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THE DETECTION OF DENSITY-DEPENDENCE FROM A SERIES OF ANNUAL CENSUSES[1]

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Abstract. We report a distribution-free approach to the detection of density-dependence in the variation of population abundance, measured by a series of annual censuses. The method uses the correlation coefficient between the observed population changes and population size and proposes a randomization procedure to define a rejection region for the hypothesis of density-independence. It is shown that the use of the proposed statistic under the randomization approach is equivalent to the likelihood ratio test for a particular family of time series models.

The randomization test is compared with two other recently proposed tests. Using computer-generated density-independent and density-dependent data, it is shown that, unlike the other tests, the randomization test is effective whether or not there is a marked trend in the observed data. Arguments are presented showing how one of the other two tests can be further improved.

Caution is urged in the use and interpretation of any test for detecting density-dependence in census data because (a) the tests depend on assumptions about population processes, (b) errors of measurement may lead to spurious detection of density-dependence.

Key words: annual census; correlation; density-dependence; distribution-free tests; likelihood ratio tests; randomization; regression; simulation.

Introduction

As many populations persist for long periods, yet remain finite, there can be little doubt that they experience some form of density-dependent limitation (Royama 1977). However, such density-dependence might be very rare, occurring between periods of density-independence, or frequent and manifest in most or all generations. Hence, the role of density-dependent factors in animal populations has been of critical interest in population ecology for many years (Smith 1935, Andrewartha and Birch 1954, Krebs 1979). In spite of this interest, all proposed methods to detect density-dependence appear unsatisfactory. Thus, even in the apparently simple case of census data consisting of "error-free" counts made in successive annual generations at the same stage in the life-cycle, there is no satisfactory method of detecting density-dependence in the variation of population abundance.

Slade (1977) and Vickery and Nudds (1984) have reviewed the variety of methods that have been proposed by a number of research workers. However, having examined the effectiveness of six different tests of density-dependence, Vickery and Nudds concluded "No single, simple test has been described which can differentiate between DD (density-dependent) and DI (density-independent) data from a series of population censuses." They found that tests based on the estimators of the regression statistic were effective only if the population showed a pronounced trend in time, and that Bulmer's autoregression test (Bulmer 1975) was best only when the population showed no growth or decline.

The main purpose of this paper is to report a simple, efficient, and distribution-free approach to the detection of density-dependence in the variation of population abundance measured by a series of annual censuses. We show that our proposed technique is satisfactory for populations showing no growth as well as for populations that are growing (or declining). We also develop and discuss the relevant statistical theory underlying a family of time series processes considered by, or implied in the proposals for detecting density-dependence by, other research workers. This gives an understanding of the reasons why some of the methods proposed by other research workers are unsatisfactory, and leads also to the possibility of further improvements of the earlier methods.

Definition of "density-dependent"

Huffaker and Messenger (1964:79) define "density-dependent" action as "... the actions of repressive

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environmental factors, collectively or singly, which intensify as the population density increases and relax as this density falls. . . ." We accept this definition, which is in accord with our own view that, in testing for density-dependence, the central question we need to consider is whether the magnitudes of the per capita changes in the size of animal populations are dependent or independent of the density of the population itself. For brevity, we shall refer to such populations as density-dependent or density-independent populations.

If a population size is $N(t)$ at time t, then the relative rate of change, at time t, in the population size, with respect to time, is given by $r(t) = \frac{1}{N}\frac{dN(t)}{dt}$. Writing $x(t) = \log_e N(t)$, it follows that $r(t) = \frac{dx(t)}{dt}$. Hence, if a series of annual census values of a population, over n years, is given by the count values $N_1, N_2, \ldots, N_n$, then, writing $x_i = \log_e N_i$ $(i = 1, 2, \ldots, n)$, the relative rate of change (or the relative growth rate of the population) between years i and $(i + 1)$ is given by $(x_{i+1} - x_i)$, with time measured in units of 1 yr. For a density-dependent population, the relative growth rate $(x_{i+1} - x_i)$ is dependent upon the population size x_i, while for a density-independent population, $(x_{i+1} - x_i)$ is independent of x_i.

To illustrate this definition of density-dependence, and also to describe the development of the subject by other authors in recent decades and our own proposals in this paper, it is useful to consider the three populations arising from the following family of time series processes:

$$x_{i+1} = x_i + e_i \tag{1}$$

$$x_{i+1} = r + x_i + e_i \tag{2}$$

$$x_{i+1} = r + \beta x_i + e_i \qquad (\beta \neq 1). \tag{3}$$

In these equations, x_i denotes the natural logarithm of the population size in year i. The terms e_i are independent random variables with mean zero and variance equal to σ^2, while r and β are the model parameters.

Population 1 will perform "a random walk" in time and is density-independent. The relative growth rate $(x_{i+1} - x_i) = e_i$, which is independent of x_i and of any other e_j. For population 2, $(x_{i+1} - x_i) = r + e_i$, which is again independent of x_i; the march of this density-independent population through time is described as "a random walk with a drift" with the drift parameter r. For population 3, $(x_{i+1} - x_i) = r + (\beta - 1)x_i + e_i$, which obviously depends upon x_i since $\beta \neq 1$, and hence, this population is density-dependent.

