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SPATIAL SCALING AND ANIMAL POPULATION DYNAMICS

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Studies of changes in animal population size over time (population dynamics) are conducted primarily for three reasons: (1) to make predictions of population persistence (Lande 1988), (2) to investigate the mechanisms causing population fluctuations (Royama 1992), and (3) to calculate sustained yield harvests (Bailey 1984). The spatial scale of the investigation has important consequences in all cases. This chapter reviews our current understanding of how the spatial scale of a study of population dynamics affects the conclusions one is able to draw from it.

Spatial Structure of Populations

To understand how the spatial scale of an investigation affects the conclusions it engenders about population dynamics, it is first necessary to understand how populations themselves are scaled. First, we must distinguish between the spatial scale of an experiment or census, as opposed to the scaling of a population. The spatial scale of an experiment or census is chosen by the investigator and may or may not be appropriate for investigating the population dynamics of a species. The scaling of a population is the spatial structure of the population itself. Populations can be organized into different hierarchical levels (figure 9.1), each with its own typical scale. The lower and upper limits of a species' spatial scales are the scale of the individual and of the global population. The spatial scale of the individual is the range over which it moves during usual (nondispersal) activities; this has been referred

to as the ecological neighborhood by Addicott et al. (1987). The spatial scale of the global population is the scale over which all movements of all individuals in the species occur, that is, the range of the species. Between these two limits there may be two additional population scales: the local population and the regional population.

A local population is a collection of individuals with a high probability of encountering each other during usual activities (Andrewartha and Birch 1984; Wiens et al. 1986; Addicott et al. 1987). The encounter probability must be high relative to the probability of dispersal, where dispersal refers to movements of individuals between local populations. Therefore, most individuals remain within the local population and only a small fraction (e.g., less than 5 percent) move between local populations. Examples of this type of population structure have been reported for a wide range of insects (Addicott 1978; den Boer 1981; Cappuccino and Kareiva 1985; Cappuccino 1987; Harrison et al. 1988;

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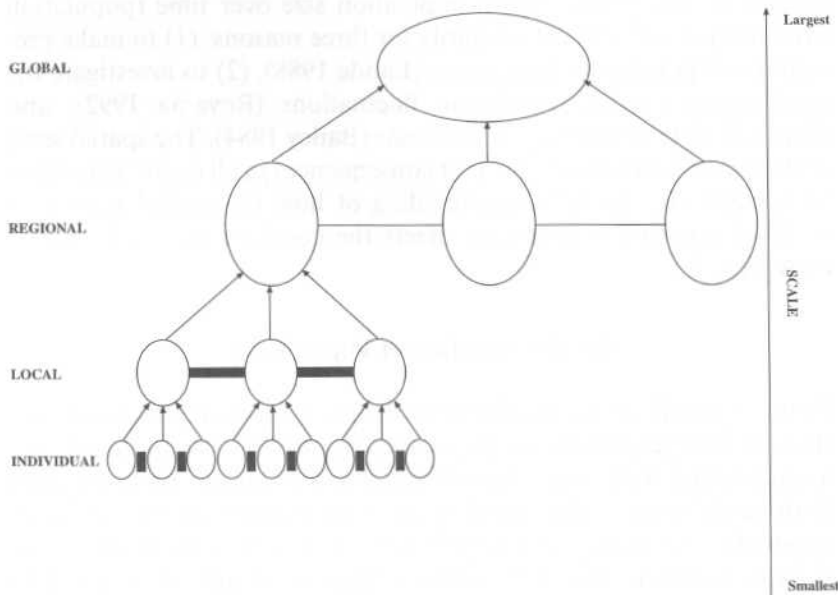to separate, and [...]

FIGURE 9.1
Schematic representation of the organization of a species. Levels higher in the hierarchy are at larger spatial scales. The thickness of the interconnecting lines indicates the degree of interaction within levels; thicker lines indicate a greater probability of interaction.

