10
Three Axes of Ecological Studies
Matching Process and Time in Landscape Ecology

MELISSA J. REYNOLDS AND MICHAEL S. MITCHELL

Abstract. The spatiotemporal resolution of observations should match the level of the ecological process under study to yield reliable insights. We present a concept of designing ecological studies that integrates three axes: temporal resolution of the study, spatial resolution of the study, and the resolution of the ecological process addressed. Focusing on the integration of the temporal axis in landscape ecology, we provide two examples from our long-term research on black bears (*Ursus americanus*) where erroneous selection of temporal resolution yields inaccurate results. In both examples, we incorporate temporal dynamics into spatial phenomena to understand complex systems. We synthesize demographic and behavioral results from our bear research and invoke hierarchy theory to understand the effects of timber harvesting on habitat quality for bears. We propose that the temporal scales at which different vital rates are manifested in a bear population may differ, which may affect the way perturbations (e.g., clear-cuts, roads, etc.) affect habitat quality for bears.

10.1. Introduction

10.1.1. Three Axes of Ecological Studies

Ecological processes operate over various spatial and temporal scales (Turner, 1989; Allen and Hoekstra, 1992; Levin, 1992; Wiens, 1996). We often overlook the fact that data collected to understand these processes are also proscribed by specific spatial and temporal scales that define the observation window through which ecological processes can be evaluated reliably (O'Neill et al., 1986; Allen, 1998). The spatiotemporal scaling that defines the observation window of a particular study should depend on the resolution of the ecological process being addressed. Thus, it is easy to visualize that for ecological studies, three axes should be considered explicitly; the resolution of the ecological process of interest, as well as the temporal and spatial resolutions of the study (Fig. 10.1A). All three axes should match closely to yield reliable insights.

Ecological processes can be conceptually organized according to hierarchy theory (Allen and Starr, 1982; O'Neill et al., 1986; King, 1997), a framework of

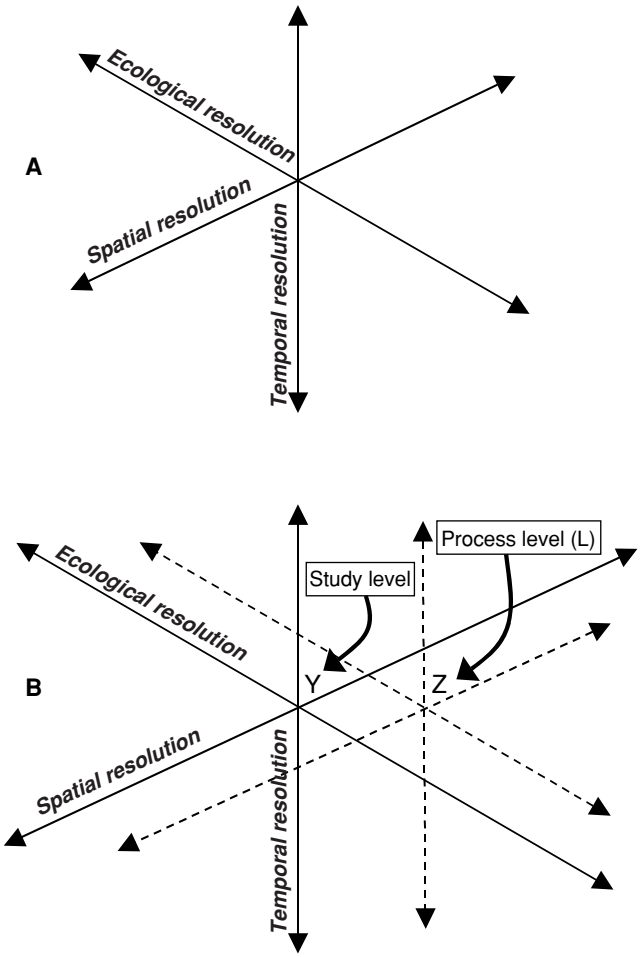

FIGURE 10.1. (A) The 3 axes implicit in every study design for ecological research: temporal resolution of the study, spatial resolution of the study and the resolution of the ecological process under study. (B) Three axes are inextricably linked. When the focal level changes along the ecological resolution axis, complementary movements in spatial and temporal resolution axes also occur. If the focal level moves from Y to Z along the ecological resolution axis, the temporal and spatial resolutions must also move from Y (solid lines) to Z (dotted lines). Study designs are flawed when the focal level of the process (L) occurs at a spatiotemporal resolution that differs from the spatial and temporal resolutions of the study.

system organization whereby ecological processes are understood in terms of both lower-level mechanisms and higher-level constraints. The framework comprises a triadic structure such that the focal level (L) includes the ecological process of interest; the $L - 1$ level includes lower-level mechanisms, defined by faster process rates and stronger interactions than those seen at L; and the $L + 1$ level includes the