Existing methods

In a series of papers, Morris (1959, 1963*a*, *b*) described his technique of "key-factor analysis," which in our notation amounts to plotting x_{i+1} as an ordinate value against x_i as an abscissa value, fitting a straight line to the resulting scatter of points, and then examining the magnitude of the departure of the slope of the fitted line from 1. Solomon (1964) discussed Morris's method and focussed particular attention on its implications for analysis of density responses of animal populations. While Morris stated that a slope of 1 is to be interpreted as complete density-independence, Solomon pointed out that deviations from 1 in either direction are a measure of density response (dependence) in a population: if the slope is >1, the population is positively density-dependent (i.e., the relative growth rate increases as the population size increases), while, if the slope is <1, the population is negatively density-dependent. In this paper, we are concerned with "negative" density-dependence and we will not consider further the case of slope >1. A number of authors have shown that while the logic underlying Morris's method appears correct, in practice any attempt to test for density-dependence in a population is subject to a difficulty. This difficulty is, that if the sample observations are used to estimate the true slope β by the regression coefficient b, i.e., by

$$b = \sum_{i=1}^{n-1} (x_i - m_1)(x_{i+1} - m_2) \Big/ \sum_{i=1}^{n-1} (x_i - m_1)^2 = b_{21} \tag{4}$$

where

$$m_1 = \sum_{i=1}^{n-1} x_i/(n - 1)$$

and

$$m_2 = \sum_{i=1}^{n-1} x_{i+1}/(n - 1),$$

then, even if the true slope β were to be 1, the estimate b (of β) is liable to be <1 because of random variation in data. Hence, the method is increasingly unreliable as the variation increases or as the number of census points decreases (Eberhardt 1970, Maelzer 1970, St. Amant 1970, Kuno 1971, Reddingius 1971, Ito 1972, Bulmer 1975). Varley and Gradwell (1963) suggested regressing x_{i+1} against x_i, and also x_i against x_{i+1} and proposed that the hypothesis $\beta = 1$ should be rejected only if both (a) the slope of x_{i+1} against x_i, and (b) the reciprocal of the slope of x_i against x_{i+1}, are significantly <1. Varley and Gradwell's test has been shown by Slade (1977) and by Vickery and Nudds (1984) to identify too few significant results. These authors have also examined other alternatives to b as estimator of β. These include the slope of the major axis (Deming 1943), the standard major axis (Ricker 1973, 1975; citing Teissier 1948) and an estimator based on the first-order serial correlation (Bulmer 1975). None of these tests proved satisfactory in trials using simulated density-independent and density-dependent data. The two major axis tests were considered by Slade to be the best available, although neither was considered to be capable of detecting density-dependence in the absence of periods of growth or decline in the simulated population data.

In his study of the statistical analysis of density-dependence Bulmer obtained a good approximation to the distribution of the statistic R, the reciprocal of von Neumann's Ratio, for the random walk model 1 with normally distributed errors, and he used this ratio as a criterion for testing density-dependence. Writing $V = \sum_{i=1}^{n} (x_i - \bar{x})^2$ and $U = \sum_{i=1}^{n-1} (x_{i+1} - x_i)^2$, Bulmer's R is given by the ratio V/U, with small values of R indicating density-dependence. His testing procedure amounts to testing the random walk model $x_{i+1} = x_i + e_i$ (our model 1 [i.e., Eq. 1]), against our model 3, with the intercept r in model 3 considered as $\mu(1 - \beta)$ where $\mu = E(x)$, the expected value of x under model 3.

In their simulation studies, Slade (1977) and Vickery and Nudds (1984) found Bulmer's method to be ineffective where there is a trend in the data. As tests based on estimators of β are acceptable only when there is pronounced trend in x_i values in time, and Bulmer's method only when there is no pronounced trend, Vickery and Nudds pointed out that the potential user has a difficult preliminary decision to make about the presence or absence of trend in a particular data set. They suggested that where no such decision can easily be made, a simulation test, which they describe, should be used.

Vickery and Nudds' paper can be interpreted to mean that their simulation test is based on the comparison of the simple regression coefficient b, calculated from the observed data, with the same statistic calculated from a large number of simulated sets of density-independent data. These simulations are generated with the same length, the same expected mean, and the same expected variance as the observed data. Their density-independent model is the same as that used by Bulmer, i.e., model 1, with an expected growth rate of zero and with normally distributed errors. As is the normal practice, they define the rejection region by the most extreme 5% (or $[\alpha \times 100]$%, for testing at a different level of significance) values of the test-statistic calculated using the simulated sets of data. We have found such use of the regression coefficient b_{21} as a test statistic unsatisfactory, but W. L. Vickery (*personal communication*) informs us that the procedure used by Vickery and Nudds (1984) was first to compute b_{21} and then to compute Student's t statistic, $t = (b_{21} - 1)$/(standard error of b_{21}), for the observed and simulated sets of data. The t statistic is then used as a test statistic in the simulation procedure.

In this paper, we show that both Bulmer's test and Vickery and Nudds' test (even using t) yield unsatisfactory results. We propose, instead, a randomization test and present the appropriate statistical arguments to show that this approach is preferable to the alternatives discussed above. To demonstrate this, we used simulated density-independent and density-dependent data to provide Monte Carlo comparisons of the proposed randomization test with Bulmer's and Vickery and Nudds' procedures.

