Detection of density-dependent effects on caribou numbers from a series of census data

François Messier

Department of Biology, University of Saskatchewan, Saskatoon, Sask., Canada S7N 0W0

Abstract: The main objective of this paper is to review and discuss the applicability of statistical procedures for the detection of density dependence based on a series of annual or multi-annual censuses. Regression models for which the statistic value under the null hypothesis of density independence is set *a priori* (slope = 0 or 1), generate spurious indications of density dependence. These tests are inappropriate because low sample sizes, high variance, and sampling error consistently bias the slope when applied to a finite number of population estimates. Two distribution-free tests are reviewed for which the rejection region for the hypothesis of density independence is derived intrinsically from the data through a computer-assisted permutation process. The "randomization test" gives the best results as the presence of a pronounced trend in the sequence of population estimates does not affect test results. The other non-parametric test, the "permutation test", gives reliable results only if the population fluctuates around a long-term equilibrium density. Both procedures are applied to three sets of data (Pukaskwa herd, Avalon herd, and a hypothetical example) that represent quite divergent population trajectories over time.

Keywords: density dependence, census, randomization test, permutation test

Rangifer, Special Issue No. 7: 36–45

Introduction

Population studies of ungulates generally aim at identifying causes of population fluctuations, and density-dependent effects that lead to population regulation (Messier 1991a, b). The first objective requires the investigation of processes that quantifiably influence the population rate-of-increase, hence revealing their *limiting effect.* The second objective is more specific; it addresses density dependence of dominant population processes, such as food competition, predation, parasitism, and dispersal, to assess their *regulatory effect* on animal numbers (Fowler 1987; Messier 1989; Sinclair 1989). Density dependence may be revealed by analysis of changes in sources of mortality with population density (Sauer and Boyce 1983; Messier and Crête 1984, 1985; Skogland 1985, 1986; Freeland and Choquenot 1990). Alternatively, density dependence can be assessed at the population level using a series of census data (Vickery and Nudds 1984; Gaston and Lawton 1987; Pollard *et al.* 1987; Reddingius and den Boer 1989).

The population dynamics of caribou or reindeer *(Rangifer tarandus)* has been reviewed by many authors in recent years (Bergerud 1980, 1983; Leader-Williams 1980; Skogland 1985, 1986, 1990; Messier *et al.* 1988). Food exploitation, predation, and winter snow accumulation have been identified as primary limiting factors, although most authors stressed that the respective impacts of these agents on population growth likely differ according to caribou densities, presence of alternate prey, geographic region, and environmental factors (e.g., Van Ballenberghe 1985; Bergerud and Ballard 1988). However, the density relationships of dominant causes of mortality, primarily those involving biotic interactions, are still poorly documented (Messier *et al.* 1988). This lack of information continues to restrict our capacity to empirically understand the demography of caribou in North America, particularly the mechanisms involved in the regulation of caribou numbers.

The principal objective of this paper is to review and discuss the applicability of statistical methods for the detection of density dependence based on a series of annual or multi-annual censuses. Such analyses would be warranted when the density relationship of individual causes of mortality cannot be assessed due to limited information. Yet, the detection of overall density dependence would imply that one or a number of mortality agents reduce the population rate-of-increase at elevated densities, and *vice versa.* Mechanisms of population regulation are exhibited only when density dependence actually operates, not during periods of unlimited growth. Therefore, such tests may suggest the most appropriate time period to initiate a demographic study aimed at revealing feedback mechanisms in caribou population dynamics.

Tests of density dependence

The hypotheses

An animal population is said to be density independent if its growth rate is independent of the density of the population itself. Let N_t be the size of an animal population at a specific time in the annual cycle. A simple model of density independence is:

$$X_{t+1} = r + X_t + \epsilon_t \qquad [1]$$

where $X_t = \ln(N_t)$ $(t = 1, 2, ..., n)$, ϵ_t is an independent normal random variable with mean zero and variance σ^2, and r denotes a "drift" factor. A population governed by [1] follows a random walk through time with and average drift of r; there is no tendency for the population to return to a long-term equilibrium value.

