Measuring Temporal Variability of Population Density: A Critique

Xuhua Xia; Rudy Boonstra

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NOTES AND COMMENTS

MEASURING TEMPORAL VARIABILITY OF POPULATION DENSITY: A CRITIQUE

Many authors (e.g., Connell and Sousa 1983; Hansson and Henttonen 1985*a*, 1985*b*; Schoener 1985; Ostfeld 1988; Mackin-Rogalska and Nabaglo 1990) have recently compared temporal variation in population density among different taxa or among different populations within the same taxon. There are many problems associated with this approach, and most generalizations made in these articles are not valid. In this note, we analyze in detail one specific example and highlight inherent problems associated with such an approach.

ONE SPECIFIC EXAMPLE

Hansson and Henttonen (1985*a*) and Henttonen et al. (1985) analyzed long-term demographic data sets of microtine populations (*Clethrionomys glareolus* and *Microtus agrestis*) in Fennoscandia and found a clear latitudinal trend: microtine populations in northern Fennoscandia showed (1) greater temporal variability in density and (2) longer cycle periods than those in southern Fennoscandia. These findings have been widely accepted by microtine ecologists, who have then proceeded to explain why there should be such a latitudinal trend (e.g., Hansson and Henttonen 1985*b*; Henttonen 1986, 1987; Erlinge 1987; Hansson 1987; Henttonen et al. 1987; Hansson and Henttonen 1988; Korpimäki et al. 1990; Hanski et al. 1991).

For temporal variability in density, Hansson and Henttonen (1985*a*) calculated the standard deviation of log-transformed density data collected over years, that is,

$$s = \sqrt{\frac{\Sigma[\log N_i - \text{MEAN}(\log N_i)]^2}{n - 1}}, \quad (1)$$

where N_i is the density of the microtine population at year i and n is the number of years in the sample. They replaced N_i in equation (1) by indices of density (e.g., number of voles caught per 100 trap nights in snap traps [*DI*, hereafter]) and found a significant positive correlation between s and latitude.

There are two problems with the use of this calculation of *DI*. First, *DI* in-

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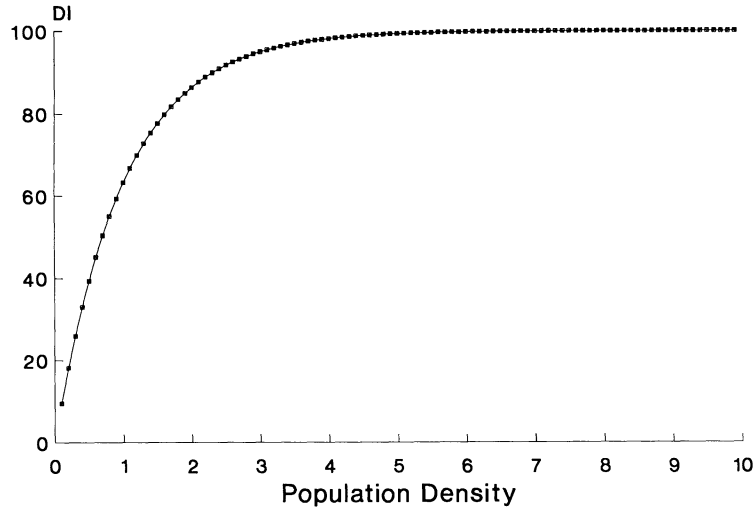

FIG. 1.—Relationship between *DI* (number of voles caught per 100 trap nights) and population density.

creases with population density at a decreasing rate (fig. 1), because each time an animal is caught one trap is no longer available to capture other animals and the number of active traps is progressively reduced (Southern 1973; Caughley 1977; Southwood 1978). This relationship has been documented for rodent populations in Fennoscandia by Hansson (1975) and for North American microtines by Krebs and Boonstra (1984), who showed that trapping success decreases with increasing population density in both *Microtus townsendii* and *Microtus californicus*. Thus, *DI* underestimates population density as density increases. Second, the standard deviation (s) of *DI* underestimates temporal variability of population density progressively as mean density increases. For example, when population density fluctuates between 0.1 and 1, *DI* changes from 9 to 63 (fig. 1), but when the density of a population fluctuates between 4 and 10, *DI* changes only from 98 to 100. In the extreme case, when population density is sufficiently high so that all traps are occupied by voles every night, *DI* reaches its maximum of 100 and no longer changes with density, in which case the standard deviation of *DI* equals 0. Thus, even when two populations of different densities have exactly the same temporal variation in population density, s of *DI* will be smaller for the high-density population than that for the low-density population.