Proposed randomization test

If the observations $x_1, x_2, \ldots, x_n$ are from density-independent populations such as those described by models 1 and 2, then starting with the initial observation x_1, the observed changes $(x_2 - x_1)$, $(x_3 - x_2)$, $\ldots$, $(x_n - x_{n-1})$ are random fluctuations that have collectively displaced the population size from the initial value of x_1 to the final value of x_n. Thus, writing $d_i = (x_{i+1} - x_i)$, $(i = 1, 2, \ldots, n - 1)$, the observed set $(x_1, x_2, \ldots, x_n)$ is a random realization due to a particular ordering $d_1, d_2, d_3, \ldots, d_{n-1}$ of the d_i values. For a density-independent population the d_i values could have occurred in a different order, yielding a different, but equally likely, pattern of x_i values, with the initial and final values of x_i (i.e., x_1 and x_n) remaining unchanged.

The rationale underlying the randomization test is to consider whether, using an appropriate test-statistic, T(say), the observed set of x_i values should be judged as a significantly extreme arrangement when compared with all the possible arrangements of the x_i values. Given $x_1, x_2 \ldots, x_n$, there are $(n - 1)!$ number of arrangements of the $(n - 1)$ d_i values, and hence $(n - 1)!$ possible sets of x_i values, conditional upon the initial value being x_1. Even for a relatively moderate value of n such as 10, there will be $9! = 362\,880$ arrangements of x_i values. Our approach is to obtain a sample of the random permutations of the d_i values, and for each permutation of the d_i values, generate a corresponding set of simulated x_i values.

Thus, to test the null hypothesis that the observations x_i $(i = 1, 2, \ldots, n)$ arise from a completely density-independent population, our procedure is:

a) Use the observed values $x_1, x_2, \ldots, x_n$ to compute the value of the test-statistic, T.
b) Either calculate the $d_i = (x_{i+1} - x_i)$ values and enumerate the $(n - 1)!$ possible sets of x_i values, or randomly permute the d_i values, and corresponding to N such permutations, obtain a sample of N simulated sets of x_i values. The latter constitutes a Monte Carlo test (Barnard 1963). Guidelines for the choice of N are given by Marriott (1979).
c) For each simulated set of x_i values, compute the test-statistic T.
d) If less than (say) 5% of the T values calculated

under (c) are smaller than or equal to the computed T value under (a), then provisionally (see Discussion) reject the null hypothesis of density-independence, at 5% level of significance.

Nearly all research workers, except Bulmer, have used the slope of x_{i+1} upon x_i as the test-statistic T. However, since density-independence implies no relationship between population changes (d_i) and the population size (x_i), either the regression or the correlation coefficient of d_i on x_i are plausible alternatives. It is shown later that if the error terms e_i in Eqs. 1, 2, 3 are assumed to be normally distributed, then the correlation coefficient (r_{dx}) is equivalent to the likelihood ratio test statistic for a given set of observed changes.

Statistical Considerations

Eqs. 1, 2, and 3 describe a family of time series processes in which Eq. 2 is a special case of Eq. 3 with $\beta = 1$, while Eq. 1 is a special case of Eq. 2 with $r = 0$. We have seen that while populations described by models 1 and 2 are density-independent, model 3 describes a density-dependent population.

Given the observations $\boldsymbol{X} = x_1, x_2, \ldots, x_n$, if the null hypothesis, H_r, states that the observations are from a population generated by some model r, and if the alternative hypothesis, H_s, states that the observations are from a different population generated under a more general model s (i.e., if the parameters in model r form a subset of the parameters in model s), then the maximum likelihood of the observations under model r must be less than or equal to the maximum likelihood of the observations under model s, i.e.,

$$L_{\max}(\boldsymbol{X}/H_r) \leq L_{\max}(\boldsymbol{X}/H_s).$$

The Likelihood Ratio method of test construction (see Kendall and Stuart 1961) requires that to test the null hypothesis H_r against the alternative hypothesis H_s, the test should be based upon the distribution of the ratio $L_{\max}(\boldsymbol{X}/H_r)/L_{\max}(\boldsymbol{X}/H_s)$.

For the family of the three models described above, if the error terms e_i are assumed to be normally distributed, then given observations $\boldsymbol{X} = x_1, x_2, \ldots, x_n$, the maximum likelihoods are inversely proportional to the same power ν [$\nu = (n-1)/2$] of the corresponding residual sums of squares obtained by least squares fitting of the models to the observations. These are:

Model 1:

$$L_{\max}1 = L_{\max}(\boldsymbol{X}/x_1, r = 0, \beta = 1) \propto \left[\sum_{i=1}^{n-1} (x_{i+1} - x_i)^2\right]^{-\nu}. \quad (5)$$

Model 2:

$$L_{\max}2 = L_{\max}(\boldsymbol{X}/x_1, \hat{r}, \beta = 1) \propto \left[\sum_{i=1}^{n-1} (x_{i+1} - x_i)^2 - (x_n - x_1)^2/(n-1)\right]^{-\nu}, \quad (6)$$

where

$$\hat{r} = (x_n - x_1)/(n-1).$$

Model 3:

$$L_{\max}3 = L_{\max}(\boldsymbol{X}/x_1, \hat{r}, b) \propto \left[\sum_{i=1}^{n-1} (x_{i+1} - m_2)^2 - b\sum_{i=1}^{n-1} (x_i - m_1)(x_{i+1} - m_2)\right]^{-\nu}, \quad (7)$$

where $\hat{r} = m_2 - bm_1$ (see Eq. 4 for definition of m_1, m_2, and b). Eqs. 5, 6, 7 give the following results:

i) To test model 1 against model 2, the appropriate likelihood ratio test-statistic is $(x_n - x_1)^2$, or equivalently $(x_n - x_1)$. This is as expected, for the maximum likelihood estimator of the drift parameter r is given by $\hat{r} = (x_n - x_1)/(n-1) = \sum_{i=1}^{n-1} d_i/(n-1) = \bar{d}$. It is readily shown that the statistic $T(1, 2)$ to test model 1 against model 2, is given by

$$T(1, 2) = (x_n - x_1)/\sqrt{\sum_{i=1}^{n-1} (x_{i+1} - x_i)^2},$$

which has a t distribution with $(n-1)$ degrees of freedom.