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Solbreck and Sillén-Tullberg 1990), amphibians (Gill 1978; Laan and Verboom 1990; Sjögren 1991), birds (Saunders and Ingram 1987; Villard et al. 1992), and mammals (Henderson et al. 1985; Arnold et al. 1993). The spatial scale of the local population is defined by the scale over which all its individuals move during their usual (nondispersal) activities.

Of increasing interest to ecologists is the regional population scale, which consists of all the local populations within a particular region (Gurney and Nisbet 1978; Taylor 1988a). The scale of the regional population is arbitrarily determined by the total area (or region) of interest to the researcher. If the region includes the whole range of the species, then the regional and global populations are the same.

The spatial structure of a regional population is determined by the combined effects of the spatial pattern of the population and the rate of successful dispersal between local populations, which in turn depends on the interaction between the dispersal characteristics of the organism and the landscape structure (Merriam 1984; Burel 1989; Taylor et al. 1993; Fahrig and Merriam 1994). Population spatial structure is determined functionally by the set of probabilities of movement between all pairs of local populations. For example, a population of birds inhabiting 10 small forest patches could have a spatial structure similar to that of a population of dung beetles inhabiting 10 dung pats in a field, if their abilities to disperse relative to interpatch distances were equal. Also, a population of frogs inhabiting 10 ponds at 1-km spacing within a large forested area could have a spatial structure similar to that of a population of the same species inhabiting 10 ponds at 100-m spacing but separated from each other by roads or other barriers to movement, causing the probability of successful dispersal over 100 m to be the same as that over an unimpeded kilometer.

The spatial structure of a population is not static; it changes over time. It is necessary, therefore, to consider population dynamics within an appropriate temporal frame. The appropriate temporal scale is the generation time of the organism (McArdle et al. 1990). It has been suggested that populations should be censused once per generation (Connell and Sousa 1983); however, with overlapping generations, this concern can be relaxed (Gaston and McArdle 1993). Before making any inferences about population dynamics, it is necessary to study a population over an appropriately long time frame by gathering data on several generations of a species. Spatial and temporal scaling are difficult to separate, and the investigator needs to keep both in mind when de-

signing a study. This chapter focuses on spatial scale; in our discussion, we assume that the population is sampled at an appropriate frequency and for an appropriate duration.

Scales of Population Studies

Two components of measurement scale can be identified: extent and grain (Wiens 1989, Gardner, chapter 2; Vande Castle, chapter 13). Extent refers to the range over which measurements are taken or how much area is covered in the sampling scheme. Grain often refers to the amount of area sampled per quadrat or the size of quadrats used (Wiens 1989). This definition of grain is most applicable to sessile organisms. Mobile organisms are usually censused using traps or visual counts. These methods produce estimates of abundance, but it is difficult to determine how much area they sample effectively. In the case of mobile animals, it may be more appropriate to think of grain as the number of samples per unit of length or area. Increasing the grain of a sampling scheme increases the resolution of the observations made. More sampling points must be added to maintain a constant grain and to increase extent. If the number of sampling points is restricted, the only way to increase extent is to decrease grain. In general, when population ecologists refer to the spatial scale of a study, they are in fact referring only to its extent (Kareiva and Andersen 1986; Taylor 1988; Rose and Legget 1990).

Studies of population dynamics are conducted at a variety of scales relative to the actual spatial structure of the population. An important problem in the interpretation of population dynamic studies is that the scale of observation often does not coincide with one of the population scales. For example, the samples might cover only part of a local population (Bach 1980), or only part of a regional population (Gill 1978).

Population ecologists use a variety of criteria when deciding on the sampling scale for a study. The most common is probably expediency and cost. Kareiva and Andersen (1986) reviewed 6 years of experimental community ecology studies published in *Ecology* and found that half of the studies used plots no larger than a meter in diameter. Although Kareiva and Andersen were not examining studies of population dynamics *per se,* their review demonstrates that many ecologists do investigate populations at scales smaller than the scale of a single local population. This inequity between the scales of most ecological investigations and population structure is mostly caused by high costs

of and logistical constraints on larger-scale studies (Kareiva and Andersen 1986; May 1994). The scale of such studies may be too small to quantify properly, let alone understand the mechanisms driving population dynamics.