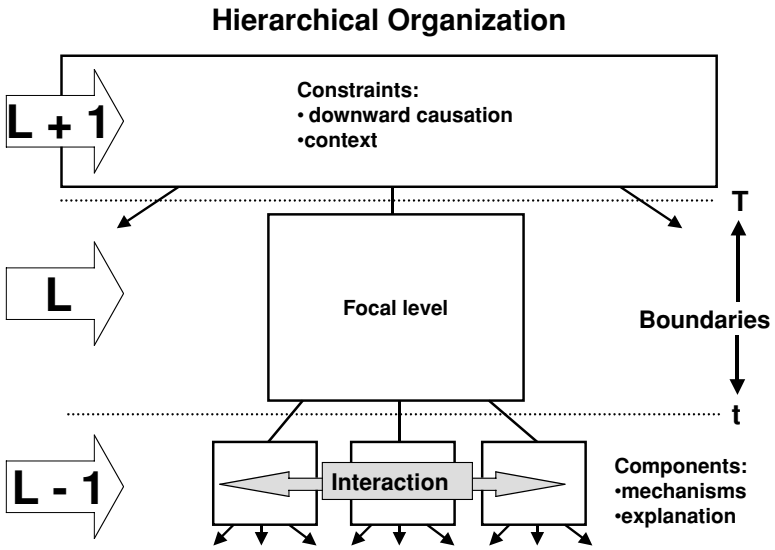

FIGURE 10.2. Hierarchical organization of ecological systems, where the focal level of the ecological process is explained by processes occurring at L − 1 levels and constrained by processes occurring at L + 1 levels.

higher-level constraints, defined by slower process rates and interactions that constrain those seen at L (Fig. 10.2). We define T to represent the spatial and temporal extent (i.e., the dimensions in space and the length in time over which observations are made), whereas t represents the spatial and temporal grain (i.e., the smallest spatial or temporal intervals in an observation set). Each level, and each holon (i.e., strongly interacting processes: Allen and Starr, 1982) within levels, is demarcated by differences in rate structure. If an ecological process is hierarchically organized, the focal level (L) of the process dictates the resolution of its temporal and spatial axes (O'Neill and King, 1998).

The range of focal levels of an ecological process is represented along the ecological resolution axis (Fig. 10.1A). The spatial and temporal resolution axes represent the spatial and temporal grain and extent of the study. All three axes are inextricably linked. As the focal level (L) of an ecological process changes along the axis, complementary movements along the spatial and temporal resolution axes are required. For example, if the focal level of an ecological process moves from Y to Z in Figure 10.1B, then corresponding movements along the spatial and temporal resolution axes must occur. Conceptually, this concerted movement is similar to movements required to fly a helicopter, with respect to three axes of orientation, up/down, left/right, and fore/aft. Movement of a control to change orientation of a helicopter along one axis automatically requires complementary movements of controls for the other two axes. Applying this analogy to the three axes of ecological studies, shifting the ecological resolution automatically implies a shift in the spatial and temporal resolution axes, too.

Similarly, shifts in the spatial and temporal resolution axes automatically imply a shift in the ecological resolution axis. If funding or logistics constrain the spatial and temporal resolutions such that a chosen focal level of an ecological process cannot be appropriately addressed, then the focal level of the ecological process must be shifted to match that of the spatiotemporal resolutions of the study.

10.1.2. Implications for Study Design

Failure to design studies without considering all 3 axes may underlie much of the contradictory or confusing insights often generated by ecological studies. Studies whose focal level is characterized by a certain ecological resolution, but that use spatial resolutions that are too small, can erroneously generalize highly localized phenomena to broader spatial scales. Consequences of failure to acknowledge choice of resolutions explicitly can be compounded if the study design includes the erroneous selection of resolution for >1 axis. For example, Figure 10.1B represents what may be the most common error in designing ecological studies, choosing the duration and spatial scope of a study that is inappropriate to the ecological resolution of the problem (e.g., attempting to model population growth of a large mammal in a year-long study conducted in a 1-ha study area). Clearly, incorrect alignment of the three axes within a given study can result in misleading inferences. Because so few studies address each axis explicitly in their design, the confidence which we can have in the bulk of empirical research to date becomes less certain (even, and perhaps most dangerously, for those studies with results that appear to make good sense).

Whereas defining spatial resolution has been widely discussed in landscape ecology, similarly defining the temporal axis in ways appropriate for landscape-scale research is commonly neglected. We devote the remainder of this chapter to an evaluation of how extent and grain of the temporal axis is best understood in the context of landscape ecology. We demonstrate the importance of matching the resolutions of ecological processes with appropriate temporal resolutions of data by providing two examples from our long-term research on black bears (*Ursus americanus*) where erroneous selection of temporal resolution yields inaccurate results. After providing background information on our research necessary to understand our two examples, we evaluate the effect of resource availability on demography of bears over three temporal extents. In our second example, we evaluate resource selection by female bears over two temporal grains. In both examples, we incorporate temporal dynamics into spatial phenomena to understand complex systems. We conclude by synthesizing our results within the framework of hierarchy theory and offering suggestions for the design of research that fully integrates all three axes.

10.2. Temporal Scale in Landscape Ecology

The role of time and the importance of temporal scale have received considerably less attention in landscape ecology than issues of spatial scale, even though relationships between landscape patterns and ecological processes, if they exist,

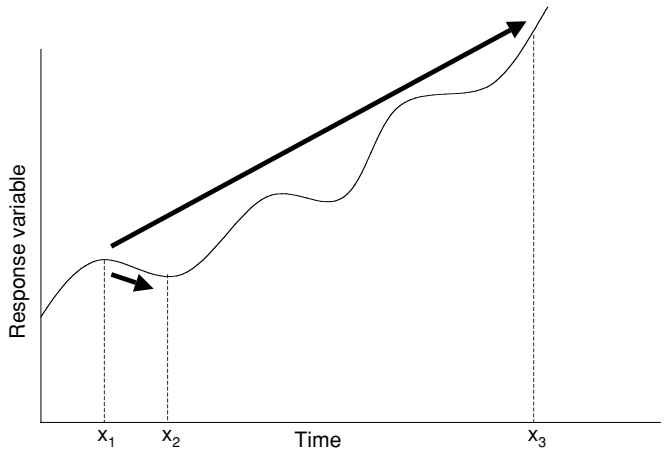

FIGURE 10.3. Contrast between inferences about an ecological process drawn at different temporal extents. Observations collected from time points X_1 to X_3 would correctly capture process variation, those collected from X_1 to X_2would not.