A numerical example can illustrate quantitatively how severe such underestimation could be. Suppose there are a total of N voles in the trapping area, and the density per trap site is then $D = N/T$, where T is the total number of traps in the trapping area. If voles are distributed randomly, then the percentage of traps that have no vole visiting is

$$p = e^{-D}, \tag{2}$$

according to Poisson distribution, and the percentage of traps that have at least

TABLE 1

NUMERICAL EXAMPLE DEMONSTRATING HOW THE USE OF *DI* AND LOG-TRANSFORMATION UNDERESTIMATES TEMPORAL VARIABILITY

Year	D_l	D_h	DI_l	DI_h	$\log(DI_l)$	$\log(DI_h)$
1	.318	.918	27	60	1.43	1.78
2	.164	.764	15	53	1.18	1.72
3	.101	.701	10	50	1.00	1.70
4	.256	.856	23	58	1.36	1.76
5	.030	.630	3	47	.48	1.67
6	.144	.744	13	52	1.11	1.72
7	.208	.808	19	55	1.28	1.74
8	.185	.785	17	54	1.23	1.73
9	.241	.841	21	57	1.32	1.76
10	.136	.736	13	52	1.11	1.72
$\bar{X}$	.178	.778	16.08	53.95	1.15	1.73
s	.083	.083	6.97	3.82	.27	.03

NOTE.—Values are as follows: D is number of voles per trap site, DI is number of voles caught per 100 trap nights, $\ln(DI)$ represents natural log-transformation of DI, and s is standard deviation of corresponding variables. Subscripts l and h refer to low- and high-density populations, respectively.

one vole visiting will be $1 - p$. Because each snap trap can catch only one vole, the expected number of voles caught per 100 trap nights is

$$DI = 100 \times (1 - p). \tag{3}$$

Now suppose we have one low-density (D_l) and one high-density (D_h) microtine population with equal temporal variability in density. Temporal changes in density over 10 yr for both populations are generated so that both populations have different mean densities (0.178 and 0.778 for the low-density and high-density populations, respectively; table 1) but the same standard deviation of density (0.083 for both populations). The value of DI (i.e., number of voles caught per 100 trap nights) and its standard deviation are calculated for both populations (table 1). The standard deviation of DI for the low-density population is almost twice as large as that for the high-density population (6.97 vs. 3.82; table 1). If log-transformation is applied to DI as in equation (1), then s for the low-density population is nine times as large as for the high-density population (0.27 vs. 0.03; table 1). This occurs even though the largest DI value in table 1 is no more than 60 voles caught per 100 trap nights. Thus, the latitudinal trend shown in Hansson and Henttonen (1985*a*) may simply be an artifact caused by different degrees of trap "saturation" between the north and the south. An appropriate method for estimating density from trapping data in the form of DI_l and DI_h in table 1 is provided in the Appendix.

Do Southern Fennoscandian Populations Have Higher Density than Northern Populations?

The northernmost population of *Clethrionomys glareolus* (66°N) studied by Hansson (1969) had its peak density in 1966 with a total of 194 traps catching a

total of 108 voles in two nights. The *DI* was therefore

$$100 \times \frac{108}{194 \times 2} \approx 28(\text{voles}/100 \text{ trap nights}).$$

The southernmost population of *C. glareolus* (56.5°N) studied by Hansson (1971) had its peak density in 1964 with a similar trapping method yielding a *DI* of 29 voles/100 trap nights. Superficially, this would suggest that peak density in the northern population was similar to that in the southern population (28 vs. 29) and that there was no indication that the southern population experienced a greater degree of trap saturation than the northern population. A close examination, however, shows otherwise. There are other species of small mammals "competing" for traps with *C. glareolus* in both the southern and the northern study sites. In the northern site, the sum of all six species of small mammals other than *C. glareolus* gave a *DI* of 5 animals/100 trap nights, whereas, in the southern, *Apodemus sylvaticus* alone had a *DI* of 60 voles/100 trap nights (Hansson 1971). Hansson mentioned that *Microtus agrestis* is also common in the southern site. Of 1,070 animals captured for diet analysis, 366 were *A. sylvaticus,* 307 were *C. glareolus,* and 397 (37%) were *M. agrestis*. Thus, there are apparently many more rodents "competing" for traps in the south than in the north.