An animal population is said to be density dependent if its growth rate is correlated with its size. The correlation must be negative to create population stabilization. A model of density dependence frequently cited in the literature takes the following form:

$$X_{t+1} = r + \beta X_t + \epsilon_t \qquad [2]$$

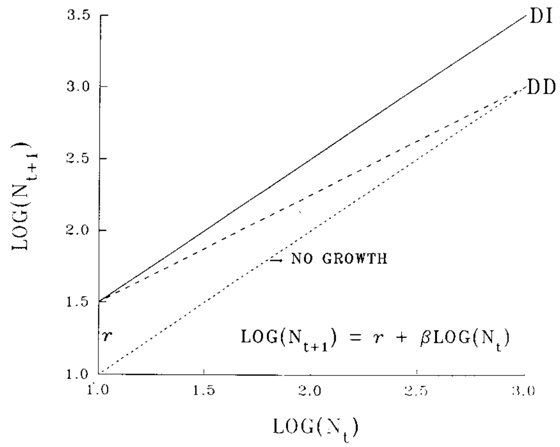

Figure 1. Test of density dependence proposed by Morris (1959, 1963), when applied to a series of censuses (N_t). It is hypothesised that $\beta = 1$ for a density independent (DI) population, and $\beta < 1$ for a density dependent (DD) population.

where β is a constant reflecting the degree of density dependence, and r, X_t, and ϵ_t conform to model [1]. Here, the population growth rate depends upon X_t when β #1. If $\beta = 1$, then model 2 converges to model 1. A population governed by [2], when $\beta < 1$, will tend to fluctuate around an expected value of $e^{r/(1-\beta)}$ (Fig. 1), which can be taken as the ecological carrying capacity (KCC, Macnab 1985). The variable r represents the population rate-of-increase assuming no density dependent effects, or $r_{\max}$ as defined by Caughley (1977: 53).

Models [1] and [2] essentially form the null and the alternative hypothesis to test for the presence of density dependence at the population level. Specifically, we are asking the following question: does the sum of negative feedback mechanisms affecting population growth outweigh the sum of the positive feedback mechansisms, thus creating population regulation (Berryman *et al.* 1987; Berryman 1991)?

Regression models

Regression analysis has been used by many authors to analyse population data (review in Itô 1972, Slade 1977). A first approach, proposed by Morris (1959, 1963), consisted of regressing $\ln(N_{t+1})$ on $\ln(N_t)$ for a series of annual censuses (Fig. 1). Density-independent populations should generate a slope (β) of one, and a y-intercept equal to r (the exponential rate-of-increase). Density dependence should be indicated by $\beta < 1$. Here, β is estimated by b, the slope of the regression line computed by standard least squares procedure (Sokal and Rohlf 1981: 468). Maelzer (1970), St. Amant (1970), and Itô (1972) noted four important weaknesses to this approach: (1) a problem of autocorrelation because each estimate of population size (except the first and the last ones) is used successively as x- and y-value; (2) the test is largely unsuitable for populations with large, stochastic fluctuations in numbers; (3) a density-dependent process frequently generates a curvilinear relationship on a log-log graph because of an accelerating impact at high densities, hence producing a relationship not appropriately described by a linear regression model; and (4) a population with a low intrinsic rate-of-increase, but with potentially wide displacements in densities through time (like caribou), will always be associated with a b-value close to unity. The major weakness of this approach, however, is the assumption that b is an unbiased estimator of β, and should equal 1 for a density-independent population (i.e., the null hypothesis). Computer simulations showed that such an assumption was in fact incorrect for finite sample sizes

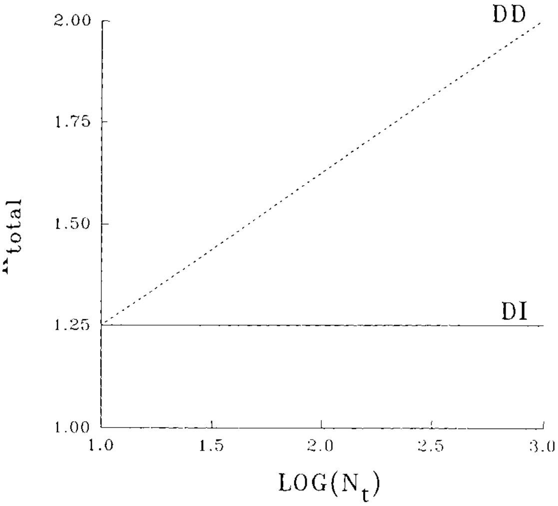

Figure 2. Test of density dependence proposed by Varley and Gradwell (1960), when applied to estimates of annual total mortality rates (k_{total}) versus log population size (N_t). Density independence (DI) should be associated with a slope of 0, whereas density dependence (DD) should be indicated by a slope greater than 0.