typically change through time due to disturbance, succession, and other temporal dynamics (Reice, 1994). Understanding complex systems requires linking space with time, over the appropriate spatial and temporal scales (O'Neill et al., 1986; King et al., 1990). Mismatches in temporal scale can yield biased results similar to those stemming from mismatches in spatial scale. For example, when the temporal extent over which data were collected is smaller than the temporal extent of the ecological process under study, the results may reflect only a brief glimpse of a long-term process and can be problematic, depending upon whether temporal patterns are consistent across scales.

10.2.1. Incorrect Selection of Temporal Extent

Consider the hypothetical scenario in Fig. 10.3 where the temporal extent over which the ecological process operates is the time between x_1 and x_3. If the response variable were measured between x_1 and x_3, the overall trend would be positive. If, however, the response variable were measured during the time period between x_1 and x_2 (i.e., a mismatch in temporal extent), results would indicate a declining trend. By definition, many studies within the field of landscape ecology examine processes occurring over relatively large spatial extents, which often correlate with large temporal extents (Urban et al., 1987; Bissonette, 1997; George and Zack, 2001). Yet most ecological studies last only 2 to 3 years.

10.2.2. Incorrect Selection of Temporal Grain

Similarly, mismatches in temporal grain may yield unreliable insights. For example, consider a scenario where fall and summer foods are evaluated to determine

whether their landscape pattern affects resource selection by a population of wild animals. For the landscape pattern to be effective (Ritchie, 1997; Bissonette, 2003), the arrangement of the foods (not just the amount) must influence resource selection by the animals. To test if spatial arrangement of foods is effective, clustering of food-bearing patches within home ranges might be estimated. If the temporal grain of 1 year is used (i.e., annual home ranges), which is common among studies of resource selection, information critical for testing whether pattern is effective may be masked. For example, seasonal foods may be distributed in numerous ways within the annual home range, 2 of which are demonstrated in Fig. 10.4 (A1 and B1; Reynolds, unpublished data). In A1, summer foods are clustered with summer

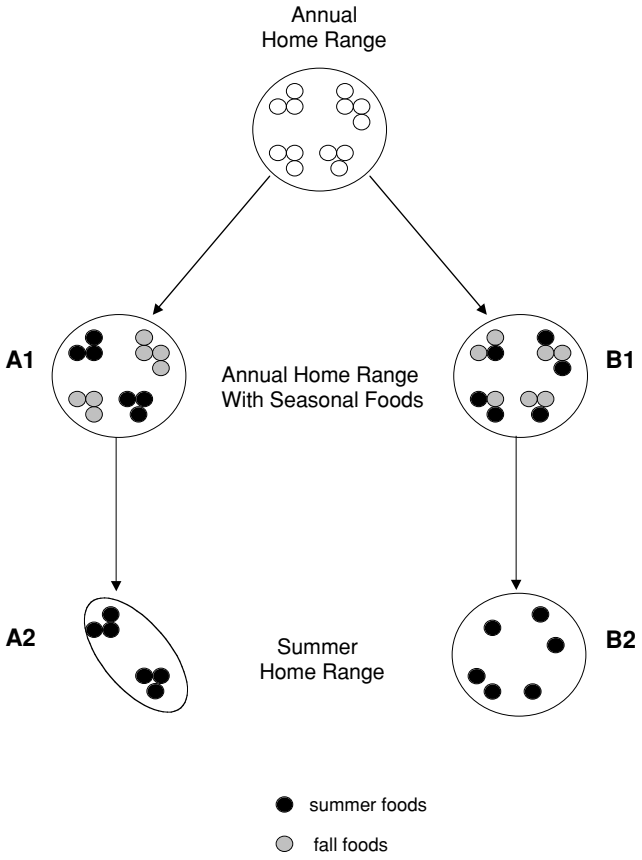

FIGURE 10.4. Hypothetical spatial arrangement of seasonal foods within annual and seasonal home ranges for 1 animal. A1 represents an annual home range where summer foods are clustered with summer foods and fall foods are clustered with fall foods, B1 represents an annual home range where summer foods are spatially intermixed with fall foods. A2 represents the summer home range that would be estimated from A1, B2 represents the summer home range that would be estimated from B1.

foods and fall foods are clustered with fall foods. Alternatively, summer foods are spatially intermixed with fall foods in B1. Although amount of each seasonal food is equal between A1 and B1, seasonal foods in A1 are more clustered than those in B1; therefore, the seasonal home range A2 differs considerably from the annual home range A1, whereas B1 and B2 are essentially the same. Differences between A1 and A2 could be masked if the larger temporal resolution is used; the temporal resolution of 1 year is not appropriate for evaluating effects of resource clustering on resource selection when animals select foods seasonally.

