

## A GENERAL MODEL FOR ANALYZING TAYLOR'S SPATIAL SCALING LAWS

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**Abstract.** Taylor's spatial scaling law concerns the relation between the variance and the mean population counts within areas of a given size. For a range of area sizes, the log of the variance often is an approximately linear function of the mean with a slope between 1 and 2, depending on the range of areas considered. In this paper, we investigate this relationship theoretically for random quadrat samples within a large area. The model makes a distinction between the local point process determining the position of each individual and the population density described by a spatial covariance function. The local point process and the spatial covariance of population density both contribute to the general relationship between the mean and the variance in which the slope may begin at 1, increase to 2, and decrease to 1 again. It is demonstrated by an example that the slope theoretically may exceed 2 by a small amount for very regular patterns that generate spatial covariance functions that increase in certain intervals. We also show how properties of population dynamics in space and time determine this relationship.

**Key words:** *covariance function; migration; point process; population counts; population density; population dynamics; Taylor's spatial scaling law.*

### INTRODUCTION

One of the few general patterns in ecology is based on the observation by Taylor (1961) that the variance in abundance is proportional to a power of the mean abundance. Considering populations sampled at many different localities, on a logarithmic scale, this will give a linear relationship between variance and mean. An examination of these relationships for a wide range of taxa suggests that the slope on the log scale typically lies between 1 and 2 (Taylor et al. 1978, Hanski 1980, 1982, Taylor 1986, Krasnov et al. 2006), although a wide range of variation is found (Taylor 1986, Taylor et al. 1980). This indicates more aggregation for samples conducted among larger than among smaller areas. If individuals are randomly distributed, according to a Poisson model, the variance will be equal to the mean giving a slope on the log scale equal to 1. If the individuals show patchiness on some scale in their spatial distribution relative to the Poisson model, then the Poisson model may still apply for quite small areas, but the variance will be larger than the mean for larger areas giving a slope larger than 1. Hence, the general pattern of slopes larger than 1 strongly indicates that individuals do not distribute themselves completely

independently in space. Identifying the processes contributing to such nonrandom distributions is important for understanding spatiotemporal variation in abundances that affects many general characteristics of populations (Engen et al. 2002a).

One of the first attempts to explain these power laws was provided by Taylor and Taylor's (1977) suggestion that aggregation occurred because individuals tend to move in a density-dependent way to areas in which their fitness is maximized. Hence, individuals congregate in localities with abundant resources for reproduction and survival. By such an adaptive movement pattern, both the probability of migration and settlement are likely to be density dependent (Taylor and Taylor 1977). Simulations suggest that such a density-dependent movement pattern can result in relationships between the variance and mean population size that on a logarithmic scale have slopes larger than 1 (Taylor 1981).

However, other hypotheses also can explain Taylor's spatial power laws. Theoretical analyses have shown that if there is consistent spatial heterogeneity in the mean abundance (or in the carrying capacity  $K$ ), a linear positive relationship between the variance and mean appears on a logarithmic scale (Anderson et al. 1982, Perry 1988, 1994, Keeling 2000, Ballantyne 2005). For instance, assuming no density dependence, and a simple birth-and-death process at a given locality in a constant environment, the log-log plot of variance against mean

Manuscript received 20 September 2007; revised 19 December 2007; accepted 2 January 2008. Corresponding Editor: B. E. Kendall.

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is approximately linear with a slope between 1 and 2 (Anderson et al. 1982).

Another factor contributing to Taylor's spatial scaling laws is spatial fluctuation in environmental conditions that can induce spatial autocorrelations in population fluctuations (Hanski 1987). For instance, theoretical analyses have shown that spatial correlation in environmental stochasticity strongly affects the spatial synchrony in population fluctuations (Moran 1953, Ranta et al. 1997, 1999, 2006, Lande et al. 1999, Engen et al. 2002*a, b*, 2005, Engen and Sæther 2005). Simulation studies reveal that under the influence of such variation in either carrying capacities (Perry 1988, Anderson et al. 1992), or in population growth rates (Perry 1988, Keeling 2000), the relationship between the logarithm of the variance and the logarithm of the mean abundance is again approximately linear.

Thus, several mechanisms affect the slope of the spatial relationship between the variance and mean of population size. This has probably prevented an understanding of the ecological basis for the substantial differences in the slopes of these relationships (Taylor 1961, 1986, Hanski 1982, Taylor and Woivood 1982). One reason for this is that most of the analyses are based on a log-log plot of variance against mean abundance (Taylor 1961, 1986). In contrast, many of the statistical properties of spatial scaling laws in population ecology depend on distance or area (e.g., Lande et al. 1999, Engen et al. 2002*a*). This occurs because it is the spatial scaling of the autocorrelation function of environmental stochasticity (Lande et al. 1999, Engen and Sæther 2005) that determines the spatial scaling in the population dynamics. Thus, empirical analyses of Taylor's spatial scaling laws will be influenced by the unit of sampling (Sawyer 1989, McArdle et al. 1990, Yamamura 1990). Here we will extend the theory to examine how the sampling design relates to the spatial scaling of the autocorrelation functions.

However, theoretical studies of spatial synchrony of population fluctuations usually deal with population density rather than individual counts (Lande et al. 2003, Liebhold et al. 2004, Ranta et al. 2006). To give a precise description of the distribution of counts in sampling units such as squares, we also need to include the point processes determining locations of individuals and the dependence between neighbors through competition for space or resources or tendency for aggregation. Spatial point processes describing dependence between individuals were defined almost half a century ago by Bartlett (1960, 1975). The temporal changes in local population densities which are affected by birth, death, and migration of individuals, typically need to be described on the time scale of years. On the other hand, for animal populations the point process defining individual locations depending on the local density typically acts on a much shorter behavioral time scale such as days or weeks. For plants, the point process is related to local competition for space or clustering in the dispersal of seeds.

Here we unify the description of these two rather different types of spatial population processes, the spatial autocorrelation of population sizes and the local point process for individuals. We show how they both contribute to the spatial autocovariance function, leading to a full analysis of the relation between the mean and variance in quadrat counts. This reconciles the traditional quadrat sampling approach used in many areas of ecology (Bartlett 1936, Iwao 1978, Taylor et al. 1978) with the more recent approach of describing spatial structure by spatial autocorrelation functions (Lindström et al. 1996, Sutcliffe et al. 1996, Lande et al. 1999, 2003, Engen 2001, Engen et al. 2002*a, b*, Engen and Sæther 2005) focusing on the slope in the spatial regression of the variance on mean population size.