ii) To test model 1 against model 3, the appropriate likelihood ratio test-statistic is

$$T(1, 3) = \left[\sum_{i=1}^{n-1} (x_{i+1} - m_2)^2 - b\sum_{i=1}^{n-1} (x_i - m_1)(x_{i+1} - m_2)\right] \Big/ \sum_{i=1}^{n-1} (x_{i+1} - x_i)^2,$$

which is comparable to Bulmer's R, except that:

a) in his statistic, R, Bulmer uses $\sum_{i=1}^{n} (x_i - \bar{x})^2$ instead of $\sum_{i=1}^{n-1} (x_{i+1} - m_2)^2$, but this difference is unimportant;

b) Bulmer appears to omit the second term in the numerator. This term, $b \sum_{i=1}^{n-1} (x_i - m_1)(x_{i+1} - m_2) = b^2 \sum_{i=1}^{n-1} (x_i - m_1)^2$, is the "sum of squares due to regression" in the regression of x_{i+1} upon x_i. Under model 1, the expected value of $b \approx 1$, and hence the expected value of this term is nearly $\sum_{i=1}^{n-1} (x_i - m_1)^2$, which is not negligible unless x_i's are all nearly constant, in which case there will be no marked trend in time. Thus, for a particular data set $x_1, x_2, \ldots x_n$, if there is no trend in data, $\sum_{i=1}^{n-1} (x_i - m_1)^2$ and the calculated value of b will both be small (we show this later), and hence the omission of this second term will be less serious. On the other hand, if there is a strong trend in data, both $\sum_{i=1}^{n-1} (x_i - m_1)^2$ and the calculated value of b will be large, making the omission of this second term an unacceptable distortion. Obviously, if the x_i values show a trend in time, Bulmer's omission of the second term in the numerator of $T(1, 3)$ amounts to a distortion of the likelihood ratio statistic. In this case, Bulmer's R will be dominated by the numerator $\sum_{i=1}^{n} (x_i - \bar{x})^2$, which will tend to be large, and so R will be large. Thus, in the presence of trend, Bulmer's test will tend to fail to reject the null hypothesis of density-independence. This was observed by Slade (1977) and Vickery and Nudds (1984), in their simulation studies.

iii) To test model 2 against 3, the appropriate likelihood ratio test-statistic is

$$T(2, 3) = \frac{\sum_{i=1}^{n-1} (x_{i+1} - m_2)^2 - b \sum_{i=1}^{n-1} (x_i - m_1)(x_{i+1} - m_2)}{\sum_{i=1}^{n-1} (x_{i+1} - x_i)^2 - (x_n - x_1)^2/(n - 1)}$$

The sampling distribution of the statistic $T(2, 3)$ is not tractable mathematically, but it can be shown that this statistic is equivalent to using $(1 - r^2_{dx})$, where r_{dx} is the correlation coefficient between d_i and x_i values (Appendix). As we are concerned only with negative density-dependence (see Existing Methods), r_{dx} rather than r^2_{dx} is the appropriate statistic, small values of r_{dx} indicating density-dependence.

The hypothesis testing procedure is thus based upon the likelihood of the observations having arisen from a density-independent population, as described by model 1 or 2, or from a density-dependent population, for which, like all other researchers, we use model 3. For the null hypothesis of no density-dependence, it is always preferable to use model 2, rather than model 1 as is used by Bulmer, and Vickery and Nudds, for model 1 is a particular case of model 2. Thus, it is the test-statistic $T(2, 3)$ that is preferred to the test-statistic $T(1, 3)$. However, under the randomization test, these two statistics give identical results, because they have the same numerator, and because the denominators are constant under the randomization procedure.

Simulations

Comparison of randomization test with other tests

The randomization test, Bulmer's test, and Vickery and Nudds' test were compared in trials using data known to be from density-independent or density-dependent populations. For the randomization test, in addition to using the likelihood ratio statistic (r_{dx}), we have also used the slope statistic, b, which has featured widely in the literature, for comparative purposes. The results presented here (Tables 1, 2, and 3) are from computations carried out on the University of Cambridge Computer Laboratory's IBM 3081 mainframe computer. We used Numerical Algorithms Group's (1984) FORTRAN subroutine G05DDF to generate random normal variates with specified mean and variance, and the subroutine G05EHF to perform random permutations of the integral suffices of the d_i values for the randomization test. The same computations were carried out on a BBC Model B microcomputer, but using the random number generators described by Vickery and Nudds. The two independent sets of results were very similar; we present only the IBM mainframe results.

Data from density-independent populations.—Two hundred sets of density-independent data were generated using the random walk model (Eq. 1), with e_i as normal independent variates with mean = 0 and variance = 0.01, and with n (the number of census points) = 10.

For each data set, the null hypothesis of density-independence was tested using Bulmer's test, Vickery and Nudds' test, and the randomization test using the test-statistics r_{dx} and b. Both Vickery and Nudds' test and the randomization test require the generating of further appropriate simulated data sets, and for each of these two tests, and each of the 200 data sets, we used 100 further simulated data sets. Thus, these computations amounted to considering 200 + (200 × 100) for Vickery and Nudds' test +(200 × 100) for the randomization test = 40 200 data sets, each of 10 census points. We consider this extent of simulations as adequate for our purpose, which is to demonstrate practically the validity of our theoretical arguments.