More generally, using the appropriate temporal grain for studies of resource selection increases the accuracy of preference indices. Most studies of resource selection calculate preference indices using a ratio of resource use and resource availability. Availability of resource i, for 3rd order selection (i.e. resource selection within a home range; Johnson, 1980), is typically estimated as the proportion of the home range containing resource i (Manly et al., 1993). The spatial extent of the home range, therefore, affects estimates of resource availability, which in turn affects estimates of preference. Availability of resource i will be smaller in a large home range (Fig. 10.4; A1) compared to that in a small home range (Fig. 10.4; A2), all else equal. This is the critical point because spatial extents of home ranges often depend upon temporal grains. If the temporal grain is inappropriate, the spatial extent may be biased, which will subsequently bias estimates of preference.

10.3. Habitat Quality and Black Bears

We have studied habitat quality and how forest management affects habitat quality for black bears in Pisgah Bear Sanctuary (PBS) in western North Carolina (35°17′ N, 82°47′ W) since, 1981. Habitat quality is the capacity of an area to provide resources necessary for survival and reproduction, relative to the capacity of other areas (Van Horne, 1983). Forest management includes timber harvesting and roads building, which can influence bear fitness by affecting food availability and exposure to people and vehicles, respectively. Because we defined habitat quality in terms of fitness (e.g., survival, reproduction, etc.), our goal was to determine how forest management affected bear survival, reproduction, and population growth rate (λ).

10.3.1. Understanding How Timber Harvesting Affects Habitat Quality

The relationship between timber harvesting and habitat quality for bears is complex. Distilling this complexity requires understanding how timber harvesting affects the availability of resources that are important to bears and also understanding how bears respond, demographically and behaviorally, to changes in resources through time. Resources important to bears include foods, escape cover, and den sites. Early research on PBS bears focused on habitat quality by considering all three life requirements (Zimmerman, 1992; Powell et al., 1997; Mitchell et al.,

2002), but we focus on only foods in this chapter to make our point because foods are probably the most important resources for most bear populations (Rogers, 1987; Powell et al., 1997). In the southern Appalachian Mountains, foods important to black bears include herbaceous vegetation, squaw root (*Conopholis americana*), soft mast (fleshy fruit), hard mast (acorns and nuts), insects, and carrion (Beeman and Pelton, 1977; Eagle and Pelton, 1983). Of these foods, hard and soft mast have been shown to affect reproduction or survival of different bear populations (Jonkel and Cowan, 1971; Rogers, 1976; Eiler et al., 1989; Elowe and Dodge, 1989; Pelton, 1989; Clark and Smith, 1994; Costello et al., 2003). To understand how timber harvesting affected habitat quality for PBS bears, we focused on the relationships between timber harvesting, hard mast, soft mast, and bears.

10.3.2. Temporal Availability of Soft Mast and Hard Mast Within Clear-Cuts

Timber harvesting affects the availability of soft mast differently than hard mast. Clear-cutting (removal of all trees within a stand) was the primary harvesting technique in PBS so we measured percent plant cover and estimated berry production of soft mast genera within 100 clear-cuts (ranging from 0 to 121 years old) across PBS and used these data to develop statistical models for predicting the availability of soft mast in clear-cuts as it changed through time. The availability of soft mast was highest in 2–9-year-old clear-cuts, lowest in ∼10–49-year-old clear-cuts, and moderate in 50+ year old clear-cuts (Fig. 10.5; Reynolds et al., unpublished data).

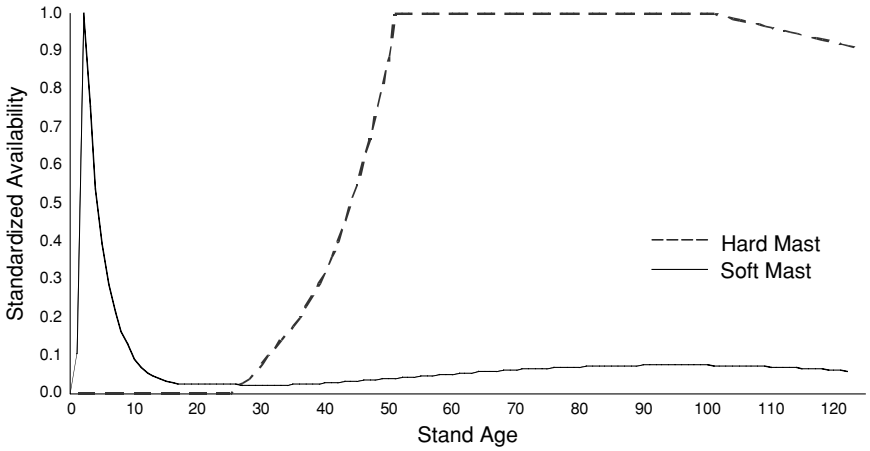

FIGURE 10.5. Temporal availability (standardized) of soft mast (*Gaylussacia* spp., *Vaccinium* spp., and *Rubus* spp. combined) and hard mast in clear-cuts in western North Carolina. The statistical model for soft mast availability was developed from field data collected in 100 clear-cuts throughout PBS in western North Carolina 2001–2002 (Reynolds et al., unpublished data), whereas the statistical model for hard mast was taken from Burns and Honkala (1990).

Alternatively, clear-cuts produce little to no hard mast for 25–50 years, the time required for regenerating hardwoods to reach reproductive age in the Southern Appalachians (Burns and Honkala, 1990).

10.3.3. Demographic Response of Bears

Because clear-cutting affects availability of soft mast and hard mast differently, the overall effect of clear-cutting on habitat quality for a bear population will depend, in part, on whether hard mast, soft mast, or both limit the population. A resource is limiting if changes in its availability affect the population equilibrium level (Williams et al., 2002), which is a function of individual survival and reproduction. Therefore, linking estimates of bear demography with estimates of resource availability as they change over time should provide insights into resource limitation.