#### PARTITIONING OF THE SPATIAL COVARIANCE FUNCTION INTO POINT PROCESS AND DENSITY CONTRIBUTION

##### *General formulation*

To study the relation between mean and variance in counts all the way from very small to large areas, it is necessary to combine the discrete point process operating on a small spatial scale with the covariance function for continuous population densities as function of geographic distance. The distinction between population density and point locations of individuals is essential for obtaining a proper description of individual counts within areas of different sizes. However, Bartlett (1960) pointed out that it is impossible to make a purely statistical distinction between the two processes from samples taken in a single year. For example, the negative binomial distribution can be generated as the Poisson mixture where the underlying density is gamma distributed among sites and the points are independently scattered with mean proportional to the density. On the other hand, the same distribution applies if parent plants are Poisson distributed in space and their number of offspring scattered in their neighborhood has a modified form of Fisher's logarithmic series distribution (Fisher et al. 1943). In the first case, the density is varying in space, and the points are independent given the density. In the other case, the density is constant, but the points are scattered in a dependent way. Nevertheless, the distinction between point process and density variation is important for studying the relation between spatio-temporal population processes using the population density function as the relevant variable (Lande et al. 1999, 2003, Engen 2001), and quadrat counts where the point process also is important, at least for small areas. In the present analysis, we consider the spatial field of population densities as given, resulting from spatiotemporal processes including birth and deaths of individuals, density regulation, migration, and spatially correlated environmental stochasticity, as well as permanent spatial variation in population parameters such as carrying capacity. For stationary spatial processes the spatial correlation of population density at a given time will then tend to zero at large distances.

Let  $\Lambda(\mathbf{u})$  be the given field of population densities in space, with mean  $\mu$  and variance  $\sigma^2$  for a randomly chosen point  $\mathbf{u}$ . Then, by definition (Bartlett 1960) the expected number of individuals  $dN(\mathbf{u})$  (points) in an infinitesimal area of size  $d\mathbf{u}$  at a given location  $\mathbf{u}$  is  $\Lambda(\mathbf{u})d\mathbf{u}$ , while the unconditional expectation is  $\mu d\mathbf{u}$ . Assuming that the individuals are separated in space, these expressions are also the probabilities that there is exactly one individual in  $d\mathbf{u}$ . Formally, we write this as  $E_p[dN(\mathbf{u})] = \Lambda(\mathbf{u})d\mathbf{u}$ , where  $E_p$  denotes expectation with respect to the point process for a given density function.

The simplest model for the point process is the inhomogeneous Poisson process (the two-dimensional spatial process), representing the completely independent positioning of individuals according to a given spatial density function  $\Lambda$ . For this model, the distributions of the numbers of individuals in any two given disjoint sampling areas  $S_1$  and  $S_2$  are independent Poisson variates with mean values  $\int_{S_i} \Lambda(\mathbf{u}) d\mathbf{u}$ ,  $i = 1, 2$ . Unconditionally, however, when the two areas are chosen randomly in the field with a given distance between them, the two counts are generally dependent and the distributions, the so called Poisson mixtures (Bartlett 1960:7–8), show overdispersion relative to the Poisson distribution. If  $S$  is an area of given size and shape chosen randomly in the field, the quantity  $\lambda = \int_S \Lambda(\mathbf{u}) d\mathbf{u}$  is a stochastic variable. Areas with the same  $\lambda$  may then have different individual numbers following the Poisson distribution,  $\lambda$  being their expected number of individuals. For example, if the distribution of  $\lambda$  among random areas can be approximated by a gamma distribution, the counts will follow a negative binomial distribution (Anscombe 1949, Bartlett 1960) and if  $\lambda$  is lognormally distributed, then the counts are Poisson lognormally distributed (Grundy 1951, Bulmer 1974). Generally, the unconditional (not conditioning on  $\lambda$ ) mean number of individuals in  $S$  equals  $E(\lambda)$  and the variance is  $E(\lambda) + \text{var}(\lambda)$ , where  $E$  and  $\text{var}$  are the expectation and variance with respect to the random location of the area.

Although independent positioning may be realistic for some species, interspecific competition or tendency for grouping occurs in many of organisms (Perry and Taylor 1985). To describe the dependence of each individual's position on other individuals, conditional on the field of densities, we follow the presentation of Bartlett (1960), who introduced the concept of product density at two locations  $\mathbf{u}$  and  $\mathbf{v}$  ( $\mathbf{u} \neq \mathbf{v}$ ) defined as  $E_p[dN(\mathbf{u})dN(\mathbf{v})] = f(\mathbf{u}, \mathbf{v})d\mathbf{u}d\mathbf{v}$ . This concept was used to define the spatial covariance function for the point process as  $g(\mathbf{u}, \mathbf{v}) = f(\mathbf{u}, \mathbf{v}) - \Lambda(\mathbf{u})\Lambda(\mathbf{v})$ , which is the covariance between  $dN(\mathbf{u})/d\mathbf{u}$  and  $dN(\mathbf{v})/d\mathbf{v}$ . Accordingly, we define the point process covariance function for a random point  $\mathbf{u}$  and a given displacement  $\mathbf{z} \neq 0$  as the mean value,

$$C_p(\mathbf{z}) = E_{\mathbf{u}}[g(\mathbf{u}, \mathbf{u} + \mathbf{z})]$$

where  $E_{\mathbf{u}}$  refers to the random choice of the point  $\mathbf{u}$  in the field. Here we have used the subscript  $p$  to emphasize

that this component of the spatial covariance function is made up of covariances that are generated by the point process, that is, by local displacement of individuals.

We base our analysis on the assumption that at any given time the spatial field  $\Lambda(\mathbf{u})$  of population densities is a stationary field across the entire plane defined by its mean density and spatial covariance function. It remains to evaluate the unconditional covariance function, also taking into account this spatial covariance function  $C_d(\mathbf{z}) = \text{cov}_{\mathbf{u}}[\Lambda(\mathbf{u}), \Lambda(\mathbf{u} + \mathbf{z})]$  of this density field, where  $d$  denotes density and  $\text{cov}_{\mathbf{u}}$  indicates that the covariance refers to the random choice of  $\mathbf{u}$ . We define the total spatial covariance function, taking into account the point process as well as the random choice of  $\mathbf{u}$ , as

$$C(\mathbf{z}) = \text{cov}[dN(\mathbf{u}), dN(\mathbf{u} + \mathbf{z})]/[d\mathbf{u}d(\mathbf{u} + \mathbf{z})].$$