The results are summarized in Table 1, in which the 200 data sets are classified by the observed range $x_n - x_1$. The observed range is a convenient measure of trend; it is also a *sufficient* statistic (i.e., it contains all the required information) to estimate the drift param-

TABLE 1. The frequency distribution of the probability that the observed data set is from a density-independent population, based upon 200 data sets from the random walk model (Eq. 1) with 10 census points. The testing is carried out by three different procedures. Results are classified by the total displacement values (observed range) $|x_n - x_1|$, a convenient measure of trend.

Total displacement $\lvert x_n - x_1 \rvert$	Mean slope $\bar{b}$ ± SE*	Bulmer's test				Vickery and Nudds' test				Randomization test using statistic T ($T = t$)				($T = r_{dx}$)				($T = b$)			
		Probability intervals† 1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
<0.1	0.30 ± 0.04	19 (6)‡	11	8	1	14 (4)	12	11	2	12 (2)	10	5	12	11 (2)	10	8	10
0.1–0.2	0.44 ± 0.04	11 (3)	16	14	3	12 (2)	14	14	4	9 (2)	12	15	8	8 (4)	17	9	10
0.2–0.3	0.62 ± 0.04	3 (0)	7	21	15	9 (2)	12	10	15	12 (3)	11	13	10	6 (2)	15	14	11
0.3–0.4	0.69 ± 0.05	1 (0)	6	9	19	7 (2)	8	6	14	11 (2)	7	8	9	12 (2)	6	8	9
>0.4	0.83 ± 0.04	1 (0)	0	3	32	9 (2)	2	7	18	12 (2)	8	7	9	12 (2)	10	5	9
	Total	35 (9)	40	55	70	51 (12)	48	48	53	56 (11)	48	48	48	49 (12)	58	44	49

* Mean slope $\bar{b}$ is the average of the slopes of x_{i+1} on x_i over the data sets in the given displacement class.
† The probability interval values are 1: 0–<0.25; 2: 0.25–<0.50; 3: 0.50–<0.75; 4: 0.75–1.0.
‡ The numbers in parentheses show the number of cases when the null hypothesis of density independence is rejected at 5% level of testing.

eter r in model 2 (see Eq. 6). In the randomization tests, this statistic remains constant through all simulations because the random permutations of the d_i values leave x_1 and $x_n = x_1 + \sum_{i=1}^{n-1} d_i$ unchanged.

If the tests are satisfactory, we would expect the four frequencies for each displacement class to be comparable, because for each testing procedure the probability intervals (1, 2, 3, 4) are equal in width, i.e., these frequency distributions should be uniform. If the frequencies are examined separately for each displacement class, it is seen that for Bulmer's test and Vickery and Nudds' test, the distributions are highly positively skew for low values of $|x_n - x_1|$ (rows 1 and 2), and as the displacement values increase (rows 3, 4, 5) the distributions change to being negatively skew. Examining the results at the commonly used 5% significance level, we expect 10 out of 200 data sets to be judged as significantly different from those arising from a density-independent population. The realized numbers of 9, 12, 11, and 12 for the four tests are thus satisfactory, but when their breakdown by the displacement values is examined, only the randomization tests yield results independent of displacement class. Thus, out of 39 data sets with range <0.1, Bulmer's test and Vickery and Nudds' test give respectively 6 and 4 significant results, i.e., 15 and 10%, respectively, instead of the "expected" 2 (5%), as in both the randomization tests. The results for Bulmer's test are generally more extremely affected by trend (displacement) than those for Vickery and Nudds' test.

Thus, both Bulmer's test (as expected) and Vickery and Nudds' test (contrary to their claim) are influenced by the presence of trend in the observed values $x_1, x_2, \ldots, x_n$. If the observed values show no marked trend in time, both these test procedures are more likely to identify the data wrongly as having arisen from a density-dependent population. Hence, if the observations from a density-independent population show a marked time trend, these two tests are likely to reject the null hypothesis in fewer than the expected ($\alpha \times 100$)% of cases. To verify this, the computations for Table 1 were repeated, but using the density-independent model 2 with $r = 0.4$, i.e., using the model $x_{i+1} = 0.4 + x_i + e_i$. With the inclusion of the drift parameter $r = 0.4$ and with $n = 10$, the expected value of $|x_n - x_1| = 9 \times 0.4 = 3.6$. As expected, the frequencies corresponding to the four probability intervals (Table 2) are highly negatively skewed for Bulmer's and Vickery and Nudds' tests, but the randomization test yields satisfactory results.

Data from density-dependent populations.—The type, method, and the extent of computations were exactly the same as for the data arising from density-independent populations, but we now used the density-dependent model 3 with $r = 0.4$ and $\beta = 0.8$ (i.e., we used the model $x_{i+1} = 0.4 + 0.8x_i + e_i$ with e_i as independent normal variates with mean = 0 and variance = 0.01, and with $n = 10$). For this population the expected value of $x = \mu = 2$. Since $r = 0.4$, and $\beta = 0.8$, it will be seen that $r = \mu(1 - \beta)$. Whatever the initial value x_1, such a population will eventually fluctuate around the expected value of 2. Thus, while the comparison of the four tests for the density-independent population in the last section did not require any consideration about the magnitude of the initial value x_1, for the present case of the density-dependent population, with a finite value of $n = 10$, the results are dependent upon the choice of x_1. If we use x_1 = the expected value of $x = 2.0$, then the generated observations $x_1, x_2, \ldots, x_n$ will tend to fluctuate around 2 with the observed trend close to zero, while a choice of a very low or high value of x_1 will tend to yield data with a marked positive or negative trend, respectively.

