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The need to improve our attention to scale of resolution in grouse research

Daniel M. Keppie & Jonathan M. Kierstead

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A principal focus of ecological research should be to learn the influence of scale on ecological processes and to determine appropriate spatial and temporal scales with which to study the problem of interest. To date, little attention has been given to scale issues in grouse research, and we conclude that this is a major weakness. The problem affects not only our interpretations of individual events and processes, but also our interpretation of relative effects of various factors and processes, which likely act at different scales. Investigators should provide evidence for the choices made for the scale of resolution/grain used in field studies and analyses, and should conduct analyses at multiple scales. The current research problem also hinders the quality of forecasts that can be made about management interventions. To help illustrate the effect that scale of resolution can have upon research results, we provide two examples on grouse, one temporal and the other spatial.

Key words: research, ruffed grouse, scale dependency, scale of resolution, spruce grouse

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Research and understanding in science advance in part by searching for general patterns. We should continuously want to learn novel ways to improve our research in the system being studied, which in turn could help enhance predictions about other systems as well. One step toward advancing the calibre of our research would be to give much greater attention to the concept of scale, that is the temporal and spatial limits to an environment or system (its extent) and the fineness with which it is measured (resolution; see Wiens 1989, Kotliar & Wiens 1990, King 1997, for further descriptions and definitions). Scale is fundamental to learning: it is "...the fundamental conceptual problem in ecology, if not in all of science" (Levin 1992: 1944). But ecologists did not seem to formally use the concept of scale much until the 1980s (Schneider 2001). Bissonette (1997) concluded that wildlife biologists still act as if scale somehow does not matter. If the intent is only to monitor annual changes in abundance of some single species then, seemingly, all we need to do is count. But as Hayek & Buzas (1997: Fig. 1.1) illustrate, scale influences what we interpret from even these simple numbers. Even though Wiens, Stenseth, Van Horne & Ims (1993) used capercaillie *Tetrao urogallus* to help promote a new research framework based on spatial patterns and scale, there has been little use of this in the design of grouse research.

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Studies by Hagen, Kenkel,Walker, Baydack & Braun (2001) and Storch (2002) are perhaps the first to clearly build upon scale as a central theme. Yet, even when biologists speak of scale in ecological research and conversation, it usually applies only to the extent of study. Much less attention has been given to assessing the importance of resolution, which greatly determines what is interpreted from data gathered (e.g. Turner, O'Neill, Gardner & Milne 1989). As a coarse generalisation, we propose that any object or process not distributed uniformly in time or space is scale dependent. Our point is, that wildlife ecologists seldom test for scale dependency.

There are many reasons for the general rise in interest for scale in ecology (see Levin 1992, Schneider 2001), but one prominent motivation was Mandelbrot's (1983) demonstrations about fractal geometry and nature. One classic example of scale dependency in nature is the now-famous query, "How long is the coast of Britain?" (Mandelbrot 1967: 636). In effect, the length is whatever we choose it to be, as measured by the resolution of the ruler. This should cause us to wonder whether biological objects and processes are measured in ways that do instruct us about the real system or whether we measure them only at a scale that is traditional or convenient for us (e.g. 1:12,500 aerial photographs).

To help us realize more fully that scale of resolution is meaningful to the answers that are generated from data collected, we provide two very simple examples on grouse. One employs multiple temporal scales of resolution and the other multiple spatial scales. We chose these particular examples because they exemplify many common research questions. Both were selected without first knowing the extent to which their analyses would show scale dependency.

The two examples

Temporal analysis of fluttering

In spring, male spruce grouse *Falcipennis canadensis* advertise themselves with a short flight from tree to ground; they land with an exaggerated, but soft flutter or a loud wing clap (Boag & Schroeder 1992). In 1989-1990 at Sevogle, New Brunswick, and Woman River, Ontario, Canada (Keppie 1992), males were watched continuously in early morning at their individual display locations. We recorded the time of flutters and associated social and environmental events. For the present purpose, fluttering was reanalysed within: 1) 6-21 May, a period overlapping principal courtship and egg-laying, and 2) 65 minutes before (-65) to 140 minutes after (+140) local sunrise time. Both constraints serve to reduce variance in the data set, putting at greater risk our conjecture of a scale effect upon fluttering.

