner 1991, Hargis et al. 1997) dwarfs research on animal responses to spatial patterns, especially landscape mosaics (Ims 1995). A variety of theories (Optimal Search, Optimal Foraging, Habitat Selection and Dispersal, Source and Sink, Meta-population) provide useful predictive frameworks to test observations of how animals respond to what structures (see Table 1 for a small sample). What kind of structure and at what scale an animal responds to it depends on the life process involved. In the Everglades, wading birds make decisions at micro-scales (food capture in littoral zones), meso-scales (which pond in which to forage?), and macro-scales (migration). Similar hierarchies relate spatial scale to movement response for a variety of taxa (Senft et al. 1987, Kotliar and Wiens 1990, Ims 1995).

Table One

What process links hierarchies of landscape structure and scale-dependent animal decision-making? Holling (1992) proposed that scale-dependent animal perception is a key link. If animal perception and use of habitat is scale dependent, and perception of landscape structure is allometric with body size, then animals in a lumpy landscape should cluster into sizes that can sense and exploit specific scale domains. As opposed to separate and unique connections between single species and landscape features, lump analysis can help define which animal groups are linked with which sets of habitat features or landscape structures. Sendzimir (1998) used lump analysis to contrast two mammal assemblages in African woodland ecosystems. Despite the lack of species overlap, the lump patterns of the two assemblages were highly similar (Figure 3). Not only do the lumps and gaps occur in very similar locations on the size axis, but the landscape texture used by different species in each ecosystem is best predicted by the lump (size class) they occur in. The discrete jumps in size that separate lumps are associated with qualitative differences in landscape structure used, with larger size classes using coarser and coarser textures in the ecosystem. For example, mammals in the lump containing the smallest species sizes used micro-scale architectures like grass runways while those in the next larger lump exploited cavities between rocks and under logs. Species in the third largest lump associate with meso-scale linear features like ecotones between wetlands and water bodies or forests and open spaces.

Figure Three

1.3.1.2 Maintenance Of Ecological Pattern And Architecture

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Animals within a size-class may perceive and use ecological architecture within a range of scale, but how they use it may reinforce and maintain that architecture as well. Landscapes are structured by a variety of processes. Vegetative processes of growth and senescence, and disturbance processes of wind throw, flooding, and fire all contribute to the architecture of landscapes. However, certain landscape structures are also sustained over time by animal-mediated processes that reinforce the distribution of structure at several scales (Table 2). Note that the structuring effect does not necessarily scale with animal body size. Large animals can effect small-scale patterns (bear browsing and defecation reinforcing patch spatial distributions of alpine flowers), and small animals can effect large scale patterns (defoliating insects can denude vegetation over 100,000 km^2 in the boreal forest over a 7 year outbreak (Ludwig et al. 1978)). In the latter case, over-development of biomass during succession can over-connect an ecosystem, making it vulnerable to contagious spread of processes that usually work at small scales. Spruce budworm outbreaks in most years may create patches less than several hectares if there is any outbreak at all.

Table Two

1.3.1.3 Resilience Of Ecosystems

Lumpy body size patterns may link aggregations of animal species with processes that structure the landscape at specific scales. Understanding the distribution of function both within and across lumps provides a framework for understanding how resilience

is generated in ecological systems. Resilience is the capacity of an ecosystem to absorb a shock while retaining the sets of processes that structure and maintain its character (Holling 1973, 1992, Peterson et al. 1998). The resilience of ecosystems depends upon the distribution of functional groups within and across scales. If the species that comprise a functional group operate at different scales, they provide mutual reinforcement that contributes to the resilience of a function, while at the same time minimizing competition among species within the functional group. For example, while small foliage gleaners such as kinglets and warblers forage for spruce budworm at low larval densities, a larger class of birds, such as corvids, converges to forage on budworm when an outbreak aggregates individual budworms so that they constitute a large-scale resource. This cross-scale resilience complements a within-scale resilience that is produced by an overlap of function among species of different functional groups that operate at the same scales (Peterson et al. 1998). Within-scale resilience arises from a 'fuzzy' redundancy because each species within a scale has similar but not at all identical effects. They differ in function, as well as degree of influence and sensitivity to change. We propose that this resilience can be assessed by analyzing the distribution of function within and across lumps in the body mass distribution of an animal assemblage.