Using the general formula for unconditional covariances, first conditioning on  $\mathbf{u}$ , we then find that

$$C(\mathbf{z}) = C_p(\mathbf{z}) + C_d(\mathbf{z}). \tag{1}$$

Although this partitioning appears quite simple, the two terms are not independent, because evaluation of the point process requires information about population density, so that  $C_p$  actually depends on  $C_d$ . To see this, we can for example assume that knowing an individual is located at a given displacement from another individual has an effect that is independent of the density. More precisely, for given positions  $\mathbf{u}$  and  $\mathbf{v}$  we assume that  $P\{dN(\mathbf{v}) = 1 \mid dN(\mathbf{u}) = 1\} = \Lambda(\mathbf{v})\beta(\mathbf{v} - \mathbf{u})d\mathbf{v}$ , where  $\beta$  is a function of the nonzero displacement that is one for the inhomogeneous Poisson process, larger than 1 if there is a tendency for clumping, and less than 1 if the individuals are more regularly spread than the Poisson process, e.g., due to competition for resources or space. This assumption leads to the following relation:

$$C(\mathbf{z}) = [\beta(\mathbf{z}) - 1][\mu^2 + C_d(\mathbf{z})] + C_d(\mathbf{z}). \tag{2}$$

Combining Eqs. 1 and 2, it appears that the contribution from the point process is

$$C_p(\mathbf{z}) = [\beta(\mathbf{z}) - 1][\mu^2 + C_d(\mathbf{z})].$$

Hence, we see that this contribution and the spatial variation in density cannot be chosen independently as  $C_p(\mathbf{z})$  in the present example is affected by the density field.

Note that this covariance function is only valid for  $\mathbf{z} \neq 0$ . For  $\mathbf{z} = 0$ , we have simply  $E[dN(\mathbf{u})dN(\mathbf{u} + \mathbf{z})] = E[dN(\mathbf{u})]$  because  $dN(\mathbf{u})$  is either 0 or 1, a relation we need for the evaluation of the variance of the total counts within an area.

*An example of a point process with spatially varying density function*

To provide an example and illustrate the concepts in the previous section, consider a given population density field  $\Lambda(\mathbf{u})$  as in Fig. 1a. For simplicity we choose  $\Lambda(\mathbf{u}) =$

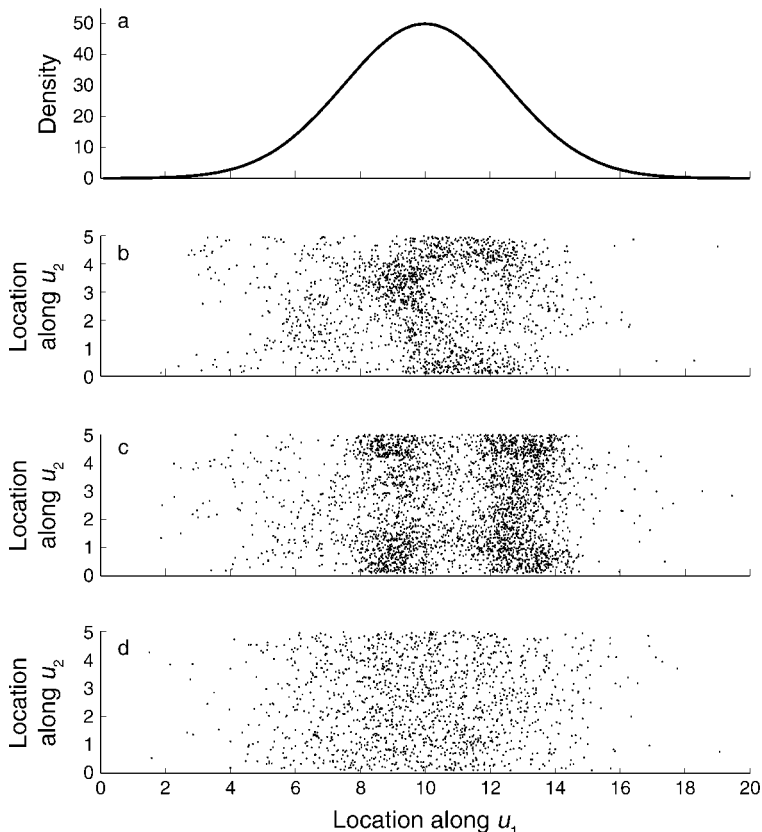


FIG. 1. (a) A spatial density function  $\Lambda(\mathbf{u})$ ,  $\mathbf{u} = (u_1, u_2)$ , in a given year is exemplified by a curve being constant along the  $u_2$  axis and varying according to a Gaussian function along the  $u_1$  axis with a peak at  $u_1 = 10$ . The form of this curve is chosen to illustrate the point process and has no relation to any specific model. The graph shows the density function  $\Lambda(u_1, u_2) = 50 \exp[-0.5(u_1 - 10)^2/5^2]$  plotted against  $u_1$ . (b, c) Two independent scatter plots of points for the above density function based on the lognormal field  $\Omega$  with variance parameter  $\tau^2 = 1$ ,  $\rho(\mathbf{z}) = \exp[-0.5(z_1^2 + z_2^2)]$  and  $\beta(\mathbf{z}) = \exp(0.5 \exp[-0.5(z_1^2 + z_2^2)])$ . (d) Inhomogeneous Poisson process with the density function shown in panel (a).

$\Lambda(u_1, u_2)$  constant in  $u_2$  and show it as a function of  $u_1$ . The point process can then mathematically be defined as follows: Let  $\Omega(\mathbf{u})$  be a stochastic field, independent of the density field  $\Lambda$ , with lognormal stationary distribution with mean 1 constructed by choosing  $\ln \Omega(\mathbf{u})$  as a Gaussian field with mean  $-\tau^2/2$  and spatial covariance function  $\tau^2 \rho(\mathbf{z})$ , so that  $\rho(\mathbf{z})$  is the spatial autocorrelation function of  $\ln \Omega(\mathbf{u})$  (Engen 2001). Then let points be spread in this field according to an inhomogeneous Poisson process with mean  $\Lambda(\mathbf{u})\Omega(\mathbf{u})$ . The probability of finding an individual in  $d\mathbf{u}$  is then for a given field  $\Lambda$  equal to  $\Lambda(\mathbf{u})d\mathbf{u}$  since the expected value of  $\Omega(\mathbf{u})$  is 1, so the population density is actually  $\Lambda(\mathbf{u})$ . The way in which the points are spread, however, is determined by the field  $\Omega(\mathbf{u})$ . We show below that, if the field  $\ln \Omega(\mathbf{u})$  has spatial covariance function  $\tau^2 \rho(\mathbf{z})$ , then the point process determined by  $\Omega$  for a given  $\Lambda$  is a process of the type given by Eq. 2 with  $\beta(\mathbf{z}) = \exp[1/2(\tau^2 \rho(\mathbf{z}))]$ . Fig. 1b and Fig. 1c show two realizations of the point process for the same density function,  $\Lambda$ , which could occur for example if the individuals changed positions over a short period of time. Fig. 1d shows a realization of the inhomogeneous Poisson process with the same density function.