A total of 1,826 flutters were recorded for a total of five males within -65 - +140 over 35 days, all days summed together herein. To investigate scale effect, total flutters heard and the 206 minute period of extent were held constant, and the period was divided into consecutive intervals at three scales of resolution, of 1) 1-minute duration (N = 206 intervals), 2) 3-minute duration (N = 69 intervals), and 3) 5-minute duration (N = 41 intervals). Individual 1, 3 and 5-minute intervals from sunrise (e.g. at -36, or -38 through -36, or -40 through -36, respectively) were sampled a maximum of 35 times (days across years); exceptions were a few late starts, predator or weather-caused gaps in activity or that the bird departed early. For each time interval relative to sunrise, a probability of sounding (fluttering) was computed as the number of days on which at least one flutter occurred divided by the number of days the particular interval was observed.

Mean flutter rates for 3 and 5-minute intervals were 3 and 5-fold greater than the 1-minute rate, unchanged by resolution because total flutters and extent of listening (206 minutes) remained constant. Furthermore, as also expected, mean ± SD probabilities of fluttering over the total period increased with coarseness of scale: 0.27 ± 0.13, 0.45 ± 0.15, and 0.52 ± 0.14, at 1, 3 and 5-minute intervals, respectively. But it was instructive that probabilities differed substantively at peak fluttering times as follows. A peak period of fluttering was identified for each scale, being the longest span of time within which all individual probabilities were equal to or exceeded the mean value computed for the respective scale over the full period of -65 to +140 (see values above). We did this in order to reduce the magnitude of variances for the three scales of analysis, again serving to put at greater risk the conjecture of a scale effect upon fluttering. Mean ± SD probabilities of fluttering during peak periods were 0.38 ± 0.07 (N = 26 during -5 to +20), 0.56 ± 0.06 (N = 26 during -14 to +63) and 0.61 ± 0.06 (N = 20 during -40 to +59), for 1, 3 and 5-minute analysis intervals, respectively (Fig. 1). These mean probabilities differed substantively (one-way analysis of variance: $F = 108.9$, $MS = 0.375$, $df = 2$, $P = 0.00$). Residuals of probabilities were plotted and showed no trend across scales. It is noteworthy that the highest single probability for a 1-minute resolution (0.58 at -25) occurred outside the peak periods identified by 1-minute and 3-minute analyses (see Fig. 1). Relative variance of fluttering during peak periods

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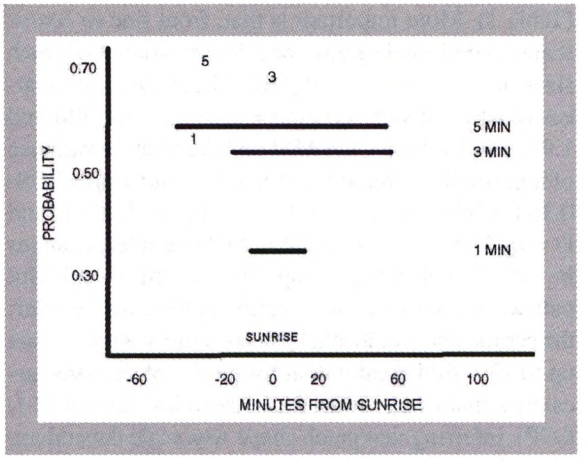


Figure 1. Fluttering by spruce grouse from 65 minutes before sunrise through 140 minutes after sunrise, from 1,826 flutter situations by five males over a period of 35 bird-days within the period of 6-21 May 1989-1990 at Sevogle, New Brunswick, and Woman River, Ontario, Canada. Horizontal lines illustrate mean probabilities across periods of time in which all individual probabilities for the particular scale of resolution (1, 3 and 5-minute analysis intervals) equalled or exceeded the mean value computed for that scale over the entire -65 through +140 period (see text for mean values). Numbers 1, 3, and 5 indicate the level and time of occurrence of the highest individual probability for 1, 3 and 5-minute scales, respectively.

decreased by half as resolution became coarser: coefficients of variation = 0.18 (N = 26), 0.11 (N = 26) and 0.09 (N = 20), for 1, 3 and 5-minute intervals, respectively.