A second common criterion used is the human-centered view of habitat structure. Researchers often define the boundaries of populations based on landscape elements obvious to human observers, such as woodlots, clearcuts, agricultural fields, or urban areas (Opdam et al. 1984; Fahrig and Merriam 1985; Saunders et al. 1987; Fahrig and Paloheimo 1988; Szacki and Liro 1991; Villard et al. 1992). There is no guarantee that the population structure of the organism of interest coincides with these landscape elements. In such instances, a study of the local population dynamics of a particular species may in fact be a study of only a small part of a local population. For example, populations of *Peromyscus leucopus* (white-footed mouse) were thought to occur primarily in wooded areas (Graves et al. 1988), so studies of *P. leucopus* dynamics were rarely performed outside of forested areas (Wegner and Merriam 1990). It has recently been found that *P. leucopus* utilizes some crop types in agricultural areas (Wegner and Merriam 1990), and, therefore, the population structure does not match the spatial structure of forest. A large woodlot could contain a number of local populations, or a collection of small woodlots and fields could contain only one local population. For a small organism with limited dispersal, a study of a local population in a landscape element could actually represent a study of a regional population composed of several local populations. Such a species may divide a patch more finely than the observer would: a patch that appears homogeneous might actually be heterogeneous for the species and contain a number of local populations.

The third possible criterion for selecting the scale of a study is to match the scale of the study to the actual spatial structure of the population. As we will argue, this is the most useful criterion. Unfortunately, it is difficult to do because it requires two pieces of information that are seldom available: (1) information on the actual spatial distribution of the population, and (2) information on the rates of dispersal of the organism. The latter depends not only on the intrinsic dispersal characteristics of the species, but also on the structure of the particular landscape in question (Fahrig and Merriam 1994). Once this information is available, one can adjust the scale of observation to match a single local population or an entire regional population.

Sampling Scale and Population Predictability

The growing emphasis on scale issues in ecology can, in most cases, be reduced to a concern over the appropriate scale to investigate a particular ecological problem (Morris 1987; Hastings 1988; Smith and Urban 1988; Wiens 1989; Rose and Legget 1990; Taggart and Frank 1990). In the case of population dynamics, the "correct" scale is the scale that permits prediction of population persistence based on a statistical or mechanistic model of the population. But how can one select the scale of the study to maximize predictability?

Success of model predictions depends on the importance of factors internal to the system relative to the influence of external factors (Allen and Starr 1982; Wiens 1989; Levin 1992). In general, predictability is highest at the scale of the global population and lowest at the scale of the individual (Levin 1986). The decline in predictability from global to individual is not monotonic (figure 9.2). Relative increases in pre-
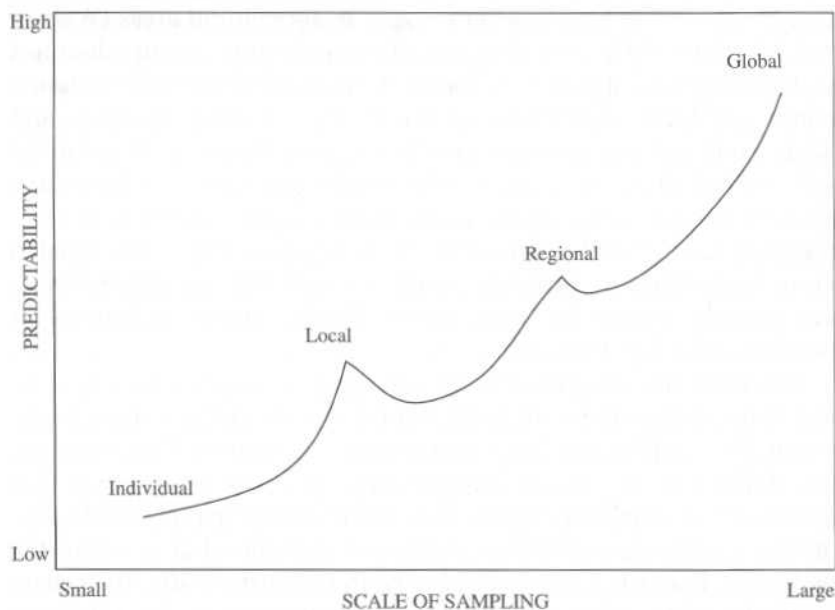
FIGURE 9.2