To find the function  $\beta(\mathbf{z})$ , consider two given locations  $\mathbf{u}$  and  $\mathbf{u} + \mathbf{z}$  with densities, say  $X$  and  $Y$ , following the bivariate lognormal distribution with mean values 1, so that the log densities have the binormal distribution with means  $\mu_x = \ln \Lambda(\mathbf{u}) - \tau^2/2$  and  $\mu_y = \ln \Lambda(\mathbf{u} + \mathbf{z}) - \tau^2/2$ , variances  $\tau^2$  and correlation  $\rho(\mathbf{z})$ . The marginal distribution of  $X$  is then lognormal:

$$f_X(x) = \frac{1}{\sqrt{2\pi\tau}} \left(\frac{1}{x}\right) e^{-1/2[(\ln x - \mu_x)/\tau]^2}.$$

Let  $B$  denote the event that there is a point in  $d\mathbf{u}$ . Then  $P(B | X = x) = x d\mathbf{u}$ , and according to Bayes' formula, the distribution of  $X$  given the event  $B$  is therefore proportional to  $x f_X(x)$  (the so-called first moment distribution) which is the lognormal distribution  $f_X(x)$  with  $\mu_x$  replaced by  $\mu_x + \tau^2/2$ . From binormal theory, the conditional distribution of  $\ln Y$  given  $X = x$  is normal with mean  $\mu_y + \rho(\mathbf{z})(\ln x - \mu_x)$  and variance  $\tau^2[1 - \rho(\mathbf{z})^2]$ . Using the above conditional distribution of  $X$  given  $B$ , we then see that the marginal distribution of  $\ln Y$  given  $B$  is normal with mean  $\mu_y + \rho(\mathbf{z})\tau^2/2$  and variance  $\tau^2$ . The expected value of  $Y$  given  $B$  is then  $\exp[\mu_y + (1/2)\tau^2 \rho(\mathbf{z}) +$

$(1/2)\tau^2]$ . For a given value  $y$  of  $Y$ , the probability of finding a point in  $d(\mathbf{u} + \mathbf{z})$  is  $yd(\mathbf{u} + \mathbf{z})$ , and conditioning on the event  $B$ , this probability becomes  $E(Y|B)d(\mathbf{u} + \mathbf{z}) = \Lambda(\mathbf{u} + \mathbf{z}) \exp[\tau^2\rho(\mathbf{z})/2]d(\mathbf{u} + \mathbf{z})$  showing that  $\beta(\mathbf{z}) = \exp[\tau^2\rho(\mathbf{z})/2]$ .

THE MEAN AND VARIANCE OF COUNTS IN AN AREA

General formulation

Following Bartlett (1960), we now evaluate the mean and variance of the number of points  $N$  in a sampling unit  $S$  with area  $A$  and a given shape at a random location in the field. As  $E[dN(\mathbf{u})] = \mu d\mathbf{u}$ , integration over the entire sampling unit gives simply  $E(N) = \mu A$ . The variance is derived from the continuous analogue to the general formula for the variance of a sum (Bartlett 1960: Eq. 8):

$$\text{var}(N) = \int \int C(\mathbf{z}_1 - \mathbf{z}_2) d\mathbf{z}_1 d\mathbf{z}_2 + \int_S \mu d\mathbf{z}_1$$

where the double integral runs over  $S^2$  excluding  $\mathbf{z}_1 = \mathbf{z}_2$ . The second integral represents the contribution from the points  $\mathbf{z}_1 = \mathbf{z}_2$ , which in fact is the only term different from zero if the points obey the homogeneous Poisson process in space, that is, the field  $\Lambda$  of population densities is constant and the individuals are completely randomly distributed. For such a process, we have no autocorrelation for either the point process or the population density and find  $E(N) = \text{var}(N) = \mu A$  in accordance with well-known theory for the homogeneous Poisson process.

For an isotropic model, that is, when  $C$  can be expressed as a function of the absolute value of the displacement independent of the direction, the above double integral can alternatively be expressed as  $A^2 E[C(R)]$ , where  $R$  is the distance between two points chosen at random in the sampling unit  $S$ .

Suppose now that the shape of the sampling unit is kept constant, for example as a square or a circle, whereas the area is a variable. If the area has unit size,  $A = 1$ , then the distribution of  $R$ , say  $f_1(r)$ , can in principle be derived for any shape. The variance of the number of individuals within an area of size  $A$  chosen at random in the field is then, in general for any shape:

$$\text{var}(N) = \mu A + A^2 \int_0^{r_{\max}} C(r\sqrt{A}) f_1(r) dr. \tag{3}$$

The quantity  $r_{\max}$  is the maximum distance between two points in the unit area. Hence, for the square with area = 1,  $r_{\max} = \sqrt{2}$ .

Here we shall only deal with squares, for which the distribution of the distance between two randomly chosen points is as follows (Engen et al. 2002a):

$$f_1(r) = \begin{cases} 2r(\pi + r^2 - 4r) & \text{for } 0 \leq r \leq 1 \\ 2r \left[ 2\arcsin(2/r^2 - 1) + 4(r^2 - 1)^{1/2} - 2 - r^2 \right] & \text{for } 1 \leq r \leq \sqrt{2} \end{cases}.$$

To analyze in more detail the effect of dependence between individuals in their local positioning and examine the effects of our decomposition, it is convenient to introduce the function

$$v(A) = 1 + A\mu^{-1} \int_0^{r_{\max}} C_p(r\sqrt{A}) f_1(r) dr. \tag{4}$$

This function expresses the overdispersion in the point process relative to the inhomogeneous Poisson process and will be approximately independent of the sampling area  $A$  if the scale of the individual dependence in the point process is small compared to the side length  $\sqrt{A}$  of the sampling square.

We observe immediately that  $v = 1$  for the inhomogeneous Poisson process for which  $C_p = 0$ . In the case of dependence between individuals, suppose that the covariance function for the point process is approximately zero for distances larger than say  $l_p$  so that appreciable contributions to the integral exist only for  $r < l_p/\sqrt{A}$ . If  $l_p/\sqrt{A}$  is much smaller than 1 then  $f_1(r) \approx 2\pi r$  for values of  $r$  that contribute to the integral. By a simple scale transformation of the integration variable,  $v \approx 1 + 2\mu^{-1} \pi \int_0^\infty u C_p(u) du$  and hence, becomes approximately independent of the area.

Inserting the general decomposition of Eq. 1 into Eq. 3 now leads to a general equation for the relation between the variance and the area:

$$\text{var}(N) = v(A)\mu A + A^2 \int_0^{r_{\max}} C_d(r\sqrt{A}) f_1(r) dr. \tag{5}$$

The first term on the right side of Eq. 5 is the contribution from the point process with overdispersion function  $v(A)$ , while the second term comes from the spatial variation in density. The form of these terms, analyzed below, depends on the spatial scale of the point process and as well as that of the density process.