To sum up, male advertising was distributed irregularly enough over time in early morning so that the probability of fluttering differed substantively according to the scale at which data were analysed. The probability that males sound (song or mechanical) is a useful metric for many questions about behaviour as well as for coarse indices of abundance (e.g. audio-index estimates for ruffed grouse *Bonasa umbellus*). These probabilities are insensitive to additional factors that might influence the rate at which active males sound (call/song rate). Although untested, we speculate that social and reproductive factors will influence probabilities inconsistently at different scales of resolution; intuitively, greatest at fine scales. Because efficient indices of abundance should be insensitive to such behavioural variance, the appropriate resolutions for estimates of abundance are likely coarser than optimal scales for behavioural studies.

Forest patch complexity

There are two ways to change resolution for spatial objects (e.g. patches); 1) change the numerical unit with which they are measured, e.g. map scale (the coastline example) or, 2) change the fineness of criteria by which patch types are defined, as in the present example.

Grouse use various plant species and structural conditions over time and space. For many reasons it may be useful to learn the degree to which individuals use particular locations, e.g. because of conditions at those respective sites or relative to their proximity to other patches, or for numerous questions about environmental patterns. It is intuitive that patch shape and the resulting pattern both influence and result from certain critical biotic and abiotic processes (e.g. Krummel, Gardner, Sugihara, O'Neill & Coleman 1987, Turner, Gardner & O'Neill 1995: Fig 5), and new ideas keep emerging about animal behaviour and environmental and vegetative heterogeneity (e.g. Clobert, Danchin, Dhondt & Nichols 2001). Almost any interest in describing spatial characteristics about physical environment forces us to define the limits (edges) to patches being studied, even if only to crudely describe a point location for an animal during a fleeting observation. The specific objective of the present exercise was to learn whether metrics used to describe patterns of patches used by grouse are scale dependent.

As part of a larger study about animal community and scale, we searched for spruce grouse and ruffed grouse and their faecal pellets along transect lines through mature forest in northcentral New Brunswick from spring 1997 into late winter 1998 (Kierstead 1999). Transect lines were scattered across two areas 11 km apart (Nalaisk Mountain (NM) of 1,990 ha and the Lower Graham Plains (LGP) of 5,220 ha). We found evidence of one or both species in 37% of the forest stands along the transect lines in each area, undoubtedly an underestimate of the total use. We were interested in measuring the complexity of shapes of patches used by grouse. But edge and shape of any individual patch is influenced by patches surrounding it. At the finest scale of description (see below), individual patches were on average surrounded by five other patches (D. Keppie, pers. obs.). Because of this effect of peripheral patches upon any individual patch of interest, we propose that the complexity of patches used by grouse is indexed well by measuring all patches within areas at each respective scale of resolution. To index complexity we used patch perimeter and area.

Three measures about patches were computed: edge density (ED; in m/ha), a coarse measure about relative perimeter and area across all patches over the entire landscape (study area); mean shape index (MSI), a measure of shape complexity generated from shape indices of individual patches (SI = perimeter/$2\sqrt{\pi * \text{area}}$); and frac-

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tal dimension (D), a measure of pattern complexity computed from a power curve of log area (y axis) regressed over log perimeter of each patch, with D = 2/slope. Equations used are from FRAGSTATS (McGarigal & Marks 1994).