Hypothesized relationship between predictability of population persistence and scale of sampling. Increase in predictability with scale is not monotonic, and local maxima coincide with intrinsic scales of organization (see figure 9.1).

dictability will occur when the scale of sampling matches the scale of an entire regional population or an entire local population.

At any scale in the population hierarchy, population persistence depends on two factors: (1) the probability of extinction of the population given that it is extant, and (2) the probability of reestablishment of the population given that it is extinct. The first of these (extinction) depends primarily on factors internal to the population, and the second (colonization) depends primarily on external factors. Therefore, as the frequency of extinction and reestablishment increases, the importance of external factors relative to internal factors increases, leading to decreasing predictability.

At the scale of the individual territory, extinction probability is the product of mortality probability and the probability of movement out of the territory. However, once the individual dies or moves, the probability of reestablishment of the area by another individual depends on the density of the local population and the movement rate of individuals within it. Because extinction rate is very high, the probability of persistence of a population within an individual territory depends almost entirely on factors external to the territory.

Similarly, if only a portion of a local population is sampled, predictability will be low unless that area of the population happens to be representative of the whole local population. The greater the extent of the local population, and the greater the asynchrony over space in factors affecting the local population, the less likely a subset of the population is to represent the whole. For example, small portions of a local population could become extinct as a result of localized feeding of a predator. Recolonization of these extinctions depends on the density of the remaining population and the movement rates within it.

At the scale of the entire local population, there is a sharp increase in predictability. By definition, movement rates between local populations are much lower than movement rates within local populations. Extinction probability depends primarily on factors operating at the scale of the local population, with the possible exception of a rescue effect through immigration (Brown and Kodric-Brown 1977). Recolonization depends on the larger regional scale, so short-term persistence is relatively predictable, whereas long-term presence or absence is not. To gain the highest possible predictability for a local population, one should conduct sampling over the entire area of the local population.

Regional population persistence depends on the overall regional population density, which is affected by the processes of growth, extinction, and recolonization of local populations within the region.
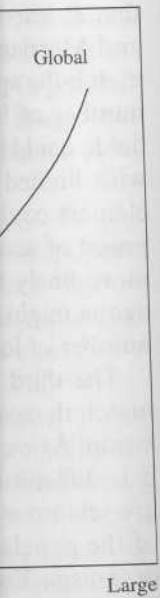
Once the population in an entire region is extinct, recolonization depends on immigration from outside the region. However, it is not clear whether one can sample a subset of local populations to make predictions of regional population persistence.

A possible method for sampling local populations to predict regional persistence has been proposed by Hanski (1994a). He developed a method for estimating regional persistence based on incidence functions, which could be applied to a subset of patches. Using patterns of presence and absence and patch arrangement, simple models can be parameterized and used to predict the regional persistence of a species. Hanski (1993) has applied these models to *Sorex* species (shrews) on islands and found these predictions to compare favorably to empirical studies. However, his model assumes a large number of local populations (more than 50) and a balance between occupied and extinct patches (between 20 and 80 percent in one state). Thomas (1994) has also raised the concern that for this model, populations must be at a steady-state equilibrium, which probably does not hold for many natural systems. Therefore, the incidence-function approach is probably applicable only to a very limited number of systems.

In subsampling a regional population, we again have the same difficulty in making predictions about the whole population. The various local populations within the regional population may be controlled by different factors. For example, within one portion of the region, the local dynamics may be primarily density dependent, and in another portion they may be primarily density independent. To obtain the highest predictability of a regional population, one should, therefore, conduct stratified sampling: the sampled strata are the local populations. This ensures that all local populations are sampled. Similarly, predictions about a global population will be most accurate when they are based on observations stratified according to the population structure.