The major literature on Taylor's power law deals with the relation between the log of the variance and the log of the mean (Taylor 1986). However, because the mean count in an area  $A$  is  $m = \mu A$  so that  $\ln m = \ln \mu + \ln A$ , we see that shifting between  $\ln A$  and  $\ln m$  only represents a simple translation of the relations on the log scale. In the following analysis, we shall consider the variance as function of the mean, writing

$$V(m) = v(m/\mu)m + m^2\mu^{-2} \int_0^{r_{\max}} C_d(r\sqrt{m/\mu}) f_1(r) dr. \tag{6}$$

Relation between  $m$  and  $V$  generated by varying the sampling area

Taylor's original formulation of the power law was based on an empirical linear relationship between variance and mean on a logarithmic scale (Taylor 1961, 1986). However, it has long been realized (Taylor and Woiwood 1982, Downing 1986, Perry and Woiwood 1992) that estimating the relationship between mean and variance for small population numbers is

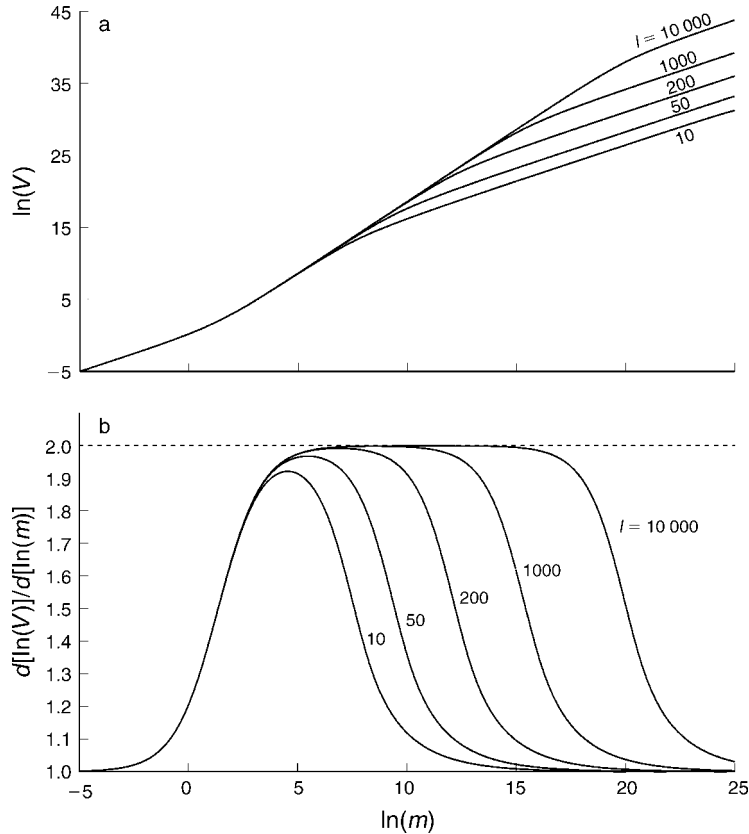


FIG. 2. (a) Logarithm of variance ( $\ln V$ ) as function of log mean ( $\ln m$ ) for increasing square size for different values of the spatial scale  $l$  of the spatial covariance function of the Gaussian form. The other parameters are overdispersion,  $v = 1$ ; mean density,  $\mu = 1$ ; and coefficient of variation for density,  $c_v = 0.5$ . Panel (b) shows the derivatives of the curves depicted in panel (a).

difficult. This occurs because the underlying processes determining these relations turn out to be different for small, medium, and large areas. For small and large areas, rather simple approximations can be derived, whereas the shape of the curve for intermediate areas only can be expressed by integration involving the covariance function, that is, by solving Eq. 6 numerically.

For small distances  $\mathbf{z}$  the correlation between  $\Lambda(\mathbf{u})$  and  $\Lambda(\mathbf{u} + \mathbf{z})$  is likely to be close to 1. Hence, for sufficiently small squares the expected value of  $C_d(r\sqrt{A}) \approx C_d(0) = \sigma^2$  for the whole range of distances  $r$ , giving the following quadratic relationship:

$$V(m) \approx vm + c_v^2 m^2 \quad (7)$$

where  $c_v = \sigma/\mu$  is the coefficient of variation for densities  $\Lambda$  in space. This relationship has previously, for the Poisson case  $v = 1$ , been proposed by Bartlett (1936), Perry (1981), and Routledge and Swartz (1991). Eq. 7 can also be derived by a simpler argument, using that the overdispersion function  $v(A)$  and the density  $\lambda$  is approximately constant over small areas. Then,  $E(N|\lambda) = \lambda A$  and  $\text{var}(N|A) = v\lambda A$ . Unconditionally, we then have  $E(N) = \mu A$  and  $\text{var}(N) = E\text{var}(N|\lambda) +$

$\text{var}E(N|\lambda) = E(v\mu A) + \text{var}(\lambda A) = A\mu v + A^2 \text{var}(\lambda)$ . Inserting  $\text{var}(\lambda) = c_v^2 \mu^2$  and  $\mu A = m$  then gives Eq. 7. As the maximum value of  $r$  is  $\sqrt{2}$  for a square, this relation is a good approximation if  $C_d(\sqrt{2A}) = C_d(\sqrt{2m/\mu}) \approx C_d(0) = \sigma^2$ .

An accurate approximation for large areas can be found by utilizing the known distribution  $f_1(r)$ . Considering the spatial distribution in a given year, we assume that  $C_d(r)$  approaches zero as  $r$  approaches infinity. If this limit is reached approximately at the distance  $\sqrt{A}$  so that  $C_d(\sqrt{A}) \approx 0$  we can simply use the formula for  $f_1(r)$  valid for  $r < 1$ , which leads to the approximation

$$V(m) \approx (v + 2\pi\alpha_1/\mu)m - 8\alpha_2\mu^{-1/2}m^{1/2} + 2\alpha_3 \quad (8)$$

for large values of  $m = A\mu$ , where  $\alpha_j = \int_0^\infty C_d(r)r^j dr$ .