We evaluated competing hypotheses about the degree to which hard mast and soft mast limited PBS bears by estimating annual demographic parameters and linking them with annual estimates of mast availability (Reynolds et al., unpublished data). Using capture-recapture data from 101 females captured during 1981–2002 and the temporal symmetry method (Pradel, 1996) in Program MARK (White and Burnham, 1999), we estimated apparent survival, fertility, and λ. We also modeled annual distributions of hard mast and soft mast across the landscape each year from 1981 to 2001, as they changed due to timber harvesting and succession. We separated productivity of soft mast in 2–9 year old clear-cuts from that of the remaining landscape to evaluate their effects on demography of bears separately. The spatial grain of our resource data was 30 meters and the spatial extent was PBS. For each demographic parameter (survival, fertility, and λ), we incorporated annual estimates of hard and soft mast availability (across the landscape and in 2–9-year clear-cuts), as well as their interactions, as covariates using methods described by Franklin et al. (2000). To evaluate competing hypotheses, we ranked models using Akaike's Information Criterion (AIC) with an adjustment for small sample sizes (Akaike, 1973). Based on the life history of bears, we incorporated a time lag in the effect of resource availability on demography. Female bears mate in the summer, but delay implantation until fall. If a female has not acquired sufficient stores of energy by fall, she will abort her pregnancy. Therefore, if availability of a food resource affects fertility during year t, the effect will be measurable during year $t + 1$ when cubs are born. Similarly, any effect of a resource on survival at time t will be measurable at time $t + 1$. Therefore, covariate estimates for year t were calculated using covariate data from year $t - 1$.

We found the additive effect of hard and soft mast across the landscape were most important to both fertility and λ. In addition, the availability of 2–9-year-old clear-cuts was important to fertility. Results for survival were inconclusive because the null model ranked relatively high for survival, indicating the null model could have explained survival as well as availability of soft or hard mast (Reynolds et al., unpublished data).

10.3.3.1. Example 1: Mismatch in Temporal Extent

Did the temporal resolution (grain and extent) of our demographic and resource data match the resolution of the ecological processes (i.e., the effect of resource availability on survival, fertility, and λ)? The temporal grain (t in Fig. 10.2) was 1 year, which was appropriate because we wanted to test whether annual availability of resources affected annual demographic rates. Determining if the temporal extent (T in Fig. 10.2), 22 years, was appropriate was more challenging because we did not know *a priori* the temporal extent of the ecological processes.

We could not extend our data set to test if our temporal extent may have been too short, nor could we compare our results with previous studies on demography of black bears because none exist with temporal extents as long as ours. Instead, we truncated our data set and evaluated how relationships between resources and demography changed as the temporal extent of the data changed. We re-ran the demographic analyses using both the first 5 years of data and the first 10 years of data and then compared results with those from the 22-year data set.

For all three demographic parameters, results from the 5-year and 10-year data sets differed qualitatively from results based on the 22-year data set. We present model results for fertility in Table 10.1, which includes only the top 3 of 15 models we evaluated for each temporal extent. All models ranked third or higher had Δ AIC_c values >4.0, indicating these models had relatively little support (Burnham and Anderson, 2002). For the two truncated data sets, the null model ranked highest

TABLE 10.1. Three models associating covariates representing productivity and availability of hard and soft mast with fertility of a black bear population, Pisgah Bear Sanctuary, North Carolina, 1981–2002*.

Data set	Model	AICc	ΔAICc	AICc weights	Model likelihood	Parameters	Deviance
5-year	Null	157.38	0.00	0.80	1.00	10	12.99
	Soft mast in young clear-cuts	160.60	3.22	0.16	0.20	11	12.20
	Hard mast + soft mast across landscape	163.27	5.89	0.04	0.05	12	10.55
10-year	Null	331.22	0.00	0.86	1.00	20	120.02
	Soft mast in young clear-cuts	335.19	3.97	0.12	0.14	21	119.66
	Hard mast + soft mast across landscape	338.79	7.56	0.02	0.02	22	118.71
22-year	Hard mast + soft mast across landscape	1012.21	0.00	0.77	1.00	46	342.05
	Soft mast in young clear-cuts	1015.67	3.46	0.14	0.18	45	349.31
	Null	1016.70	4.49	0.09	0.11	44	344.18

*Each model represents a different use of the 22-year data set; the first used only the first 5 years, the second used the first 10 years, and the third used all 22 years of the data.

and had relatively high model weight. Conversely, the model that included the additive effect of hard mast and soft mast across the landscape ranked relatively low with a Δ AIC_c value >4.0. Results for both truncated data sets suggest bear fertility was not explained well by availability of soft mast or hard mast.

In strong contrast, results from the 22-year data set showed the top ranked model was that which incorporated the additive effect of hard mast and soft mast across the landscape, whereas the null model ranked low (Δ AIC_c value >4.0) and had little model weight. Overall, the 22-year data set indicated the availability of hard mast and soft mast across the landscape affected fertility, whereas the two truncated data sets indicated neither resource was affective.