We made another comparison of population density between northern and southern populations using data collected by Henttonen et al. (1977), who snap trapped three populations at different latitudes (63°54′N, 68°03′N, and 69°03′N). Hansson and Henttonen (1985*a*) calculated the standard deviation (*s*) and coefficient of variation (*CV*) of the density index for these populations, and the mean density index for the three populations can be obtained simply by dividing *s* by *CV*. The mean density index thus calculated is 1.044, 0.566, and 0.329 for populations at latitudes 63°54′N, 68°03′N, and 69°03′N, respectively. It is also worth noting that great trapping effort (a total of 60,000 snap-trap nights) was involved in the study by Henttonen et al. (1977), and the effect of trap "saturation" should therefore be relatively small. Consequently, one should expect the study to reveal relatively accurately the true difference in temporal variation in density among populations of different latitudes. According to calculation by Hansson and Henttonen (1985*a*), *s* is greater for the southern population (63°54′N, $s = 0.95$) than that for the two northern populations ($s = 0.94$ and 0.50 for populations at 68°03′N and 69°03′N, respectively), contrary to the general latitudinal trend claimed by Hansson and Henttonen (1985*a*).

Because of the lack of a standard trapping method, it is difficult to compare population density between southern and northern populations. The number of animals caught per 100 trap nights (*DI*) is affected by trap type (e.g., snap trap, single and multiple live-traps), trap spacing, trapping intensity, and a variety of other factors. For example, given the same microtine population density, an investigator who spaced traps close together so that each animal had many traps in its home range would arrive at a lower *DI* than one who set only one trap per home range. Similarly, an ecologist who trapped for four consecutive nights would arrive at a smaller *DI* than one who trapped for only one night, because of diminishing return per trapping effort during the second, third, and fourth

nights. A comparison of *DI* between southern and northern populations can only be made when these factors are roughly the same for both northern and southern populations. The studies we quoted above (Hansson 1969, 1971; Henttonen et al. 1977) are perhaps the only three studies in which reported *DI* values can be validly compared.

Another Source of Error in Computing s

Potential difference in population density between the northern and southern populations of microtine rodents is not the only cause that might have given rise to the latitudinal trend. Another problem was with number of traps used. For example, Hansson (1969) used only five trap stations in 1966 for a northern (66°N) population of *M. agrestis* and caught no animals. A *DI* of 0 voles/100 trap stations was then reported. Similarly, when he used only eight trap stations in 1967 and caught eight voles, a *DI* of 100 voles/100 trap stations was reported. These *DI* values are highly unreliable and inflate the temporal variation in density between 1966 and 1967 simply because s is statistically expected to decrease by a factor of $N^{-1/2}$ when the number of sampling units (traps) is increased by a factor of N. For example, if a southern population is trapped with 10 times as many trap stations as a northern population, s for the southern population is expected to be 3.15 ($= \sqrt{10}$) times smaller than s for the northern population. Thus, one cannot compare s among different populations in cases in which the number of traps is not controlled.

Do Microtines Cycle in the North but Not in the South?

The second latitudinal trend found is that microtine populations in the north cycle, whereas those in the south do not (Henttonen et al. 1985). This could also be a numerical artifact because of different degrees of trap saturation at different latitudes. Once its upper limit of 100 is reached, *DI* no longer changes with increasing density (fig. 1). A simple numerical example will illustrate how multiannual cycles would fail to be detected in southern populations in which *DI* is used. Suppose that all snap traps are occupied by voles at a point at which density reaches 50/ha. If a southern population has annual densities of 50/ha but peaks of 500 voles/ha every 4 yr and a northern population has annual densities of 2/ha but peaks of 20/ha every 4 yr, the cycle would be detected in the north but not in the south. Thus, the finding by Henttonen et al. (1985), that microtine populations in northern Fennoscandia have multiyear cycles while those in southern Fennoscandia have only annual fluctuations may also be due to the failure of the method in detecting cycles in populations with high mean density.