From Eqs. 7 and 8, we see that  $\ln V$  is approximately linear in  $\ln m$  for very small and very large  $\ln m$  (Fig. 2). For small  $\ln m$ , the intercept is  $\ln v$  and for large  $\ln m$ , the intercept is  $\ln(v + 2\pi\alpha_1/\mu)$ . The quadratic term in Eq. 7 makes the difference between  $\ln V$  and  $\ln v + \ln m$  increase with  $\ln m$ , so that  $\ln V$  approaches a straight line for large  $\ln m$ . The value of  $\ln V$  computed from Eq. 7 is halfway between the two straight lines with slope 1 for  $m^* = \pi\alpha_1/(\mu c_v^2)$ . At this value of  $m$ , we should generally

expect the slope to be close to its largest value. For the Gaussian model of spatial autocorrelation, we find  $m^* = \pi l^2 \mu$ . This occurs at sampling area  $A^* = m^*/\mu$ , giving simply  $A^* = \pi l^2$ . The slope of the log variance vs. log mean relationship is therefore expected to be largest when the side of the square roughly equals the scale  $l$  of the spatial covariance function for population density. Fig. 2 depicts examples demonstrating how the curves depend on the scale  $l$ . We see that with increasing  $\ln m$  the slope first increases from 1 to 2 which is a consequence of Eq. 7. For small values of  $m$ , the first term dominates, giving slope 1 on the log scale, while the second term dominates for larger values of  $m$  giving a slope approximately equal to 2. For even larger values of  $m$ , that is, as  $m$  gets much larger than  $l\sqrt{\pi\mu}$ , the curve approaches the large  $m$  approximation given by Eq. 8, which again has slope 1 on the log scale. Thus, the curves in practice will be indistinguishable from straight lines even over rather large ranges of values of  $m$  (Fig. 2), keeping in mind that the scale on the axis is logarithmic. In empirical data the values of  $\ln V$  are estimated from sums of squares, which have a fairly large uncertainty, so the sample points will appear to be spread around a straight line.

The spatial correlation for population density may often be approximately of the Gaussian form with scale  $l$ ,  $C_d(r) = \sigma^2 e^{-r^2/(2l^2)}$ . For this model, we have  $\alpha_1 = \sigma^2 l^2$ ,  $\alpha_2 = 1/2(\sigma^2 l^3)$ , and  $\alpha_3 = 2\sigma^2 l^4$ . For an exponentially decreasing function  $C_d(r) = \sigma^2 e^{-r/l}$  the corresponding values are  $\alpha_j = (j - 1)!\sigma^2 l^{j+1}$

*Relation between m and V generated by interspecific variation in population density*

An increase in  $m = A\mu$  can alternatively occur by an increase in  $\mu$  keeping  $A$  constant. Such variation may be caused by between-species variation in growth rate or strength of density regulation because the mean value is the result of density regulation reducing the realized growth rate to zero.

In view of Eq. 3, the relation between  $V$  and  $m$  is determined by how density affects the two terms of the spatial autocovariance function  $C$  given by Eq. 2. A simple, but often realistic assumption in many biological situations, is that changes in mean values change the variances so that the coefficient of variation is kept constant. If this holds for the relation between the mean and variance of the density  $\Lambda(u)$ , the coefficient of variation  $c_v = \sigma/\mu$  should be constant so that the variance of  $\Lambda$  is proportional to the square of its mean. In that case, it is a reasonable assumption that the covariances are also proportional to  $\mu^2$  so that the spatial correlations for the field  $\Lambda(\mathbf{u})$  are the same for different densities. Writing  $C_d^*(\mathbf{z})$  for the covariance function at  $\mu = 1$ , we then have  $C_d(\mathbf{z}) = C_d^*(\mathbf{z})\mu^2$ .

Also, assuming the point process leading to Eq. 2, the relation for between-species variation in mean and variance, is again quadratic:

$$V(m) = m + m^2 \int_0^{r_{\max}} \{ [\beta(r\sqrt{A}) - 1][1 + C_d^*(r\sqrt{A})] + [C_d^*(r\sqrt{A})] \} f_1(r) dr. \tag{9}$$

*Relations to overdispersion and crowding*

Unconditionally (for a randomly chosen square), the distribution of the number of individuals in a square will in most cases be overdispersed relative to the Poisson distribution. This overdispersion is most conveniently analyzed using Eq. 9. Here, the covariance function for population density is assumed to be proportional to  $\mu^2$ , so that  $C_d^*(\mathbf{z}) = C_d(\mathbf{z})/\mu^2$  does not depend on  $\mu$ , and we have used the model for the point process expressed by the function  $\beta(\mathbf{z}) = \exp[\tau^2 \rho(\mathbf{z})/2]$ . Eq. 9 can be written as  $V(m) = m + b(A)m^2$ , where  $b(A) = [V(m) - m]/m^2$  is a measure of overdispersion for sampling squares at size  $A$ . If the distribution of the number of individuals can be approximated by some Poisson mixture,

$$P(N = n) = \int_0^\infty \frac{\omega^n e^{-\omega}}{n!} h(\omega) d\omega$$

then  $E(N) = E(\omega)$  and  $\text{var}(N) = E(\omega) + \text{var}(\omega)$ , where  $E(\omega)$  and  $\text{var}(\omega)$  are the mean and variance defined by the distribution  $h(\omega)$ . For this model,

$$b(A) = \text{var}(\omega) / [E(\omega)]^2$$

which is the squared coefficient of variation of  $\omega$ . One example of Poisson mixtures that often fits biological counts is the negative binomial distribution that can be generated as a Poisson mixture assuming that the mean value of the Poisson variate ( $\omega$ ) varies among sites according to a gamma distribution with shape parameter  $k$  and scale parameter  $a$ . The coefficient of variation for  $\omega$  is then  $1/k$ , which implies that the shape parameter  $k$  of the negative binomial, when this is used as an approximation, is the inverse of the integral in Eq. 9. For small areas, we then have  $1/k \approx c_v^2 \beta(0) + \beta(0) - 1$ . For large areas, we have  $\beta(r\sqrt{A}) \approx 1$  and  $C_d^*(r\sqrt{A}) \approx c_v^2$  giving  $1/k \approx c_v^2$ . The quantity  $\beta(0)$  can be interpreted as the density of individuals in the immediate neighborhood of an individual relative to the mean density at this position, and is therefore a kind of small scale crowding index. For comparison, the crowding index of Lloyd (1967) equals  $m[1 + b(A)]$  while that of Morisita (1962) for a large number of squares is  $1 + b(A)$ . Our general formula expresses how these indices vary with the area  $A$ , a relation depending on the autocorrelation of densities and the point process for individuals.

*Spatial patterns generated by temporal environmental stochasticity and migration*

The effect of migration on the spatial correlation of population density and hence its effect on the curve  $V(m)$  is in general complex, depending on specific assumptions about the migration process (Hanski

1980, Taylor 1981, Thórarinnsson 1986). However, in a homogeneous environment with no permanent spatial variation in local carrying capacity so that the spatial and temporal variation in population density is generated only by spatially correlated environmental stochasticity and local regulation of population density, general results for the effects of migration on the spatial correlation function of population density have been obtained (Lande et al. 1999, Engen 2001, Engen et al. 2002a, b).