1.3.2 Understanding And Predicting Vulnerability

In hierarchical complex systems, breaks between levels indicate the scales at which the processes controlling structure shift from one set to another. Scale breaks in

attributes of animal communities such as body masses correlate strongly with a set of poorly understood biological phenomena that mix contrasting attributes. These phenomena include invasion, extinction, high population variability, migration and nomadism; in other words, high variability at the species, population and community levels. Recently, Allen et al. (1999) documented that the body masses of endangered and invasive species in a community occur at the edges of body mass aggregations 2-4 times as often as expected by chance. For example, Figure 4 illustrates the locations of invasive species (arrows) within body mass aggregations (hatched polygons) of a body size distribution for south Florida mammals. That correlation is consistent in all 8 data sets examined so far. Those data include four different taxa in two different ecosystems. The strong correspondence between the independent attributes of population status and body-mass pattern in three different taxa confirms the existence of discontinuous body mass distributions. It may seem surprising that both invasive and declining species are located at the edge of body-mass aggregations. These results suggest that something similar must be shared by the two extreme biological conditions represented by invasive species and declining species. An examination of the phenomena of nomadism in birds in an Australian Mediterranean climate ecosystem (Allen and Saunders 2002) found that nomadic birds also cluster about scale breaks (occur at the edge of body mass aggregations). The clustering of these phenomena at predictable locations – the edge of body mass aggregations - suggests that variability in resource distribution or availability is greatest at scale breaks.

Rapid anthropogenic disturbance affects the processes that structure ecosystems. If animal body mass aggregations are linked to scale-specific structures, such perturbations should reveal themselves by rate changes in species turnover that affect body mass aggregation patterns, or changes in the pattern itself. Feedback from taxa adapted to the altered ecosystem structure (e.g., invasive species) can prevent return to the original system state. As more invasive species become established, they may further alter the environment and promote a new regime of processes that entrench structural change. The lower turbidity induced by zebra mussel invasion of the Great Lakes is one example (MacIsaac 1996, Budd et al. 2001). Even if original key processes are re-established, the original animal community is not likely to be re-assembled (Case 1990, Drake et al. 1996). Understanding the nature, location, and drivers of turnover in complex systems may help us understand how these systems are established and maintained.

There are unusual characteristics associated with scale breaks. The edges of aggregations may be considered zones of crisis or opportunity depending on the way a given species at these scales exploits resources and interacts with its environment. As such, scale breaks may be analogous to phase transitions. In perturbed systems, we have documented that biological invasions, extinctions, and nomadism tend to occur at aggregation edges. However, we suspect that variability in species composition and population status is higher at scale breaks (the edge of body mass aggregations) whether or not the system has been perturbed. Human landscape transformations simply heighten the inherent variability. Highly variable behavior such as this has

been demonstrated for the area between domains of scale in physical systems

(Nittmann et al. 1985, O'Neill et al. 1986, Grebogi et al. 1987), and postulated for

biological communities (Wiens 1989). This discontinuous pattern may have

predictive power: invasive species and extinct or declining species tend to be located

at the edge of body-mass aggregations, which may be transition zones between

distinct ranges of scale. Location at scale breaks affords species great opportunity, but

also potential crisis. Complex behaviors such as migration, and rapid adaptation

leading to speciation may evolve most efficiently and commonly at scale breaks,

where there is the greatest potential reward, though with the highest potential cost.