Finding the "Correct" Scale

Predicting Persistence

Based on the above description, it follows that the correct sampling scale for population dynamics should coincide with the intrinsic scales determined by the population structure, such that sampling is conducted over either an entire local population or an entire regional population. However, this approach requires knowledge of the population

structure, which is often lacking. One way to find the scales of local populations is to determine what is usable breeding habitat through autecological studies or natural-history observations, and then search out that type of habitat in the study area. This could be facilitated through the use of aerial photographs or satellite images. Capture–recapture studies could then be used to determine the rate and extent of demographic flows between habitat areas, and to determine whether the different habitat areas represent different local populations (Stern, chapter 14). Note again that the population structure depends on the landscape structure, because movement through the landscape depends on both the structure of the landscape and the movement attributes of the species (Fahrig and Merriam 1994).

If it is not clear what demarcates a local population or where a local population might occur for a species of interest, then population structure could be determined by censusing in a grid pattern and looking for aggregations of individuals that could represent local populations. The size of grid chosen and the grain of sampling should ideally be based on information about the movement scale of the organism, and it may be beneficial to determine this empirically (e.g., mark-release, radio tracking) before conducting the census. Inability to detect aggregations could be the result of either the entire sampling area being within a single local population or the grain of the sampling design being too large to detect local populations within the area (figure 9.3). These have opposite implications for changes to the sampling scheme (increased extent versus decreased grain), and in the absence of additional information on movement scale, there is no way to decide which alternative to try.

If a sampling scheme is found to yield low predictability once the scale of the local or regional population is taken into account, then forces external to the populations sampled are more important than internal forces. This indicates that to increase predictability (approach the correct scale), it is necessary to increase the scale of investigation to incorporate external forces. This is opposite to the usual scientific tradition for dealing with uncertainty, which is to further reduce the system of interest and look at a finer scale (Allen and Starr 1982). However, in studies of population persistence, this approach may indicate that the population is structured at a larger scale and needs to be studied at this larger scale.

In many cases, the appropriate scale of study will be too large to census realistically. Sometimes, this problem can be overcome through a marriage of theory and empirical study (Kareiva and Andersen

1986). Autecological studies performed at smaller spatial scales can provide parameters (e.g., reproductive rates, dispersal ability) for either simulation or theoretical models. Results from detailed studies of both movement (Kolasa and Waltho, chapter 4; Stern, chapter 14) and habitat use can be incorporated into an individual-based, spatially explicit model of population dynamics. This model can be made to reflect a larger area than what was incorporated in the garnering of parameter values, by using aerial photographs or satellite images and geographic information systems (GIS) software. The model is run by incorporating this larger area and used to produce hypotheses (Fahrig 1991) that can be tested by using a few strategic experiments or observations (Fahrig and Freemark 1995).

For example, parameters for a species could be measured either directly or gathered from the literature. Fahrig and Merriam (1985) used