Here we follow the approach of Engen (2001) who considered a model with local density regulation of the Gompertz type (May 1981), spatially autocorrelated environmental stochasticity and density-independent migration modeled as a two dimensional spatial diffusion of individuals. In the absence of migration the dynamical model for the log density  $X(\mathbf{u}, t)$  at location  $\mathbf{u} = (u_1, u_2)$  at time  $t$  is given by

$$dX(\mathbf{u}, t) = [r_0 - \gamma X(\mathbf{u}, t)]dt + \sigma_e dB(\mathbf{u}, t)$$

where  $\gamma$  expresses the strength of local density regulation,  $\sigma_e^2$  is the environmental variance, and  $B(\mathbf{u}, t)$  is a Brownian motion with expected temporal increment  $E[dB(\mathbf{u}, t)] = 0$  and variance  $\text{var}[dB(\mathbf{u}, t)] = dt$ . The environmental noise terms  $\sigma_e dB(\mathbf{u}, t)$  at two different locations separated by displacement  $\mathbf{z} = (z_1, z_2)$  are correlated with spatial autocorrelation  $\rho_e(\mathbf{z})$  defined by  $E[dB(\mathbf{u}, t)dB(\mathbf{u} + \mathbf{z}, t)] = \rho_e(\mathbf{z})dt$ . We shall assume that the environmental autocorrelation is isotropic, only depending on the distance  $r = \sqrt{z_1^2 + z_2^2}$  and will then write  $\rho_e(r)$  for the spatial autocorrelation function  $\rho_e(\mathbf{z})$ . Individuals are assumed to migrate as a continuous random walk or diffusion in space (Turchin 1998) with parameter  $M$ . More precisely, the expected migration distance during time increment  $dt$  along a given direction is zero, while the variance is  $Mdt$ . As the movement along two orthogonal axis are assumed independent, the variance of the total distance moved during  $dt$  is  $2Mdt$ . For this model, the probability that the migration distance during time  $t$  is smaller than  $d$  is  $\exp[-d^2/(2Mt)]$  (Engen 2001). The log-densities for this model compose a Gaussian field, so that population densities are lognormally distributed in space and time. Applying this theory, the effect of migration on the curve  $V(A)$  can then be evaluated numerically as demonstrated in Fig. 3. We see that increasing migration makes the transition from slope 1 to 2 occur at larger distances, which is due to increasing scale in the spatial covariance function for population density with increasing migration (Lande et al. 1999, Engen 2001, Engen et al. 2002a).

DISCUSSION

The distribution of the number of individuals in squares of different sizes has been discussed in the literature over the past 70 years (e.g., Bartlett 1936, 1960, 1975, Bliss 1956, Morisita 1962, Grieg-Smith 1964, Lloyd 1967, Iwao 1978). Here, we have investigated theoretically how such distributions are related to the

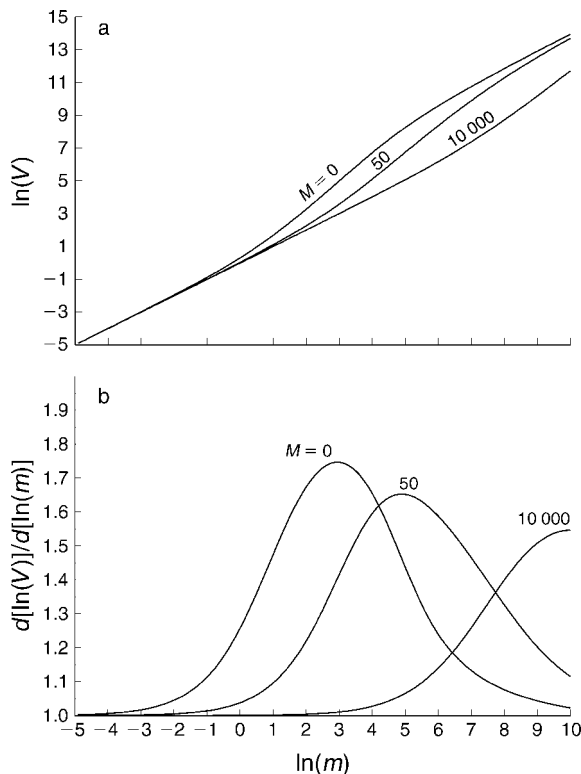


FIG. 3. (a) Logarithm of variance ( $\ln V$ ) as function of log mean ( $\ln m$ ) for three different values of the migration parameter  $M$ . The covariance function for environmental stochasticity has a Gaussian form with  $\sigma_e^2 = 0.01$  and spatial scale  $l_e = 5$ . The local strength of density regulation is  $\gamma = 0.1$  using the Gompertz model of density regulation with mean density  $\mu = 1$  and overdispersion  $\nu = 1$ . The spatial autocovariance function for the log-densities  $\zeta(r) = \text{cov}[X(\mathbf{u}, t), X(\mathbf{u} + \mathbf{z}, t)]$ , where  $r = |\mathbf{z}|$ , is found by the equation  $\zeta(r) = (1/2\pi) \int_0^\infty f_e(u) [2\gamma + Mu^2] u J_0(ru) du$  (Engen 2001, Engen et al. 2002b). Here  $f_e(u)$  is the Fourier transform of the environmental covariance function, and  $J_0$  is the Bessel function of the first kind of order zero (Abramowitz and Stegun 1972). Because  $X(z, t)$  is normally distributed, the corresponding autocovariance function for the population density,  $\Lambda = \exp(X)$ , takes the form  $c_e(r) = e^{2\eta + \zeta(r)} [e^{\zeta(r)} - 1]$ . Panel (b) shows the derivatives of the curves depicted in panel (a).

concept of spatial correlation in population density as well as properties of the point process defining the positioning of individuals, generated by tendency for grouping or overdispersion by local competition for resources or territory, given the field of population densities. These results are summarized by Eqs. 5 and 6. Although the two different mechanisms can be decomposed into additive terms as shown in Eq. 1, there is an interaction between the two mechanisms demonstrated by Eq. 2. We have shown that the overdispersion in the point process for a given density function, that is, the deviation from the inhomogeneous Poisson process, can be expressed by a single parameter  $\nu$  when the spatial scale of the point process is smaller than the side-length