Figure Three

1.3.3 Wildlife Management And Landscape Pattern

By practical imperative, protocols to manage landscape pattern tend to become diffuse

and vague as the scale of the conservation goal increases. Conservation of an

individual species mandates identifying, conserving and/or creating the specific

metrics of patch size, shape, and diversity in the landscape mosaic that favor that

species, whereas regional goals broadly aim to "preserve diversity at all scales

including the processes that create diversity" (Arnold 1995). From vegetation

distributions to patch metrics to corridor width, the work of identifying landscape

pattern types critical to conservation at different scales is relatively young, and

developing spatial pattern statistics has only begun (Turner and Gardner 1991).

Determining the metrics of critical landscape patterns separately for each species

would be an overwhelming task even if landscapes remained stable. In a world of shifting climates, nutrient and material fluxes, and land cover, how can we practically assess and manage landscapes to conserve biodiversity at the species level? And if species requirements conflict, how can they be rationalized within landscape level planning?

Complex Adaptive Systems theory may shorten the road to conservation effectiveness by integrating parallel probes of the processes, structures and species interacting in a landscape. All three show fundamental clustering patterns and hierarchical structure. Lumpiness is evident in the temporal distribution of the structuring processes, the space/time distributions of landscape patterns, and the size distributions of the animals living in the landscape. The task remains to test whether these pattern correspondences translate into functional linkages that can guide conservation research and management practice. The association between location of a species in the lumpy body size pattern and species attributes such as invasiveness or vulnerability to extinction suggests that such functional links do exist. If so, the daunting diversity of dozens of natural histories in a landscape may reduce to a small number of species groups (lumps), within which species share affinities for scale ranges of landscape pattern and structuring processes. For example, in an analysis of animal assemblages with species numbers ranging from 25 to 73 (Sendzimir 1998), the number of lumps ranged from 3 to 13, a reduction in numerical complexity ranging from a factor of 5 to 24.

The analysis of body mass patterns and their links with scales of structure in the landscape has many potential applications in wildlife management. For landscapes it may be possible to analyze the distribution of function within and across scales and estimate the relative ability of different ecosystems to cope with perturbations. We predict that systems with more lumps, greater functional group representation, and more even distribution of functional groups across lumps (Peterson et al. 1998) will be more resilient to human development, or other large disturbances. Systems with relatively fewer lumps, less functional group representation, and less even distribution of functional groups across lumps are less likely to tolerate development and more likely to need intensive management intervention following landscape change.

Even in a world in transition, it should be easier to study and manage species within groups rather than dozens of species individually. We can more easily identify critical landscape patterns if lump analysis identifies groups of animals likely to exploit such patterns. Conversely, identifying key landscape patterns simplifies monitoring the dynamics of critical or endangered populations of species related to those landscape structures. As well, it should be possible to predict those species most at risk of decline, and thus most in need of monitoring, following perturbations. Species whose body masses place them at the edge of body mass aggregations are twice as likely to be endangered, threatened or species of special concern than species whose body masses place them solidly within lumps (Allen et al. 1999). Longer-term research might identify vulnerable clusters of species whose habitat use relies on landscape structure that has begun to change, or is expected to change. Management

interventions could address endangered species and structuring processes in parallel, by protecting vulnerable species clusters while changing the degree of perturbation at critical scales. This might be done by diminishing other impacts on vulnerable species, e.g., hunting or competition for resources, while shaping resource spatial patterns through control of grazing, hydrology and/or planting.

Two examples of pre- and post- disturbance research and management illustrate how integrating analyses of lumps and landscape spatial patterns of structure and function help to assess and manage the effects of perturbations at various scales on wildlife. Efforts to anticipate or respond to perturbation effects on native fauna could use lump analysis to identify species size clusters and compare the spatial scales of movement and habitat use critical to survival of species within each cluster with those of perturbation (such as patch size and inter-patch distances). One post-disturbance opportunity to study and perhaps manage change was created when European colonization of Australia introduced new species of grazing herbivores that transformed vegetation patterns at regional scales. Introduction of cattle and rabbit drastically altered plant species composition in rare, fertile pockets of the arid landscape. These perturbations to the Australian landscape increased inter-patch distances, making resources at meso-scales inaccessible to indigenous middle-sized mammals and hastening their disappearance (Morton 1990). Lump analysis might predict species or species groups in the size range that could profit from re-establishment of pre-colonial vegetation patterns or that could better exploit existing vegetation patterns.