Using a forest planner, forest patches were mapped using Arc/Info™ on a geographic information system. The finest set of criteria used to describe patches (finest grain, scale 1) was the same set used at a 1:12,500 scale on 1998 Forest Development Survey maps available at the New Brunswick Department of Natural Resources and Energy. Criteria were then eliminated in a step-wise fashion to generate coarser levels of resolution (scales 2-5, see Kierstead 1999). As resolution decreases, adjacent patches lose their finer differences and often aggregate. Hence, patches at coarser scales generally are fewer and larger. Briefly, at scale 1, patches were defined according to percentages of the five (≤ 5) dominant tree species, development stage (e.g. young, mature and old), and canopy closure; at scale 2, by percentages of the two most dominant tree species (less dominant species classed in aggregate as conifer or deciduous), and development stage as above; at scale 3, by percentage of the single dominant tree species categorised as ≤ 30, 31-69 or ≥ 70% (less dominant species were classified in aggregate as conifer or deciduous), and development stage as above; at scale 4, by percentage of the single most dominant tree species categorised as ≤ 30, 31-69 or ≥ 70%; at scale 5, by dominant tree species categorised as either deciduous (≤ 30% conifer), mixedwood (31-69% conifer) or conifer (≥ 70% conifer). Effectively, the method simply changed the attributes used to characterise patch types, whereas the grouse locations themselves were not changed across scales.

As patch description became coarser (i.e. resolution decreasing), ED in both study areas decreased as expected, substantively and consistently, because the numbers of patches decreased and the extent remained constant (Table 1). More important is that, from fine to coarse scales in both study areas, the relative variance of patch sizes increased consistently by at least 49% within areas (coefficients of variation = 0.98-3.73 for NM and 1.97-2.94 for LGP), the MSI and the relative variance of it generally increased (coeficient of variation = 0.28-0.36 for NM and 0.39-0.64 for LGP; see Table 1) and D varied irregularly (see Table 1). For circles, changes in area do not change shape indices (SI = 1.0). But patches in both study areas certainly were not circular; the perimeters of individual patches were at least 5% and up to 13.1-fold greater than for circles of the same area (maximum shape index for an individual patch = 14.1, LGP), inferring that patch shape was scale dependent. To further test for scale dependency, a two-way analysis of variance was applied to shape indices of individual patches across scales. There was a substantial scale effect on shape index ($F = 4.32$, MS = 2.692, df = 4, $P = 0.00$), moderate study area effect (MS = 1.623, df = 1, $P = 0.11$) and no meaningful interaction of study area with scale effect (MS = 0.305, df = 4, $P = 0.74$; error MS = 0.623, df = 3161). We repeated the analysis using only scales 2-4 in order to reduce somewhat the very unbalanced number of patches across scales (see Table 1), putting the hypothesis of scale effect upon shape at greater risk. Despite this, scale effect (of scales 2-4) was still substantive on shape indices ($F = 4.70$, MS = 2.888, df = 2, $P = 0.01$). Residuals of shape indices in both analyses showed no evidence of any trend across scales. Because the fractal dimension D was computed from an exponent in a log-log regression, even small differences between the dimensions of the relationships they describe should be meaningful (Milne 1997). Increase in D between scales 1 and 4 means that the plane of the area of individual patches becomes increasingly filled with edge, quite different from the simple decrease interpreted from edge density (ED). To sum up, by holding the spatial extent constant at two areas, metrics of patch dimensions changed greatly depending on how we

Table 1. Area-perimeter metrics of forest patches at scales 1-5 of resolution (fine to coarse) at the Nalaisk Mountain (NM of 1,990 ha) and Lower Graham Plains (LGP of 5,220 ha), northcentral New Brunswick, Canada, during 1997. The fractal dimensions are from Kierstead (1999).

Area	Scale	No. of patches	Edge density (m/ha)	Mean shape index (±SD)	Fractal dimension
NM	1	236	103.0	1.84 ± 0.51	1.423
	2	220	100.1	1.85 ± 0.53	1.427
	3	141	83.3	1.96 ± 0.70	1.448
	4	92	72.0	2.07 ± 0.91	1.479
	5	17	18.3	2.17 ± 0.79	1.356
LGP	1	674	-[a]	1.83 ± 0.72	1.342
	2	664	101.8	3.44 ± 0.73	1.343
	3	542	94.7	1.88 ± 0.82	1.356
	4	422	85.2	1.93 ± 0.93	1.373
	5	164	51.9	2.02 ± 1.30	1.360

[a] Area and perimeter could not be computed because of a GIS problem, but it did not affect other scales.