(Maelzer 1970; St. Amant 1970; Slade 1977). Nonregulated populations had a mean slope significantly less than 1, and the departure was greater for low sample sizes and variable data. Therefore, the test proposed by Morris often generates spurious indications of population regulation (Bulmer 1975; Slade 1977).

Varley and Gradwell (1960) presented another method for analysing serial census data which was expanded later by Krebs (1970), Watson (1970), Podoler and Rogers (1975), and Manly (1977). This method consists of expressing each source of mortality (frequently called "submortality") as the difference of $\log_{10}$ of population size before and after the submortality has acted. Each submortality, expressed here in *k*-values for a number of years, can then be plotted against log population size before its action to assess the degree of density dependence (Podoler and Rogers 1975). For age-structured populations, the analysis can be restricted to a given age class (Sinclair 1973; Clutton-Brock *et al.* 1987; Albon *et al.* 1987) or to animals of all ages (Clutton-Brock *et al.* 1985). However, a problem arises when the study animal has a complex life cycle. In such cases it is often impossible to sequence mortality agents through time because they may act simultaneously (a notable difference compared to many invertebrate species; Varley *et al.* 1973). Nonetheless, total mortality (k_{total}) from t to $t+1$ can be plottet against $\log(N_t)$ to reveal overall density dependence (Fig. 2; Itô 1972). Note that a regression expressing the rate of population growth against log population size is mathematically equivalent to a regression involving k_{total}, assuming that the loss of breeding potential is treated as a submortality (Kuno 1971; Clutton-Brock *et al.* 1985; Messier 1991a).

There is a serious empirical difficulty in applying the approach of Varley and Gradwell. The authors assumed that a density independent population should be indicated by a slope of zero when k_{total} values are plotted against log population size. Like the model of Morris described above, the slope is biased by data that contain low sample sizes and high variance (Itô 1972), thus providing erroneous evidence for density dependence. The fact that one cannot derive the *b*-value for the null hypothesis greatly hampers statistical testing for density dependence using key factor analysis.

Other regression statistics have been used to determine density dependence. These include (1) the slope of the principal axis, (2) the slope of the standard (reduced) major axis, (3) a comparison of the slope of a double regression [$\ln(N_{t+1})$ on $\ln(N_t)$, and $\ln(N_t)$ on $\ln(N_{t+1})$], and (4) the coefficient of first order serial correlation (see Varley and Gradwell 1963; Varley *et al.* 1973; Bulmer 1975; Slade 1977). However, recent Monte Carlo simulations have demonstrated that these statistics remain largely inappropriate to reveal density dependence (Slade 1977; Vickery and Nudds 1984; Pollard *et al.* 1987; Reddingius and den Boer 1989).

Non-parametric models

Pollard *et al.* (1987) suggested a simple, distribution-free approach for the detection of density dependence based on a series of annual censuses. The method uses the correlation coefficient, or the slope of the regression line, between the observed rate of population growth and population size (Fig. 3). A distinct feature of the proposed test is that the correlation coefficient under H_0 (i.e., model 1) is derived intrinsically from the data by a randomization process.

The rationale of the randomization test of Pollard *et al.* (1987) is rather simple. Let X_t (t = 1, 2, ..., n) be $\ln N_t$) for a series of annual censuses. If model 1 applies, $(X_2 - X_1)$, $(X_3 - X_2)$, ..., $(X_n - X_{n-1})$ are random fluctuations that sequentially displace the population size from X_1 to X_n. Writing $d_t = (X_{t+1} - X_t)$ (t = 1, 2, ..., n-1), the observed displacement of X_1 to X_n is due to a particular ordering of random d_t va-