OTHER EXAMPLES OF INJUDICIOUS USE OF DENSITY INDICES

The same injudicious use of density indices has occurred in a number of other publications. For example, Mackin-Rogalska and Nabaglo (1990) studied the relationship between latitude and population demography of the common vole, *Microtus arvalis*. They used two density indices: one is the same as above (i.e., number of voles caught per 100 trap nights) and the other is the counting of

inhabited burrows per unit area. The problem with the first index is now obvious. As for the second (i.e., the counting of inhabited burrows), Mackin-Rogalska et al. (1986) have demonstrated that the relationship between the number of inhabited burrows per unit area and true density is exactly the same as is depicted in figure 1. The percentage of inhabited burrows increases with density but at decreasing rate, because the number of individuals per burrow also increases with density (Mackin-Rogalska et al. 1986). For example, when the density of the common vole in Region I of their study site increased from 0 to 100, the percentage of inhabited burrows increased from 0% to 40% (fig. 6 in Mackin-Rogalska et al. 1986). However, when the density increased from 100 to 200, the percentage of inhabited burrows increased from 40% to only 45%. It is therefore not surprising that Mackin-Rogalska and Nabaglo (1990) found exactly the same latitudinal trend of microtine population demography in Poland as that reported for Fennoscandia.

The misuse of density indices has also been found in other areas of ecology. Connell and Sousa (1983) used s (see eq. [1]) to estimate temporal variability of population density (or size) for many natural populations of animal species and found that temporal variation of population density was high (large s) and that terrestrial vertebrates were as variable as terrestrial arthropods. Many of their s values were obtained from density indices having the same property as is depicted in figure 1. For example, one of the density indices used in Connell and Sousa (1983) was the number of breeding pairs of birds in nest boxes. This density index apparently increases with population density *at a decreasing rate,* because each time a nest box is occupied it is no longer available to be occupied by other birds. Thus, s calculated from this density index underestimates temporal variability of population density progressively with increasing density. Another density index they used for parasites was the percentage of hosts infected by parasites. This density index should also have the same relationship to population density as is depicted in figure 1. Once all hosts are infected, the index assumes the value of 100% and no longer changes with the population density of parasites, and the resulting s value approaches 0. For this reason, it is not surprising to see uniformly small values of s in parasites (Connell and Sousa 1983).

Schoener (1985) compiled s values from lizard populations in a similar way and found little temporal variation of population density in lizards (small s). When he added these s values from lizard populations to the original compilation by Connell and Sousa (1983), the population density of terrestrial vertebrates became less variable than that of terrestrial arthropods. Schoener (1985) used a density index (number of home ranges per site) reported in Schoener and Schoener (1980, 1982). Adult males in those lizard species are aggressive and territorial, adult females are less aggressive but often have exclusive home ranges, and juveniles range widely. A site can only accommodate a limited number of home ranges or territories. Thus, the density index will not increase linearly with population density. Once a site is saturated, "surplus" individuals will have to range widely waiting for a vacancy. Because density estimates in Schoener and Schoener (1980, 1982) were the number of individuals that had their geometric center inside the study sites (each of which is about 100 m^2 in size), "surplus" individuals

that wander among sites were excluded from the density estimation. Thus, the fluctuation of the number of these "surplus" individuals, no matter how dramatic, contributed little to the variability of population density estimated by Schoener (1985). For populations with extraordinarily high density, such as lizard populations of *Anolis* species, the variability of population density may be severely underestimated by using this density index. Thus, the small s values reported for lizard populations in Schoener (1985) may be a reflection of the method used to assess true density.

Following Schoener's (1985) example, Ostfeld (1988) added s values calculated from microtine data collected in Europe and North America to the compilation by Connell and Sousa (1983) and Schoener (1985). Ostfeld (1988) found the surprising result that these microtine populations, which often exhibit dramatic fluctuations in density, did not have large s values. In fact, most of his s values tended to be small. These small s values reinforced the idea in Schoener (1985) that the population density of terrestrial vertebrates is less variable than that of terrestrial arthropods. Ostfeld (1988) was not aware that many of these s values underestimated temporal variability of population density of microtine species.

In conclusion, most estimates of temporal variability of population density reported for different species or for the same species in different geographical areas are not directly comparable because of the injudicious use of a variety of density indices that do not have a linear relationship to the true density. Even if population density is accurately and precisely estimated, the log-transformation in equation (1) makes it problematic to compare the resulting s values among populations of different densities because actual temporal variability of high-density populations is reduced more than that of low-density populations. We therefore recommend the use of density estimates, such as those in Seber (1982), that are not biased or, at least, those in which the bias is not density-dependent.