We anticipate the use of a similar approach prior to a planned introduction of a new disturbance regime intended to support avian biodiversity conservation efforts in the Narew River valley in north-east Poland. This experiment tests ideas (Vera 2000) that proper management of disturbance regimes can sustain and promote biodiversity. Pollen stratigraphic analysis in lake bottoms revealed that landcover in many parts of pre-historic Europe was not closed forest but more open and savanna-like, perhaps in response to mega-faunal foraging and browsing processes (Vera 2000). This suggests that habitat management might restore biodiversity to historic levels by re-establishing the full suite of processes, including browsing, which formerly structured the landscape. The impacts on biodiversity of re-introduction of browsing or traditional forms of mowing are being tested in forests, heathlands and grasslands (Bokdam and Wallis de Vries 1992, Bokdam 1995, Kampf 2001). We plan to assess the biodiversity impacts of browsing in the river floodplain of the Narew by monitoring avian populations and changes in vegetation patterns related to changes in hydrology or herbivory by local or ancient breeds of horses or cattle. Lump analysis of the avian species assemblage will be employed to identify as candidates for monitoring those individual species and species clusters that might be influenced by change in vegetation spatial distributions.

1.4   Conclusions

Ecosystems function as, and are organized as, complex adaptive systems (Levin 1998). There is compelling evidence from time-series and spatial data that the world is organized by a small set of structuring processes into a hierarchy of a limited number of spatial scales (a 'lumpy' world). Measures of clustering in the time behavior of ecological processes, the spatial distributions of landscape structures, and the size distributions of resident, animals can identify which groups of processes and landscape patterns might be associated with which groups of species over which time horizons. These clusters of process-landscape-species may prove more practical to detect and manage than efforts to marshal data on dozens of species and landscape characteristics. They may also provide a more informed context for asking specific questions about the habitat requirements of individual species. The most striking example to date of the conservation implications is the capacity that lump pattern analysis provides to predict species characteristics, such as nomadism, invasiveness and vulnerability (Allen et al. 1999, Allen and Saunders 2002). We can test the larger potential of lump analysis by using it to predict the full range of vulnerabilities across a species assemblage by linking their body size-related resource use to scales of disturbance. Wildlife managers can then incorporate changes in resource distribution associated with slower and subtler perturbations such as climate change or shifts in land use and land cover in addition to other known threats such as hunting, catastrophic disturbances, and pollution.

1.6 Summary

Landscape patterns that are different at different scales, and which change abruptly at scale breaks, entrain morphological and behavioral characteristics of species (Holling 1992). That entrainment is reflected in discontinuous animal body mass patterns (lumps and gaps in body mass distributions). Clustering patterns evident in the time/space distributions of processes and structures and the body masses of species interacting in a landscape offer opportunities to study and manage wildlife based on functional links between animals and the scales of ecological structure they utilize. The potential for lump analysis to link clusters of animal body masses with ecological processes is demonstrated in its power to predict species characteristics, such as nomadism, invasiveness and vulnerability. For managing wildlife where perturbations are shifting the landscape mosaic, this potential can be extended by linking predictions of species vulnerability and scales of habitat exploitation with analysis of the spatial scales of landscape structure changed by disturbance.

South Carolina Department of Natural Resources, Clemson University, and the Wildlife Management Institute.

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Table 1. Links between landscape patterns and patterns of animal survival, size and movement as predicted separately by Optimal Search Theory (OST), Habitat Selection and Dispersal Theory (HSD), and Metapopulation Theory (MPT).