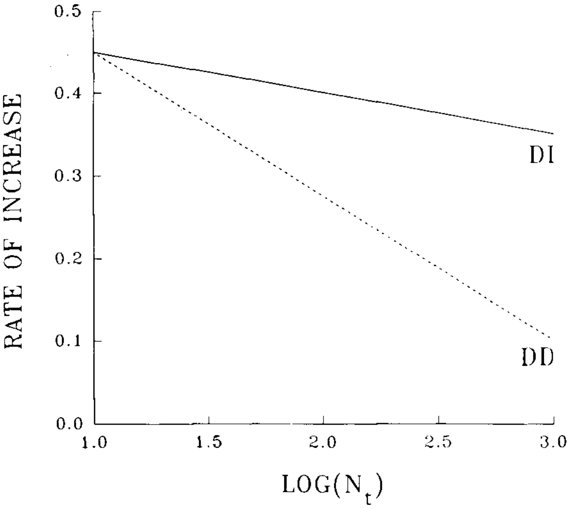

Figure 3. Illustration of the randomization test proposed by Pollard *et al.* (1987) where the annual exponential rate-of-increase is plotted against log population size (N_t). Density dependence (DD) should be indicated by a slope signifincantly lower than the slope associated with a density independent (DI) process. The density distribution of slopes under the hypothesis of density independence is derived from random permutations of the annual estimates of the population rate-of-increase.

lues. For a density independent population, d_t values could have occurred in a different order, generating a different, but equally likely, sequence of X_t values. Now we can run a large number of random permutations of d_t values to assess the correlation coefficient between d_t and X_t, symbolized here by r_{dx}. In essence, we are constructing the statistical distribution of r_{dx} under H_0, which we then use to assess to departure of the r_{dx} value computed from the original data set. If less than 5% of the r_{dx} values calculated from a randomization process are smaller than or equal to the computed r_{dx} from the original sequences of d_x, then reject the null hypothesis at 5% level of significance. In such cases, one concludes that the present survey data show evidence of density dependence.

It is important to realise that the test designed by Pollard *et al.* (1987) can be used as an alternative to a key factor analysis (Varley and Gradwell 1960) to reveal density dependence. Consider the following tautological equation:

$$k_{total,t} = r_{max} - d_t \qquad [3]$$

Clearly, k_{total} is simply the difference between the maximum rate of population growth under no ecological constraints, minus the realised growth rate for that year. The reader should notice that any loss of breeding potential is part of the total mortality in equation [3]. Thus, k_{total} and d_t are related by a constant (r_{max}), with no statistical effect on the regression analysis involving either d_t or k_{total} on X_t (Kuno 1971; Royama 1977). Monte Carlo simulations performed by the present author have indeed shown that the application of the randomization test on k_{total} values is mathematically equivalent to a test based on d_t values, with the notable exception that the slopes of the two regression lines have opposite signs (unpubl.).

Reddingius and den Boer (1989) have presented a second non-parametric test, called the permutation test, for the detection of density dependence in a series of sequential surveys. The test is closely related to the procedure described by Pollard *et al.* (1987), and for this reason I will adopt the same notation as in the previous section. Specifically, we recognize that

$$X_n = X_1 + \Sigma\, d_t, (t = 1, 2, ..., n\text{-}1) \qquad [4]$$

in which d_1, d_2, ..., $d_{n\text{-}1}$ constitute a series of random values, with a mean of r under model 1, gradually displacing population size from X_1 to X_n (above). The hypothesis of density independence states that all possible permutations of d_t values are equally likely to occur, resulting in unbounded population changes (i.e., a random walk in density through time). Under model 2, d_t values should occur in such an order that induces the population size to converge on a certain range of densities. As a measure for the amount of fluctuation under H_0 and H_1, the test uses the logarithmic range (L; $X_{max} - X_{min}$) of X_t values. The statistical question here is whether the observed logarithmic range (L_0) calculated from the original sequences of X_t values is significantly smaller than might be expected under random permutations of d_t values (i.e., a density independent population). As for the test of Pollard *et al.* (1987), the statistical distribution of L under H_0 can be assessed by performing a large number of permutations of d_t values, and then calculating L for each retrieved sequence of X_t values. The P value is based on the rank of L_0 in the population of L values generated by permutation. Specifically, P equals $a/k\text{-}1$ where a represents the number of L values smaller than or equal to L_0, and k is the number of permutations. P can also be calculated by the Mann-Whitney test (Siegel and Castellan 1988: 128–137) where one of the two samples is L_0 and the other sample is composed of the L values obtained from k permutations.