Although our results do not demonstrate conclusively the temporal extent of 22 years was appropriate to the ecological process we wanted to understand, they do strongly suggest the two shorter extents were inappropriate for estimating accurately our ecological process of interest. The temporal extents of the 2 truncated data sets were likely too short, perhaps capturing short-term dynamics that, though accurate, do not parallel longer-term dynamics (e.g., Fig. 10.3). Alternatively, differences in results could have occurred because precision in response and explanatory variables for the two truncated data sets was insufficient to detect relationships because sample sizes were too small. In the latter case, and assuming annual sample sizes could not be increased, an argument could be made that estimating vital rates would be a problem that could not be resolved, given the temporal extent of 5- or 10-year-long studies. The focal level must shift to some level below population demography, which is analogous to going from Z to Y in Fig. 10.1B. Specifically, a coarser, less data-intensive approach (e.g., patch occupancy) would need to be selected.

It is clear that relationships cannot be detected unless sufficient changes in related components have occurred (Allen and Hoekstra, 1992). In our case, understanding how resource availability affects population demography requires a temporal extent long enough to capture sufficient variability in both resource availability and demographic rates. Variability in hard mast and soft mast was relatively minimal (except availability of soft mast in 2–9-year-old clear-cuts; Reynolds et al., unpublished data) in both the 5- and 10-year data sets; this helps explain why the null model ranked highest for both truncated data sets.

Our exercise in temporal extents has important implications for ecological research. In a field where study durations typically last 2 to 3 years, a temporal extent of 10 years is considered relatively long. Yet, a decade was still too short to completely understand how resources across a landscape affected the demography of bears. As landscape ecologists, we should be very concerned about mismatches in temporal extent. On the bright side, knowing that inferences can differ across temporal extents is useful for resolving conflicting results from multiple studies that evaluated the same ecological process. Inconsistent results among studies may be explained, at least in part, by their differing temporal extents.

10.3.3.2. Example 2: Mismatch in Temporal Grain

Results from our demographic analyses showed hard mast and soft mast across the landscape limited female bears in Pisgah. The additive effect of hard mast

and soft mast across the landscape ranked highest for both fertility (Table 10.1) and λ (Reynolds et al., unpublished data). In addition, availability of 2–9-year-old clear-cuts helped explain bear fertility (Table 10.1). During years when availability of young clear-cuts was high, annual fertility increased. Our results indicated the relationship between clear-cuts and habitat quality was complex and involved tradeoffs. On one hand, clear-cuts had a negative effect because they removed hard mast (a limiting resource) for 25–50 years. On the other hand, clear-cuts had a positive effect because they increased availability of soft mast (a limiting resource), at least for ∼7 years (Fig. 10.5).

Importantly, our demographic analyses assumed bears used hard mast and soft mast when these resources were available. Similarly, we assumed bears used 2–9-year-old clear-cuts, and the resources within them, when they were available. If this assumption was invalid, our demographic results may have been spurious. Because we were interested in understanding the effects of clear-cuts on habitat quality, we needed to understand behavioral response of bears to clear-cuts.

A previous study on resource selection by PBS bears found females avoided young clear-cuts (Mitchell and Powell, 2003). The spatial grain of the resource data was 250 meters, which matched the spatial grain of the telemetry data. The Pisgah Bear Sanctuary defined the spatial extent (for 2nd order selection; Johnson, 1980). The temporal grain was 1 year and the temporal extent was 16 years.

For the study by Mitchell and Powell (2003) on resource selection by PBS bears, did the temporal scale (grain and extent) of the data match that of the ecological process? The study used a temporal extent of 16 years, which should have been long enough to incorporate both short-term and longer-term variability in resource selection. For example, if bears usually prefer hard mast stands in fall (long-term dynamic), but avoid them during years of hard mast failure (short-term dynamic), 16 years should have been sufficient to capture more than short term fluctuations. The temporal grain of the data was 1 year (annual home ranges). Though appropriate for understanding how clear-cuts affected habitat quality on an annual basis, a temporal grain of 1 year may not be the best choice for testing seasonal use of young clear-cuts by bears. During summer and early fall in the Southern Appalachians, bears forage extensively on soft mast (Beeman and Pelton, 1977; Eagle and Pelton, 1983). Assuming that soft mast is the only valuable resource available to bears in clear-cuts, the high availability of soft mast in 2–9-year-old clear-cuts in summer suggests summer home ranges should be used to understand the behavioral response of bears to young clear-cuts. By using the temporal grain of 1 year, the potential high use of clear-cuts during the summer could be obscured by low use during the rest of the year (Fig. 10.4). We re-ran analyses of resource selection by female bears in PBS using summer home ranges. If 2–9-year-old clear-cuts affected habitat quality positively by increasing availability of soft mast, we predicted females would prefer 2–9-year-old clear-cuts during summer.

We also expanded the analyses to evaluate behavioral response of bears to older clear-cuts. Although our demographic results indicated 2–9-year-old clear-cuts affected fertility positively (when the proportion of the landscape comprised <5% young clear-cuts), this analysis was insufficient for gauging the full effect of clear-cuts on habitat quality because it incorporated only the earliest portion of the

successional life of a clear-cut. Availability of resources inside clear-cuts changes through time due to succession (Fig. 10.5). Therefore, the effect of clear-cuts on habitat quality will also change through time. Assuming that a primary effect of clear-cuts on habitat quality for bears is increased availability of soft mast, the positive effect of clear-cuts should be relatively short. After clear-cuts age beyond 9 years, availability of soft mast plummets and remains low for a relatively long time (40+ years; Fig. 10.5). We predicted, therefore, that PBS females would prefer 2–9-year-old clear-cuts and avoid 10–49-year-old clear-cuts during summer.