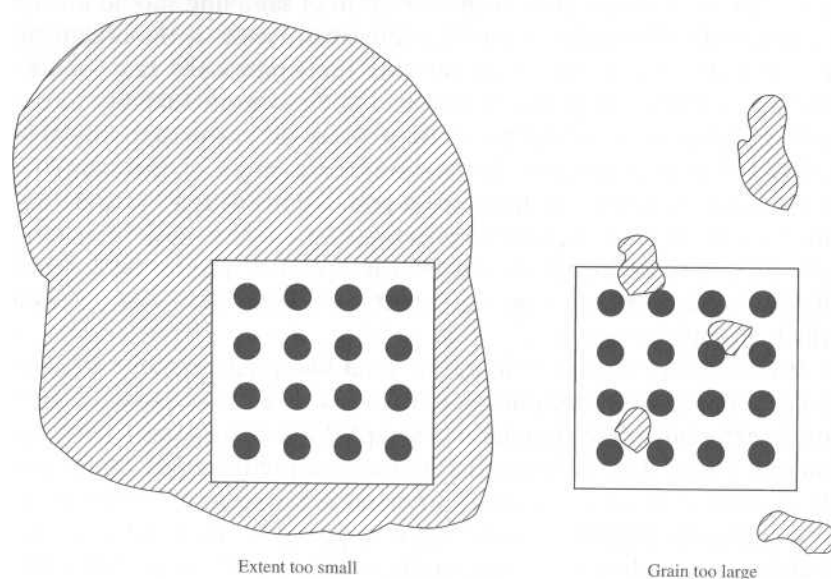Extent too small   Grain too large

FIGURE 9.3

Two possible explanations for the inability of a sampling scheme to detect local populations (*shaded areas*). The sampling scheme is indicated by the square enclosing the area sampled and the dots indicating sampling points. **(A)** Extent of the sampling scheme is too small to detect the local population, because all samples are within the local population. **(B)** Grain of sample is too large because local populations fall between the samples.

literature values to develop a model of *P. leucopus* survival in woodlots. They tested the short-term predictions of the model regarding interconnection of woodlots and survival. Lefkovitch and Fahrig (1985) then used the same model to make longer-term predictions about the survival of mice in different configurations of woodlots. If it was then necessary to attempt to understand mouse population dynamics at a larger scale, it would be possible to set up the simulation to emulate a specific landscape and then use the model to make specific predictions about population dynamics (e.g., population levels in certain woodlots). These predictions could then be tested by sampling a subset of the area. If the predictions and observations match, then the model describes the dynamics well and can be used both to reduce the fieldwork required to estimate population sizes and to make predictions about the population. A similar approach can be taken using theoretical models. For example, Kareiva and Andersen (1986) created a theoretical model explaining *Coccinella septempunctata* (ladybug) aggregations in *Solidago canadensis* (goldenrod) habitats based on fine-scale studies of movement rates, turning rates, and prey densities. The theoretical model was then successfully scaled up to explain *C. septempunctata* aggregations in larger patches of *S. canadensis.* When the model failed to work in pea fields, it illustrated to Kareiva and Andersen that plant architecture played an important role by limiting the ability of *C. septempunctata* to disperse. This failure of their model did not lead Kareiva and Andersen to reject their model but instead to be aware of another parameter (plant architecture) that would need to be considered in larger-scale extrapolations.

Investigating Mechanisms

There is no single correct scale for understanding the mechanisms driving population dynamics (Levin 1992). Mechanisms could be operating at larger or smaller scales than the scale of the local or regional population. To understand these mechanisms and how they function, it may be necessary to sample for the mechanisms at larger or smaller scales. This should not be confused with resampling the population itself at another scale. For example, population levels of a common prey species may be largely determined by predation, which makes it necessary to understand the distribution and dynamics of the predator. If the predator's population is structured at a larger spatial scale than that of the prey, then sampling for the predator (but not necessarily for the prey) must be performed at that larger scale.

One should investigate a mechanism at both the appropriate spatial scale and the appropriate temporal scale. Wiens (1989) raised the concern that factors acting at larger spatial scales may take longer to become apparent. If one is looking for a relationship between a mechanism and a population, it is clearly necessary to investigate that mechanism at the appropriate temporal scale.

There are multiple mechanisms driving population dynamics. Understanding what drives the dynamics of a population requires investigating all possible mechanisms, each at its appropriate scale. If even a few of the possible mechanisms operate at a large spatial scale, then a systematic investigation of all possible mechanisms will be impossible. To determine which mechanisms are most likely to explain population dynamics and are therefore worth investigating empirically, one could: (1) identify possible mechanisms, (2) identify their appropriate scales, (3) construct a multiscale simulation model incorporating the possible mechanisms, (4) use sensitivity analysis to determine which mechanisms are most important, and (5) test the one or two most important mechanisms with appropriately scaled field tests. If the field tests fail to demonstrate that the mechanism has a large influence on population dynamics, then it will be necessary to repeat the process while reevaluating other possible mechanisms and the structure of the model.