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APPENDIX

A Method for Estimating Density from Trapping Data

One might ask, after reading our critique, What is then the appropriate method for estimating D_l and D_h, given trapping data in the form of DI_l and DI_h in table 1? It turns out that, although general principles for deriving such a method are available in most books on probability theory, a method ready for use by field ecologists is not present in any methodological books, including the encyclopedic book by Seber (1982). Thus, a method is presented here in detail.

To estimate density of animal populations, one must first of all know the spatial distribution of the animal population. For example, if we know that animals are distributed randomly in space, then it is easy to obtain estimates of D_l and D_h from DI_l and DI_h, using equations (2) and (3). But we do not know whether the distribution is Poisson or not. Most

natural populations follow a negative binomial distribution (Elliott 1977; Southwood 1978; Seber 1982), of which Poisson distribution is a special case (in which the negative binomial exponent, k, is infinitely large). Our personal experience with rodent populations indicates that rodent populations are spatially clumped and should also follow a negative binomial distribution. Thus, we should estimate first of all the negative binomial exponent k.

To illustrate the method, we use data in DI_1 and show how to estimate D_1 from DI_1. The data are assumed to have been collected by sampling units of exactly 100 traps each. For symbolic clarity, DI_1 is, from now on, replaced by DI and D_1 by D. With negative binomial distribution, the number of traps that catch no rodent is

$$1 - \frac{DI_i}{100} = \left(1 + \frac{D_i}{k}\right)^{-k}, \tag{A1}$$

where $i = 1, 2, \ldots, 10$ in our case and D_i is then

$$D_i = k\left[\left(1 - \frac{DI_i}{100}\right)^{-1/k} - 1\right]. \tag{A2}$$

For example,

$$D_1 = k[(1 - 0.27)^{-1/k} - 1] = k(0.73^{-1/k} - 1). \tag{A3}$$

The mean of D_i is then

$$u = \sum_{i=1}^{n} D_i/n, \tag{A4}$$

where n is the total number of sampling units, which equals 10 in our case. These D_i and u values can be substituted into the following equation to obtain a maximum likelihood estimate of k:

$$n\left[\ln\left(1 + \frac{u}{k}\right)\right] = \sum_{j=1}^{m}\left(\frac{N_{D_j}}{k + D_j}\right), \tag{A5}$$

where m is the total number of distinctive DI (or D) values, N_{D_j} is the total number of sampling units with D greater than D_j, and the rest of the symbols are as defined before. The negative binomial coefficient, k, in equation (A5) is solved by iteration, that is, different values of k are substituted into equation (A5) until the two sides of the equation are balanced. In our case, we find the k to be very large (>1,000) using equation (A5). The real k is in fact infinite because the data in DI are generated from a Poisson distribution. Because a negative binomial distribution with a $k = 1{,}000$ is, for any practical purpose, not different from a Poisson distribution, one can obtain estimates of D_i either by using equations (2) and (3) for Poisson distribution or by using equation (A2) for negative binomial distribution, with k replaced by 1,000. The resulting mean and variance of estimated D_i are 0.178 and 0.082, respectively, which are very close to the true mean and variance of D_i in table 1 (0.178 and 0.083, respectively). It should be noted that some discrepancies between the real D_i and the estimated D_i are unavoidable because DI can only take integer values, that is, we can catch animals only one by one, not in halves or quarters.

One of the reviewers pointed out the importance of sampling variance in applying statistical methods to the investigation of temporal variation of population density. For example, an animal population with a negative binomial distribution of mean density u and exponent k has a variance of $(u + u^2/k)$ around the mean. This implies that we will not be able to detect temporal density variation of the same magnitude if only one sample per year is taken. To overcome this problem, one can increase either the number of sampling units (N) or the number of traps in each sampling unit so that the sampling unit will cover a

large area. The importance of sampling variance is often not taken seriously by field ecologists, and, as a consequence, within-year variation in density due to spatial heterogeneity is rarely, if ever, separated from temporal variation in density over years.

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XUHUA XIA
RUDY BOONSTRA

DIVISION OF LIFE SCIENCES
SCARBOROUGH CAMPUS
UNIVERSITY OF TORONTO
SCARBOROUGH, ONTARIO M1C 1A4
CANADA

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