Using a temporal extent of 22 years and 103 summer home ranges, we found our observations matched our predictions. Females preferred 2–9-year-old clear-cuts, avoided 10–49-year-old clear-cuts, and used >50-year-old clear-cuts randomly during summer (Reynolds and Mitchell, unpublished data). Clearly, using annual home ranges to evaluate the importance of 2–9-year-old clear-cuts represented a confounding of seasonal patterns; relative lack of use during the portion of the year when berries were not produced obscured the seasonal importance of clear-cuts to black bears revealed in the demographic analyses. Whereas clear-cuts provide few if any resources important to bears throughout most of the year and most of their successional lives, the seasonal productivity in soft mast in the years immediately following clear-cutting appears to be important to successful reproduction of the bear population. The difference between our results and those of Mitchell and Powell (2003) suggests the temporal grain of 1 year used in the earlier study was too large to adequately capture the ecological process. To make certain the differences in results between the two studies were not due to differing temporal extents, we re-ran the analyses using the same temporal extent used by Mitchell and Powell (2003; 16 years) and found results were similar regardless of which temporal extent we used. Using annual data to understand an ecological process that occurs seasonally is analogous to evaluating the focal level Y in Fig. 10.1B using data collected at Z.

The importance of using the appropriate temporal grain to answer ecological questions cannot be overstated. Using temporal grains that are inappropriate to processes adds unnecessary noise to already complex systems, and may be manifested by inaccurate results. In our case, insights differed substantively depending upon which temporal grain we used. Studies in landscape ecology commonly justify the spatial resolution of data. Our results indicate similar attention should be given to temporal resolution of data.

10.4. Synthesizing Results Using Hierarchy Theory

We invoked hierarchy theory, which posits that levels of ecological processes are demarcated by differences in temporal rates, to understand the effects of clear-cuts and roads on habitat quality for bears in our study area. Hierarchy theory provides a framework for objectively defining levels of explanation (O'Neill and King, 1998). It is important to note that traditional notions of biological hierarchy (i.e., community, population, individual, organs, tissues, cells, etc.) may not be relevant

to a study and could actually be inappropriate for understanding ecological systems with hierarchical levels defined by rate structures (King, 1997).

10.4.1. Defining Hierarchical Organization for Black Bears

For our study, we defined habitat quality in terms of survival and fertility, each of which are probably hierarchically organized. The temporal resolution at which each vital rate is manifested for bears, however, is likely to differ.

10.4.1.1. Survival Hierarchy

To understand how clear-cuts and roads affect habitat quality for bears in our study area by understanding the effect on bear survival, one can visualize a realistic hierarchy for bear survival as follows:

Phylogeny	$L + 1$
Annual survival rate	L
Daily survival	$L - 1$
Daily energy intake	$L - 2$
Daily avoidance of mortality factors	$L - 2$
Foraging efficiency	$L - 3$

If we take annual survival to be the focal level (L), then it is constrained by phylogeny ($L + 1$), which occurs slowly over evolutionary time. Bear survival is a day by day, minute by minute process, however, so annual survival is explained by daily survival, which is intimately linked with daily energy intake and daily avoidance of mortality factors (e.g., predators, hunters, and automobile collisions). Hence, daily energy intake and daily avoidance of mortality factors might be visualized to occur at the $L - 2$ level, and, foraging efficiency at the $L - 3$ level. If bear survival is hierarchically organized, then effects on L that occur at $L - 2$ and $L - 3$ levels will be relatively difficult to discern because $L - 2$ and $L - 3$ are buffered from the focal level (O'Neill and King, 1998).

10.4.1.2. Fertility Hierarchy

Alternatively, annual fertility for bears in our study area may be hierarchically organized as follows:

Phylogeny	$L + 1$
Annual fertility rate	L
Energy intake	$L - 1$
Foraging efficiency	$L - 2$

Annual fertility rate is constrained by phylogeny ($L + 1$). Unlike bear survival, bear fertility is not a day-by-day occurrence. If females do not acquire sufficient stores of energy during the year, they will abort their fetuses. Therefore, daily

energy intake affects annual fertility, but only as a cumulative effect. Therefore, unlike the day-by-day processes that best explain annual survival for bears, annual fertility is most strongly linked with average energy intake over a year. Average energy intake is explained by foraging efficiency.

10.4.1.3. Combining Demographic and Behavioral Results

Results from our demographic analyses on PBS bears showed availability of 2–9-year-old clear-cuts affected annual fertility positively but had relatively little effect on annual survival. In other work (Reynolds and Mitchell, unpublished data), we have also evaluated the effect of roads on annual survival of PBS bears because roads may increase risk of mortality due to hunting, poaching, and automobile collisions (Pelton, 1986; Brody and Pelton, 1989). We found road use affected annual survival of PBS females negatively ($n = 66$; Reynolds and Mitchell, unpublished data). During years when females avoided areas near gravel roads, annual survival increased.

Results from resource selection analyses showed adult females preferred 2–9-year-old clear-cuts during summer. Because availability of soft mast may be a function of both its amount and arrangement on the landscape, the spatial pattern of 2–9-year-old clear-cuts (in which soft mast was highly available) may affect bear fitness. We tested this hypothesis by comparing resource selection between reproductively successful and reproductively unsuccessful female bears. Because foraging effort is minimized and energy accumulation maximized when foods are relatively clustered (Stephens and Krebs, 1986), we predicted soft mast would be relatively more clustered within home ranges of reproductively successful females if landscape pattern affected reproduction. Our results matched our predictions, but our sample size was small ($n = 10$; Reynolds and Mitchell, unpublished data) so conclusions should be viewed with caution.