Applications

In this section, I apply the randomization test and the permutation test to three sets of data, two obtained from the literature and one hypothetical. Field data were from the Avalon caribou herd in Newfoundland (Bergerud 1971; Bergerud *et al.* 1983; Mercer *et al.* 1985; S. Mahoney, pers. comm.) and from the Pukaskwa herd in Ontario (Bergerud 1989; A. T. Bergerud, pers. comm.). The fictitious data set was generated by a computer simulation on the basis of model (2) where $n_0 = 10$, $r = 0.4$, $\beta = 0.9$, and ϵ with a mean of zero and σ of 0.05. Here, my intention is to analyse extremes of population trajectories (Fig. 4), from fluctuations within density bounds (Pukaskwa herd) to unlimited growth (Avalon herd). The hypothetical example illustrates a case of an expanding population for which the respective role of density dependence and environmental vagary on population growth requires statistical assessment (Fig. 4). Population estimates are summarized in Appendix I.

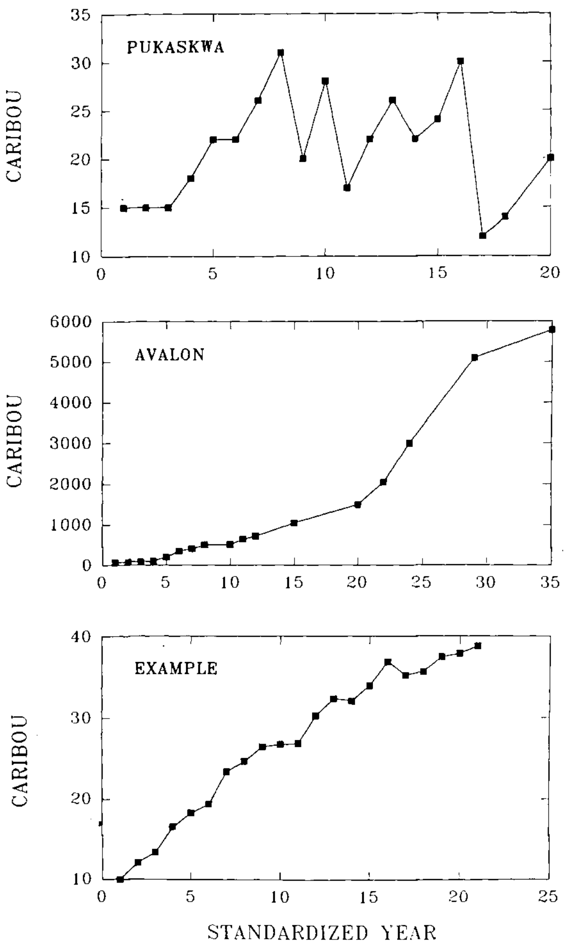

Figure 4. Fluctuations over time of caribou numbers for the Pukaskwa herd in Ontario, the Avalon herd in Newfoundland, and the computer-constructed example.

One minor modification to the randomization test was required to accommodate multiyear censuses. In these cases d_t relative to a multiyear interval was divided by the number of years in that interval to calculate correctly the exponential rate-of-increase. Such modification would affect the variance of d_t values, but not the underlying relationship between d_t and X_t. As the randomization test is a distribution-free statistical analysis (Pollard *et al.* 1987), any differences in the variance among d_t values, when annual and multiannual censuses are treated simultaneously, should not affect the test results. Note, however, that the original d_t values were used to generate the permuted sequences of X_t.

Pukaskwa herd

The Pukaskwa herd ranged from 12 to 31 animals during the period 1972–1991 (Fig. 4). The density independent model was rejected at $P < 0.05$ by both the randomization and the permutation test (Table 1). It is, therefore, quite unlikely that this series of population censuses could have originated simply from random fluctuations. The evidence for density dependence is also reflected by the decline of d_t with X_t (Fig. 5).

Avalon herd

The Avalon herd increased from 71 to 5782 animals during the period 1956–1990 (Fig. 4). Contrary to the previous example, there was a marked trend in the observed data set, typical of a population experiencing unlimited growth. The probability of rejecting the null hypothesis of density independence varied from 0.09 to 0.14 for the randomization test (Table 1). Consequently, the herd may have experienced reduced growth in recent years, but the change was not strongly expressed statistically.

The permutation test gave quite a different result. None of the permuted series of d_t produced a range of X_t values more extreme than that observed in the original sequences of X_t. In fact, this example points to a major weakness of the permutation test; the test loses its power when the population shows a pronounced trend over time. Indeed, when all d_t values are positive, as it is in this example, permutation of d_t values has no effect on the L statistic.