Using the above model, we generated three series of

TABLE 2. The frequency distribution of the probability that the observed data set is from a density-independent population, based upon 200 data sets from the density-independent model 2 (Eq. 2) with $r = 0.4$, i.e., $x_{i+1} = 0.4 + x_i + e_i$.

Procedure used	Probability intervals†			
	1*	2	3	4
Bulmer	0 (0)	0	0	200
Vickery and Nudds	11 (4)	11	21	157
Randomization: r_{dx}	51 (12)	47	59	43
Randomization: b	53 (11)	48	55	44

* Expected number of significant results ($\alpha = .05$) = 10; observed number given in parentheses.
† Probability intervals as in Table 1.

200 sets of density-dependent data corresponding to initial values of x_1 as 1.0, 2.0, and 3.0.

The results are presented in Table 3. Since the observations are generated using the density-dependent model (Eq. 3), we would desire the test procedure to reject the null hypothesis of density-independence as often as possible. For the data generated with the starting value of $x_1 = 2$, both Bulmer's test and Vickery and Nudds' test produce more significant results than did the randomization tests (21 and 18, against 12 and 15). However, if the initial value of x_1 is taken well away from the expected value of x, Bulmer's test performs totally inadequately, with no significant results, while Vickery and Nudds' test produced 48 and 29 significant results for $x_1 = 1.0$ and $x_i = 3.0$, respectively. The randomization tests, using the statistics r_{dx} and b, respectively, successfully identified 76 and 50 significant results for $x_1 = 1.0$, and 55 and 38 significant results for $x_1 = 3.0$.

GENERALIZATION OF VICKERY AND NUDDS' TEST

Vickery and Nudds' procedure is superior to that of Bulmer and it is possible to improve their simulation procedure further. They use the test statistic $t = (b_{21} - 1)/$(standard error of b_{21}) (W. L. Vickery, *personal communication*). Following the notation used in the Appendix, and bearing in mind that the variance of b_{21} is estimated, via regression analysis, by (residual mean square)/S_{11}, it follows that

$$t = \sqrt{n-3}(b_{21} - 1)/\sqrt{(s_{22} - b_{21}{}^2 s_{11})/s_{11}},$$

from which

$$t = \sqrt{n-3}\, r_{dx}/\sqrt{1 - r^2_{dx}},$$

which is a monotonic transformation of r_{dx}. In other words, Vickery and Nudds' statistic is effectively the same as the test statistic we propose in our randomization procedure. However, the two methods use entirely different procedures to generate simulated populations for testing for the presence of density-dependence.

The simulation procedure of Vickery and Nudds is unsatisfactory and can be improved. They use a complex variance expression developed in their Appendix 1. This is unnecessary, as the correlation between any two variables x and y is invariant under any change of scale or origin for either variable. Thus Vickery and Nudds' procedure can be simplified by using an arbitrary starting value for the simulations

$$x_{i+1} = x_i + \delta_i,$$

where δ_i values are normally distributed with zero mean and *any* constant variance.

The proposal described above achieves computational simplicity. To improve the procedure itself, it is necessary to adopt the general density-independent model 2: $x_{i+1} = r + x_i + e_i$, thus taking any displacement of the population into account. This generalization of Vickery and Nudds' approach is as follows

TABLE 3. The frequency distribution of the probability that the observed data set is from a density-independent population, based upon 200 data sets from the density-dependent model (Eq. 3), with 10 census points. The testing is carried out by three different procedures.

Starting value of x_1*	Bulmer's test				Vickery and Nudds' test $T = t$				Randomization test using statistic T: $T = r_{dx}$				$T = b$			
	Probability intervals†															
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
1.0 (positive trend)	0 (0)‡	1	5	194	103 (48)	49	25	23	164 (76)	27	6	3	162 (52)	30	5	3
2.0 (no trend)	86 (21)	51	39	24	68 (18)	59	46	27	54 (12)	56	42	48	59 (15)	50	46	45
3.0 (negative trend)	0 (0)	0	4	196	96 (29)	54	29	21	159 (55)	26	12	3	139 (38)	45	13	3

* The expected value of x is 2.
† Probability intervals as in Table 1.
‡ The numbers in parentheses show the number of cases when the null hypothesis of density-independence is rejected at the 5% level of testing.

TABLE 4. Results corresponding to those in Tables 1, 2, and 3, using a generalization of Vickery and Nudds' procedure to test the null hypothesis $x_{i+1} = r + x_i + e_i$ against the alternative hypothesis $x_{i+1} = r + \beta x_i + e_i$, ($\beta < 1$) . . . . (see Generalization of Vickery and Nudds' Test).