We also partitioned the female population into survival groups (i.e., bears that survived and bears that did not survive) and compared resource selection for areas near paved, gravel, and gated roads, as well as resource selection for 2–9-year-old clear-cuts, between the two survival groups. We found females that were known to have survived ($n = 26$) avoided areas near gravel roads in fall more than females that were known to have died ($n = 15$), suggesting gravel roads exerted a selective pressure on survival. Conversely, preference for 2–9-year-old clear-cuts did not differ between the two survival groups, which corroborated our demographic results.

10.4.1.4. Survival, Time, and Space

We found gravel roads affected annual survival, but not annual fertility. Gravel roads affected annual survival negatively (demographic results) at the $L - 2$ level by affecting daily avoidance of mortality factors (i.e., hunters, poachers, and automobile collisions). In addition, females that were known to have died used areas

near gravel roads more than did females that were known to have survived (behavioral results). We envision the hierarchy for bear survival as follows:

Phylogeny	L + 1
Annual survival rate	L
Daily survival	L − 1
Daily energy intake	L − 2
Daily avoidance of mortality factors	L − 2 (gravel roads)
Foraging efficiency	L − 3

10.4.1.5. Fertility, Time, and Space

We found 2–9-year-old clear-cuts affected annual fertility, but not annual survival. Availability of 2–9-year-old clear-cuts affected annual fertility positively (demographic results) at the L − 1 level by affecting energy intake. In addition, adult females preferred 2–9-year-old clear-cuts during summer (behavioral results). Moreover, the spatial arrangement of clear-cuts may have been effective, so 2–9-year-old clear-cuts may also have affected annual fertility by influencing foraging efficiency at the L − 2 level. We envision the hierarchy for bear fertility as follows:

Phylogeny	L + 1
Annual fertility rate	L
Energy intake	L − 1 (availability of 2–9-year-old clear-cuts)
Foraging efficiency	L − 2 (spatial arrangement of 2–9-year-old clear-cuts)

10.4.1.6. Using Hierarchical Organization to Interpret Effects of Forest Management

Overall, 2–9-year-old clear-cuts affected annual fertility positively at L − 1 and L − 2 levels while gravel roads affected annual survival negatively at the L − 2 level. According to hierarchy theory, higher levels have a relatively large effect on the focal level. Therefore, positive effects of clear-cuts on annual fertility at L − 1 level appear to be larger than the negative effects of gravel roads on annual survival at L − 2 level.

Individual vital rates (i.e., survival and reproduction), however, may not contribute equally to λ so the overall effect of clear-cuts and roads on habitat quality for bear populations may also depend on which vital rate contributes most to changes in λ. Adult survival is the vital rate with the largest potential to contribute to future changes in λ for bear populations (Freedman et al., 2003; Hebblewhite et al., 2003; Brongo, 2004). Therefore, the negative effects of gravel roads on bear survival may outweigh the positive effects of 2–9-year-old clear-cuts on bear fertility.

The hierarchies we envision for bear survival and reproduction may not be appropriate for evaluating other ecological processes. In our case, hierarchy theory

provided a framework for synthesizing demographic results with behavioral results to better understand overall effects of timber harvesting on habitat quality for bears.

10.5. Conclusion

We have presented a concept of designing ecological studies that integrates 3 axes of ecological studies: temporal resolution of the study, spatial resolution of the study, and the resolution of the ecological process under study. We have argued that research that ignores the proper alignment of these axes can result in misleading results. Focusing on the integration of the temporal axis in landscape ecology studies, we provided empirical examples of how incorrect selection of temporal extent and grain biased findings in our own work with black bears. Finally, we proposed the temporal scales at which different vital rates are manifested in a bear population may differ, which may affect the way perturbations (e.g., clear-cuts, roads, etc.) affect habitat quality for bears.

The insights we present in this chapter are best fully considered when designing research, prior to the collection of data. It may be too late to realize that the three axes are insufficiently aligned to develop robust insights, once the data are collected. In developing our examples for this chapter, we had key advantages that few researchers enjoy—a large, long-term data set, the benefit of 20/20 hindsight and its inevitable companion, the realization that things could have been done differently. The challenges posed to a researcher at the beginning of the process, where three axes must be selected *a priori*, are more daunting. Generally, precedents in the literature may suggest candidate focal levels, but unless these precedents represent good (or fortunate) integration of the three axes, the possibility always remains that focal levels they suggest could be wrong. In the end, nothing can replace sound biological reasoning and some hard thinking about what is achievable within the temporal and spatial constraints imposed on any study by funding, time limits, and logistics. The latter are generally the least flexible part of any study and biologists need to be prepared to adjust their targeted levels of the ecological processes accordingly. Doing so might mean settling for less exciting but more accurate insights, or perhaps chasing the funding and study locations needed to address the more interesting questions with accuracy. In any case, mismatched axes of ecological studies should never be acceptable; we argue that researchers reporting their work should be every bit as explicit in presenting their choices along the three axes as they are with other aspects of their study design.

We do not suggest the process we recommend is easy or simple—just necessary. Researchers in landscape ecology do it every day, whether they know it or not. Every study design is implicit with respect to the 3 axes we define although interpretation of research results rarely is. We suggest that hierarchy theory provides one conceptual foundation for explicitly integrating spatiotemporal scales of data with resolutions of ecological processes. Further, we argue that doing so as

part of research design and development would go a long way toward minimizing the ambiguous, contradictory, or ecologically questionable research in landscape ecology.

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