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chose to delimit patches. We conclude that the strength of the relationships and our interpretations about site use and the characteristics of these sites can vary simply with the resolution used to describe and partition the area studied.

Synthesis

Advances in landscape ecology should be instructive to the grouse research community, across our different research interests. Many of the general concepts about scale and closely associated hierarchy theory have now been presented (e.g. Allen & Starr 1982, Loehle 1983, Allen & Hoekstra 1992, Levin 1992, Pickett, Kolasa & Jones 1994, King 1997). These are absolutely central to the ways in which humans and other organisms learn about their daily environment, and how they act. Some will argue that biologists simply do not yet know the scale(s) that an organism uses to measure its environment or for which critical processes occur. This may be true, but the obvious response is to measure in the field and/or analyse at multiple scales (for some general thinking see Turner et al. 1989, Loehle & Wein 1994, Johnson, Tempelman & Patil 1995). To not do so, could mean that the opportunity is missed to detect possible domains (Wiens 1989) over which environmental characteristics and animal behaviour are associated uniformly and to search for scales at which potentially important (sharp) changes in these associations occur. Metrics about environment, animal behaviour and life history are often continuous variables, neither well partitioned into distinct categories nor necessarily measured well as simple integers (Loehle & Wein 1994). Whatever the problem being studied, there is a fixed amount of variation within the particular extent studied (e.g. study area or population). The degree to which subjects of interest (say, repertoire of behavioural events, patch types, population cohorts) are classified will determine the way in which total diversity in the system becomes partitioned within versus among categories and treatments (Burrough 1983, Wiens 1989) or, in turn, drive the interpretations.

Even if our attention centres narrowly within a single species, we cannot escape the issue. A good example here is home range size, whether described best by traditional, bounded Euclidian spaces or by fractal dimensions (Loehle 1990, 1994, Hagen et al. 2001). Traditional single-scale analyses also limit our ability to interpret the relative impact of different factors upon demography or process rates because such factors themselves likely operate at different rates (Holling 1992, Levin 1992). That species area curves can be described as fractal scaling laws (Milne 1997) means that numerous questions about rates of species' interactions and population-environment relationships should be studied as scale problems. We speculate that it is easier to detect scale effects for forest grouse (i.e. more sensitive to scale) than other grouse species because of the greater dimensionality of their structural environment (see Storch 2002). For species and local populations that are plastic in behaviour, with flexible diet and resource use, and broad interspecific relationships, it should also prove easy to detect scale effects. Species that specialise or are rather dependent on limited resources will likely show minor response to variable measurement scales, except at particular scales at which abrupt changes might take place in the parameter of interest (dependent variable).

Our message is not simply a worry about the ways in which research is conducted, but also about the resulting application of it. Baskerville (1994) built upon Levins's (1966) description of models to illustrate that research consists of three broad characteristics (its accuracy or realism, its generality and the precision of its expression), and that these vary relative to each other and that they can not all be maximised simultaneously. He used this to advocate that much research does not contribute to the management of natural resources because research and management communities emphasize different mixes of these attributes. This problem is one of information, and of how well it transfers across scales. There are now many schematic space-time models of processes and systems (e.g. Forman & Godron 1986: Fig. 1.8, Holling 1995: Fig. 1.3); in many, the processes operate at distinct speeds, disjunct in space and time, showing that they are sensitive to scale and inferring that information does not readily transfer across scales (also see Turner et al. 1989). Hence, much research heretofore about populations and environment can not instruct future management questions. But to argue that biologists do not yet know enough in order to make credible forecasts about populations over future time is not acceptable, even if partly true; progressive management accepts mistakes if we learn from them. There are common problems in many of the world's ecosystems, and a principal challenge is to improve our understanding of how common processes translate across scales (Gunderson, Holling & Light 1995: 525-532). Grouse species in need of conservation help (Storch 2000) often form part of larger systems that are changing. Effective management will not come from management implications that trail loosely on traditional population and environment research. As problems with grouse and ecosystems mount, management of resour-

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ces will increasingly require interventions that take place at the scale(s) (rates over time and space) at which the system is sensitive.

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