Theory	Structure	Observation(O) /Prediction from theory (P)	Ref.
	Boundary Hard edge	O - Species crosses habitat boundary only in extreme circumstances	2
HSD	Patch Size	O - Smaller habitat patches have higher rates of extinction and emigration, lower rates of immigration.	1,2
OST		P - foraging movements are scale specific, step length decreases and turning rate increases when entering a smaller size patch	2
		O - Increasing minimum patch size associated with increasing body size for occupant species	1
MPT	Patch Shape	Concave edges act as funnels to channel migration from peninsulas and facilitate boundary crossings by dispersers	2
		Convex edges are crossed more frequently by animals doing daily foraging	2
		P -Emigration rate increases with edge/area ratio	2
OST	Inter-patch distance	P – Traplining (rotational foraging along a memorized circuit) optimally exploits patchy resources (food or shelter).	2
		O - Increasing inter-patch distance associated with declining patch occupancy	1
HSD	Fragmentation	P – hampers migration of 'matrix-sensitive' or 'interior' species.	2
HSD	Corridors	P – may lower fragmentation's impact, especially as corridor width increases.	2
	Landscape Mosaic	O - fewer, large extinction-resistant patches and many, small extinction-prone patches.	1

References: 1- Ritchie (1997), 2- Ims (1995)

Table 2. Fauna-mediated processes that create and maintain patchy landscape patterns (after Johnson 1995).