Total displacement $\lvert x_n - x_1 \rvert$	Probability intervals* 1	2	3	4
a) Compare results with Table 1 (density-independent population: no drift)				
<0.1	12 (3)	14	12	1
0.1–0.2	13 (2)	15	12	4
0.2–0.3	10 (3)	14	14	8
0.3–0.4	11 (2)	8	6	10
>0.4	12 (3)	10	4	10
Total	58 (13)	61	48	33
b) Compare with Table 2 (density-independent population: drift = 0.4)				
	47 (12)	47	63	43
c) Compare with Table 3 (density-dependent populations)				
Starting value				
1.0	153 (64)	35	9	3
2.0	70 (19)	62	47	21
3.0	153 (56)	31	15	1

* Probability intervals as in Table 1.

a) Given observations $x_1, x_2, \ldots, x_n$, calculate the statistic t (or r_{dx})
b) Under $H_0: x_{i+1} = r + x_i + e_i$ where $e_i \approx N(0, \sigma^2)$ the maximum likelihood estimate of r is $\hat{r} = (x_n - x_1)/(n - 1) = \bar{d}$. Since $x_{i+1} - x_i = d_i = r + e_i$, an estimate of σ^2 is $\sigma^2 = \sum_{i=1}^{n-1} (d_i - \bar{d})^2/(n - 2)$. Hence, use $x'_1 = x_1$, as an arbitrary starting value, and generate $x'_{i+1} = \hat{r} + x'_i + \Delta_i$; where Δ_i values are normally distributed with zero mean and variance $\hat{\sigma}^2$.

(c) and (d), as for the randomization procedure (see Proposed Randomization Test).

The results using this generalization of Vickery and Nudds' procedure (Table 4) are much improved. In particular the frequency distribution in the case of density-independence data with trend (Table 4b) is satisfactory. However, in Table 4a, the frequencies 1 and 4, in the last column of rows 1 and 2, are extremely small, indicating a possible weakness of this generalized approach if the displacement (trend) is small.

Discussion and Conclusions

The fact that Bulmer's test is adequate only if the population shows no growth is known from the empirical studies by Slade and by Vickery and Nudds. The likelihood ratio statistic, $T(1, 3)$, derived in this paper shows why this is the case. Bulmer's statistic R is an approximation to the likelihood ratio statistic, but the approximation is good only if in the linear regression of x_{i+1} upon x_i, the sum of squares due to regression is negligible; this is so, only if there is no trend in x_i values in time. We emphasize that the likelihood ratio statistic of greater interest is given by $T(2, 3)$.

Vickery and Nudds claim (1984:102) that their simulation regression test is acceptable for both growth and nongrowth populations. However, our results show that Vickery and Nudds' test is also influenced by the presence of trend in x_i values (Tables 1 and 2). We have shown (Table 1, columns 1 and 2) that the calculated slope b of the regression of x_{i+1} on x_i tends to be small if the trend in x_i values in time is small. Vickery and Nudds' test statistic t (or r_{dx}) is closely related to b and also has this general property. Thus when the trend in the observed data is small, a likely small value of the test statistic from the observed data will be compared with a wide spectrum of values from the simulated data consisting of a full range of random walks with varying displacements. This results in the high frequency of "detection" of density-dependence in data without trend and, conversely, to a degree of failure to detect density-dependence in data with trend.

Our results (Table 2) for the data arising from the density-independent model (Eq. 2) further confirm the strong tendency in Bulmer's test and Vickery and Nudds' procedure to fail to reject the null hypothesis of density-independence if the data show a trend.

When we consider the results (Table 3) for the density-dependent model (Eq. 3), it is then not surprising that Bulmer's and Vickery and Nudds' approach succeed in rejecting the null hypothesis of density-independence if the starting value of x_1 is taken to be 2.0, which ensures an almost zero trend in the x_i values. On the other hand, if $x_1 = 1$ or 3, inducing an upward or downward trend, Bulmer's test fails to identify the density-dependence in the data, while the detection rate using Vickery and Nudds' procedure is low. If the starting value of x_1 is taken to be 2.0, the small range of the resulting x_i values should make the problem of detecting density effects inherently difficult, as shown by the results for the randomization tests.

The generalization of Vickery and Nudds' test, developed in this paper, largely overcomes the difficulties associated with trend, but does not do so entirely, e.g., once the data have been observed to have a low trend. In addition, the assumption of normality, implicit in Vickery and Nudds' proposal and in our generalization of this proposal, is satisfied in our simulations (we have generated our observations using $x_{i+1} = r + x_i + e_i$, where e_i values are obtained using a random number generator yielding normal deviates). In reality, the normality assumption is unlikely to be satisfied exactly, and the generalization of Vickery and Nudds' approach, though superior to other parametric approaches, is always likely to be inferior to the distribution-free randomization procedure.

Of course, any population described by model 3, if allowed to develop unhampered and undisturbed (i.e., if the parameters of model 3 remain unchanged), will eventually fluctuate around the expected value of $\mu = r/(1 - \beta)$. However, this does not, and should not, preclude us from examining density-dependent populations with a starting value well away from μ. Many density-dependent populations may not be close to their expected mean values. Thus, a population can be displaced from its expected mean by a catastrophy caused by exceptional weather conditions. This displacement may be followed by a more gradual return towards the expected mean. If the population is studied during this period, a trend may be observed which is strongly density-dependent in a logistic manner. A similar situation may occur when an animal colonizes a new area and increases until it is limited by shortage of resources or by predation. A different cause of trend could be a change in the habitat occupied by a population, resulting in an increase or decrease in the abundance of a given resource and so in the expected abundance of the population. The situations described are not rare, isolated possibilities; in any case, many ecological studies are initiated or continued because the species concerned fall into one of these categories.