Human Impacts

Human use of lands and resources changes landscape structure (Merriam 1988; Groom and Schumaker 1993), which can change population structure and thereby change the degree to which a particular sampling scheme coincides with population structure. Most natural habitats are reduced through human alterations, which in turn reduces local population sizes and increases the probability of local extinction at both local and regional scales. The possibility of extinction increases the relative importance of external factors affecting recolonization, which reduces predictability of population dynamics.

Loss of habitat is also often accompanied by fragmentation of habitat into a larger number of habitat patches. It is often assumed that habitat loss and fragmentation convert a single large (local) population into several smaller local populations (Robinson and Quinn 1992). However, it has also been found that habitat loss over large areas can lead to an increase in the scale of movement of some organisms. For example, it has been reported for small mammals [*Clethrionomys glareolus* (bank vole) and *Apodemus agrarius* (field mouse) (Szacki et al.

1993), and *P. leucopus* (Wegner and Merriam 1990)] that movement distances double in subdivided habitats compared to homogeneous habitat. *Calopteryx maculata* (forest damselfly) individuals in subdivided habitats have larger wings and greater thoracic mass (stronger flight muscles) than individuals in continuous forest, indicating an increased ability to move (Taylor and Merriam 1995). This switch to greater movement ability following habitat fragmentation can also change population structure, converting a regional population of several local populations into a single large, low-density local population. This change in population structure could lead to a decrease in predictability for a given sampling scheme and thus require an increase in observational scale.

In the case of harvested populations, such as ungulates and waterfowl, it is necessary to accurately estimate the population level to determine an appropriate harvest size. If the population estimate is too low, the amount harvested is less than it could be. More important, if the population estimate is too high, the amount harvested can be too great for the population to sustain, leading to the eventual extinction of the population. As we have seen above, to accurately census a population, the spatial scale of the census needs to coincide with a natural scale of the population. If sampling does not coincide with a natural scale of the population, it is possible that only part of a local population is censused, which results in low predictability. If predictability is low, then estimates of population size and subsequent calculations of harvest size will be poor. If a poor estimate of population level leads to an overestimate of the population, and subsequently an overestimate of the allowable harvest, the population could be overharvested. Therefore, it is necessary for managers to be aware of the spatial structure of the harvested population. Fisheries have long been concerned with the spatial structure of the harvested population, as evidenced by attempts to identify fish stocks (Garrod 1977) and movements between stocks (Fahrig 1993). Expansion of this spatial awareness into terrestrial populations would be beneficial.

Summary

Populations can be conceptually arranged into organizational levels including local, regional, and global populations. This spatial structure results from an interaction of dispersal ability and landscape structure. Each level has an associated spatial scale. Most studies of population dynamics are performed at scales determined either by expediency or

anthropocentric views of landscape structure. These sampling scales may be inappropriate for some animal populations and can lead to poor predictive power. Maximal predictability can be accomplished by sampling at a scale that matches an intrinsic organizational scale of the population (local, regional, or global).

Choosing an appropriate sampling scale requires specific knowledge about the spatial pattern of the population and dispersal ability of individuals, but this information is not commonly available. Studies of population persistence should be conducted to determine the appropriate sampling scale by studying habitat use and dispersal ability.

If the population study is concerned with elucidating the mechanisms controlling the population dynamics, then it will probably be necessary to take a multiscale approach. Mechanisms could be occurring at smaller or larger scales than the scale of the population. Understanding the mechanism requires studying it at the appropriate scale (or scales) for the mechanism itself. This requires thinking about, proposing, and testing hypotheses at multiple scales. Testing hypotheses can be aided by the use of theory and modeling coupled with empirical tests.

As humans change landscape structure, we change the scales of both the population structure and the mechanisms driving it. The scale of population structure could be reduced in some cases and increased in others. Sampling schemes should be adjusted to compensate for anthropogenic changes in population structure, but this will be extremely difficult if the rate of landscape change is high.

Acknowledgments

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Theory and Applications

David L. Peterson and V. Thomas Parker, Editors