| *Pattern*	*Process*	*Fauna*	*Ref.*
Patches – Surface, 2-dimensional			
Tree stems and crown	Seedling recruitment boosted by mycorrhyze enhanced by defecation	Small rodents	15
Patches of flowers in alpine meadows	Germination enhanced by higher nutrient levels from defecation	Bears	15
Small-to-Medium-sized patches (Conspecific tree patch distribution in rainforest mosaic)	Patchy defecation – Seed dispersal-Latrines	Tapirs	10, 14,
		Howler monkeys	12
	Seed predation	Collared peccaries,	10
		Agoutis	11
Medium-sized patches	Selective herbivory - Diffuse effects of single individuals	Moose	2,3
	Seed & seedling consumption -Intense effect of herd	White-lipped peccaries	10, 11, 13
	Digging, wallowing	Wild Boar	4
	Destructive browsing	Elephants	5
Medium-to-Large-sized patches	Selective herbivory - Concentrated effects of swarms	Gypsy moth, Spruce budworm	6 7
Patch Bodies – Volumetric, 3-dimensional			
Small patches	Soil-mixing	Earthworms	6
	Mounds – nutrient & water concentration	Termites, ants	6
	Den burrowing	Pocket gophers Prairie dogs	8 9
Small to large sized patches (Ponds)	Dam construction	Beavers	6
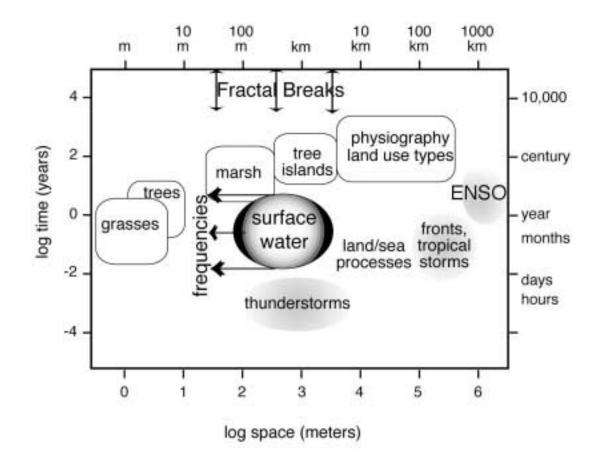
1. Paine and Levin 1981, 2. Pastor et al. 1988, 3. Bowyer et al. 1997, 4. Holling 1992, 5. Bratton 1975 , 6. Laws 1970 , 7. Ludwig et al. 1978, 8. Huntley and Inouye 1988, 9. Agnew et. al. 1986, 10. Fragoso 1999, 11. Silvius 1999, 12. Julliot 1997, 13. Fragoso 1998, 14. Fragoso and Huffman 2000, 15. Sendzimir 1998.
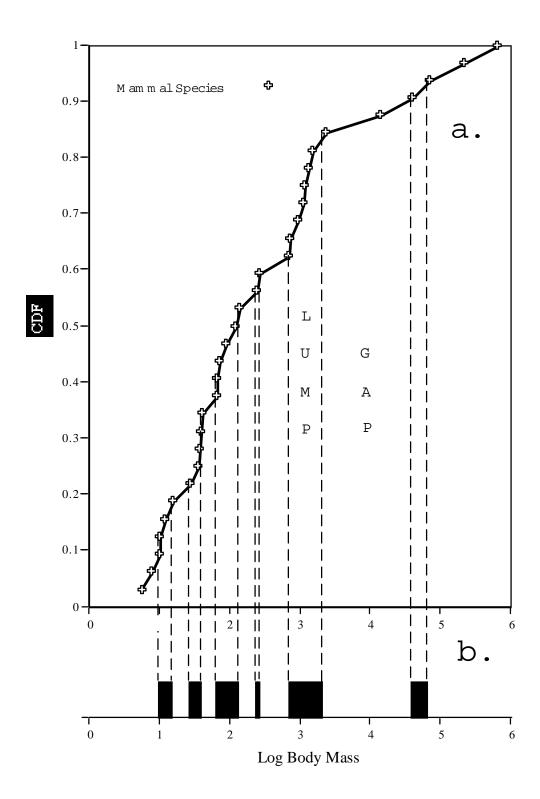
Figure 1. Stommel plot of structures and processes in the Everglades ecosystem, along dimensions of space and time. The upper set of boxes indicate vegetation hierarchy, from individual plants to physiographic groupings. The lower tier represents the scales of meteorological processes that influence ecosystem. Fractal breaks ('scale breaks', as assessed by changes in fractal dimensions) that delimit the domains of landscape features are shown.   Dominant frequencies of hydrologic processes in the Everglades are depicted as arrows from the surface water representation.
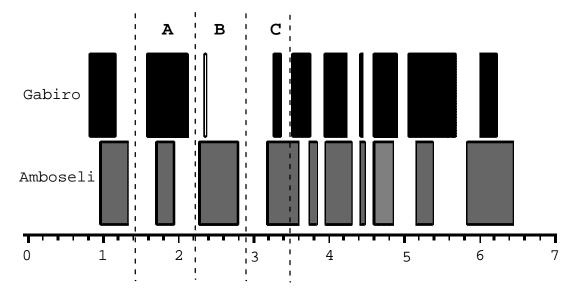
Figure 2. Extrapolation of cumulative distribution function (a) for log10 body masses of shortgrass steppe mammals from southwest Kansas to an interpretation of lump structure (b) wherein each gray box represents a distance along the size axis occupied by a cluster of species of relatively similar size (body size lump). These lumps are separated by 'gap' zones on the size axis that are occupied by no or very few species.

Figure 3. Body mass patterns for two African savanna/woodland mammal assemblages with no taxonomic overlap at the species level. Discontinuities in these lump patterns identify the distinctions in the scale and texture of landscape use of the species in the body size zones A, B, and C. With jumps in body size landscape textural use grades from very fine (A - burrows under sandy or wet soil, herbaceous mats) to fine (B - extensive ground cover, hollows, holes, crevices) to coarse (C - fringes of water, forest, and open areas).

Figure 4. Gap statistic (triangles), body mass pattern (body masses as circles), and occurrence of listed species (red) for Everglades mammals. All data is presented in the lower graphic, while the upper graphic displays a stylized version of the body mass pattern and location of listed species (arrows). Aggregations (shaded) were defined as groups of 3 or more species bordered by significant gaps; this criteria led us to disregard some high values of the gap statistic. Note, however, that changes in body mass patterns due to the above make no difference in the overall patterns detected. (Modified from Allen et al. 1999).

FIGURE ONE

FIGURE TWO

FIGURE 3

South Florida Mammals

Figure 4