Vickery and Nudds concluded: "For practical purposes, if a researcher can decide a priori whether or not his population is growing (declining), he may choose the appropriate test" for the growing (declining) or non-growth population. This is not straightforward. The observed data can be classified objectively as arising from a population with or without trend, e.g., via a testing procedure based upon a statistic such as $T(1, 2)$ used above; as a second stage of the procedure, a suitable test-statistic, T_1 or T_2, may be used depending upon whether the population is identified as growing/declining or not. These difficulties are avoided by the randomization test, the rationale for which stems directly from the definition of density-independence, irrespective of trends in the population. The procedure is simple, distribution-free, in the sense that no specific assumptions are made about the distribution of year-to-year changes, and efficient.

The outcome of the testing procedure is necessarily restricted to choosing one or the other of the models entering into the arguments used to develop the testing procedure. However, it is possible that the observed population fluctuations may be due to the operation of an entirely different process, unconsidered by the researcher. If so, the conclusion from the hypothesis testing procedure can be misleading.

Alternative models are possible. Thus, according to Maelzer (1970), a model such as

$$x_{i+1} = x_i + e_i + ce_{i-1}, \quad (8)$$

where c is a constant, describes a density-independent process. He demonstrated that the presence of serial correlations in the d_i values also influences the calculated value of the slope, b, especially in short series of data. Obviously, if, in fact, the field population being studied were to be the outcome of model 8, then all approaches based upon the consideration of models other than model 8 (e.g., Bulmer's test, Vickery and Nudds' test, randomization tests) can yield misleading conclusions. In model 8, $d_i = (x_{i+1} - x_i)$ is independent of x_i, but d_i is correlated with d_{i-1}. If the incidence of correlated d values, in the absence of density-dependence, is common in natural populations, then Maelzer's warning (which has been ignored by subsequent workers) is potentially serious.

A further assumption, in the population models considered, is that errors of measurement of population density are absent or insignificant. This ideal is rarely, if ever, achieved in population studies. We have not studied the effect of errors of measurement on the randomization test, but it is clear that large errors, relative to changes in population density, will increase the likelihood of spurious detection of density-dependence in any test. This will be because of the introduction of first-order serial correlations in the observations (due to measurement error); the effect will be similar to the effect of model 8 discussed above.

For the reasons discussed, we suggested (see Proposed Randomization Test [d]) that if a significant result is obtained from the randomization test, then the null hypothesis of complete density-independence is "provisionally" rejected. Such a significant result must always be treated with a degree of caution. An understanding of the population processes, through life-table studies or experimental manipulation, is the only way of confirming the existence and nature of density-dependence. With these qualifications, we suggest that the randomization test, based upon the correlation statistic, r_{dx}, is now the best available test for detecting density-dependence.

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APPENDIX

To show that $T(2, 3)$

$$= \frac{\sum_{i=1}^{n} (x_{i+1} - m_2)^2 - b \sum_{i=1}^{n-1} (x_i - m_1)(x_{i+1} - m_2)}{\sum_{i=1}^{n-1} (x_{i+1} - x_i)^2 - (x_n - x_1)^2/(n - 1)}$$

$$= 1 - r^2_{dx}$$

where r_{dx} = correlation coefficient between d_i and x_i values.

Notation

$$S_{11} = \sum_{i=1}^{n-1} (x_i - m_1)^2,$$

$$S_{22} = \sum_{i=1}^{n-1} (x_{i+1} - m_2)^2,$$

$$S_{dd} = \sum_{i=1}^{n-1} (d_i - \bar{d})^2$$

$$S_{12} = \sum_{i=1}^{n-1} (x_i - m_1)(x_{i+1} - m_2),$$

$$S_{d1} = \sum_{i=1}^{n-1} (d_i - \bar{d})(x_i - m_1)$$

b_{21} = regression slope of x_{i+1} upon $x_i = S_{12}/S_{11}$
b_{d1} = regression slope of d_i upon $x_i = S_{d1}/S_{11}$

Results

If $x_{i+1} = r + \beta x_i + e_i$, then $x_{i+1} - x_i = r + (\beta - 1)x_i + e_i$. Hence

$$b_{d1} = b_{21} - 1 \quad \text{(A.1)}$$

Denominator, D, of $T(2, 3)$

$$= \sum_{i=1}^{n-1} (d_i - \bar{d})^2 = S_{dd} \quad \text{(A.2)}$$

$$= \sum_{i=1}^{n-1} [x_{i+1} - x_i) - (m_2 - m_1)]^2$$

$$= \sum_{i=1}^{n-1} [(x_{i+1} - m_2) - (x_i - m_1)]^2$$

$$= S_{22} + S_{11} - 2S_{12} \quad \text{(A.3)}$$

Since $S_{12} = b_{21}S_{11}$, from (A.2) and (A.3),

$$S_{22} = S_{dd} - S_{11} + 2b_{21}S_{11} \quad \text{(A.4)}$$

Numerator, N, of $T(2,3)$

$$= S_{22} - b_{21}S_{12}$$
$$= S_{22} - b_{21}^2S_{11}$$

which, using Eq. A.4

$$= S_{dd} - S_{11} + 2b_{21}S_{11} - b_{21}^2S_{11}$$
$$= S_{dd} - S_{11}(b_{21} - 1)^2$$

which, using Eq. A.1

$$= S_{dd} - S_{11}b_{d1}^2 \quad \text{(A.5)}$$

Finally, from Eqs. A.2 and A.5,

$$T(2,3) = \frac{N}{D} = 1 - \frac{S_{11}}{S_{dd}}b_{d1}^2 = 1 - r_{dx}^2.$$