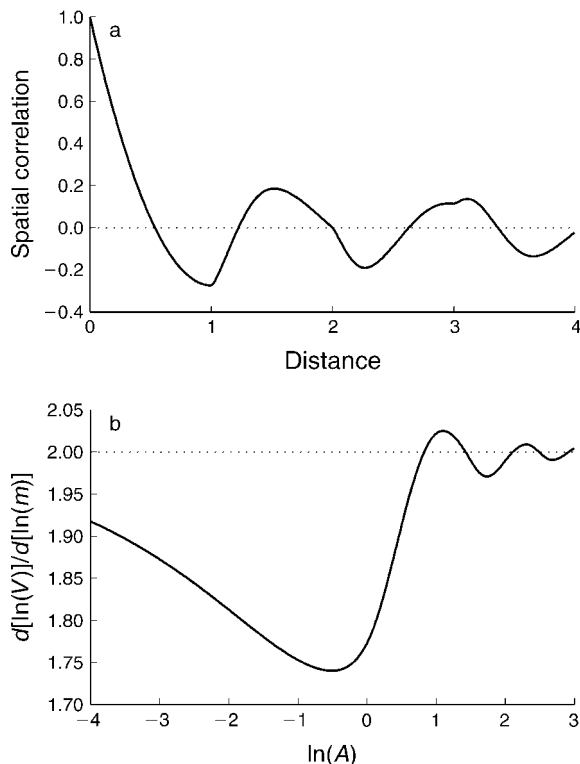


FIG. 4. Spatial autocorrelation function for the chessboard pattern with (a) square size 1 and (b) the corresponding derivative of log variance with respect to log area ( $A$ ).

of the square defining the sampling unit. In this case, the function  $v(m/\mu)$  in Eq. 6 is approximately constant.

Although our analysis shows that the slope of  $\ln V$  against  $\ln m$  is not constant for any of the wide range of models considered here, the Taylor law, or more generally, the analysis of the slope, is still interesting. Estimating spatial autocorrelations is difficult when data are summarized as counts in areas, which is often the only feasible way of data collection and density estimation. Point estimates would hardly be interesting at all, usually giving zero counts most places. Plotting the Taylor curves is therefore informative, in particular when slopes are considered in relation to the present theory linking it to the spatial autocorrelation functions and point processes.

We have seen that our general formula for the spatial autocorrelations can be used to analyze how the shape parameter depends on the area size when the distribution can be approximated by a negative binomial. This distribution can be generated by a number of different mechanisms (Boswell and Patil 1970). Such mechanisms have also been discussed in relation to Taylor's scaling laws (Anderson et al. 1982, Keeling 2000). However, these are based on birth-and-death processes, which only allow for demographic stochasticity with no environmental stochasticity (Lande et al. 2003), and deal only with stationary temporal variance among populations with varying carrying capacities. This

interpretation of the variance–mean relationship is rather different from the spatial scaling considered here. Keeling (2000) also discussed Taylor's laws in relation to spatial scaling of population densities without considering point processes, using circular areas and an exponential form of the spatial covariance function, showing numerically that the slope of log variance vs. log mean decreased from 2 to 1 as the radius increased. This is in agreement with our general results (e.g., Eq. 5). Our results are also in agreement with results from simulation studies including point processes performed by Sawyer (1989), showing increase as well as decrease in the slope with increasing sampling size.

Although the vast majority of studies have shown slopes that in general lie between 1 and 2 (e.g., Taylor 1986, Maurer and Taper 2002, Krasnov et al. 2006), some data sets also give slopes larger than 2 (e.g., Taylor 1961, Taylor et al. 1978: Appendix B). To investigate whether a slope of 2 represents a maximum, we performed a closer examination of Eq. 3. Ignoring the point process by inserting  $v = 0$ , we see that the variance  $V$  is proportional to the square of the area  $A^2$ , as well as the mean of the correlation  $\rho(r/\sqrt{A})$  with respect to the distribution  $f_1(r)$ , say  $\bar{\rho}(A)$ . Hence, the derivative of  $\ln V$  with respect to  $\ln A$  is  $2 + d\bar{\rho}(A)/d(\ln A)$ . As a consequence, the slope is larger than 2 only in intervals where  $\bar{\rho}(A)$  increases with  $A$ . For this to happen, we must have highly regular spatial patterns that produce autocorrelation functions that increase substantially in certain intervals. Fig. 4 shows the extreme case of a chessboard pattern with different constant densities in black and white squares. The direction of the sample square is random relative to the direction of the board. Fig. 4b shows the corresponding slope  $d(\ln V)/d(\ln A)$ , which has a maximum slightly larger than two at a value of  $\sqrt{A}$  between 1 and 2, which is the typical scaling of this pattern. We can conclude that slopes can be slightly larger than 2 over some intervals. In practice, however, estimates larger than 2 are most likely due to estimation errors, especially in the estimated variances, which may be rather large (Downing 1986, Perry and Woilwood 1992, Tokeshi 1995).

Theoretical analysis of dynamic models of temporal and spatial fluctuations has demonstrated that increasing migration leads to increasing scale of spatial covariance in population density (Lande et al. 1999, Kendall et al. 2000, Engen 2001, Ranta et al. 2006). As the slope of  $\ln V$  vs.  $\ln m$  is expected to be at its maximum value for areas of the order of  $l^2\mu$ , the slope is expected to increase from 1 to 2 for  $\ln m > l^2\mu$  as the migration increases. This is precisely what is shown numerically in Fig. 3.

Our approach assumes that migration is density independent. This may be a valid assumption in some taxa (e.g., in plant species with wind-mediated dispersal of seeds [Turchin 1998]). However, in vertebrates, some evidence now indicates that differences in local population size may affect emigration rates as well as

immigration rates (e.g., Clobert et al. 2004), which may strongly affect the spatiotemporal variation (Hastings 1982, Sæther et al. 1999). How such density-dependent migration rates will affect the spatial covariance function is a subject for further studies.

Here, we have primarily dealt with the spatial aspects of Taylor's power law as the sampling area increases. The spatial field of population densities is considered fixed, although it may be generated from some stochastic dynamic model. At any given time, for a stationary spatial process the spatial covariance of population density is expected to approach zero at large distances. However, if temporal sampling is included in the covariance of population density, the covariance may approach a positive value at large distances because of a common environmental factor acting over large distances, such as annual variation in regional climate, as has been demonstrated for several vertebrates (Lindström et al. 1996, Sutcliffe et al. 1996, Engen et al. 2005, Grøtan et al. 2005, Sæther et al. 2007). For a temporal sampling scheme, we will therefore find different scaling laws. However, the main difference will be that the function  $C_d(\mathbf{z})$  in Eq. 5 will approach a value  $\sigma_y^2 \rho_\infty$  for large distances (Lande et al. 1999, 2003, Engen 2001, Engen et al. 2002b). This again will create an additional term  $c_y^2 \rho_\infty m^2$  in Eq. 8, so that the slope does not return to 1 but ends up close to 2 also for very large distances.

#### ACKNOWLEDGMENTS

This project has been supported by the Norwegian Research Council, project 159571/V40, Stochastic Dynamics of Bird Communities, Strategic University Program in Conservation Biology, and the Royal Society of London.

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