Example herd

The hypothetical example was constructed arbitrarily to mimic a herd recovering from a catastrophic

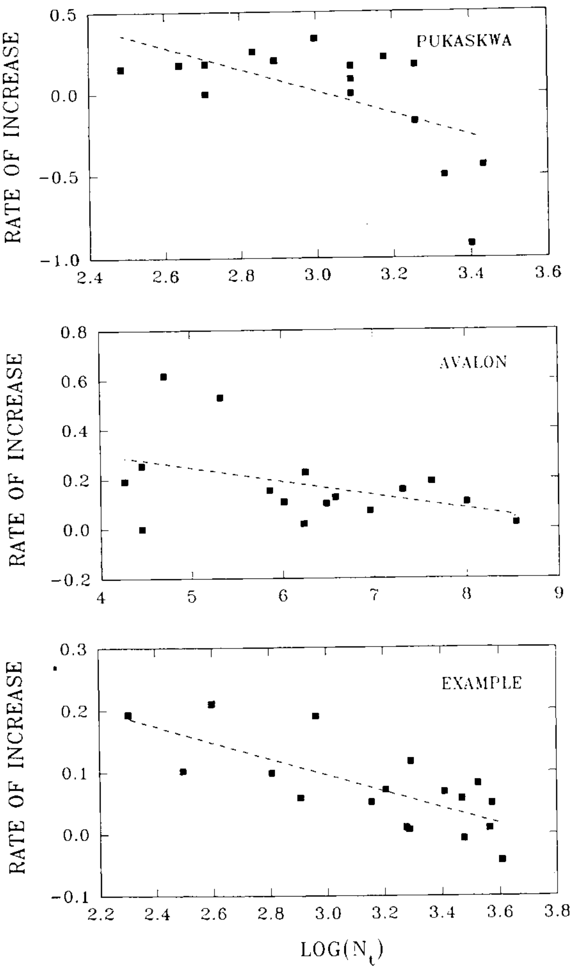

Figure 5. Relationships between the exponential rate-of-increase and log population size for the three populations illustrated in Fig. 4.

reduction in numbers. Population stabilization, in a broad sense, is not readily apparent through inspection of the graphed data (Fig. 4), and inference about density dependence needs to be assessed statistically. The randomization test clearly reveals evidence for density dependence ($P < 0.01$, Table 1). The permutation test, however, is again plagued with low power. The probability to reject H_0 is only 0.77 in spite of a clear trend in declining population growth with population size (Fig. 5). This reinforces the previous statement that the permutation test is largely ineffective when the population undergoes substantial growth without fluctuations around an equilibrium value.

Discussion

Until very recently, assessment of density dependence from a series of population estimates has been hindered by the lack of a suitable statistical procedure. All proposed regression models for which the statistic values under H_0 are set *a priori* (e.g., $b = 0$ or 1) lead to incorrect test results because of biases in the estimator of β (Morris's method, Varley and Gradwell's method), or because of low power when the population undergoes substantial growth or decline (Bulmer's test). Many authors have shown the inefficiency of these procedures (Maelzer 1970; St. Amant 1970; Kuno 1971; Itô 1972; Slade 1977; Royama 1977; Vickery and Nudds 1984; Gaston and Lawton 1987; Pollard *et al.* 1987).

The development of distribution-free, nonparametric tests by Vickery and Nudds (1984, not reviewed here), Pollard *et al.* (1987), and Reddingius and den Boer (1989) represent important contributions to population ecology. In these procedures, the rejection region for the hypothesis of density independence is defined from the data through a computer-assisted randomization process. However, these approaches are not without problems. For example, Pollard *et al.* (1987) showed that the test designed by Vickery and Nudds (1984) was affected by the total displacement in density away from a long-term equilibrium. Pollard *et al.* (1987) further demonstrated that the test proposed by Vickery and Nudds (1984) was related to the randomization test, although with a loss of generality.

The results summarized in Table 1 indicate that the permutation test as proposed by Reddingius and den Boer (1989) is largely inefficient when there is a marked trend in the series of population estimates (e.g., Avalon herd). The permutation test is best only when the study population fluctuates around a long-term equilibrium, such as the Pukaskwa herd. In view of this finding, the conclusion of Reddingius and den Boer (1989) that the permutation test has the same power as the Bulmer's test is not surprising; both tests can be applied with confidence only to a series of censuses showing no trend over time. I concur with Pollard *et al.* (1987) that, at present time, the randomization test appears to be the best available test for detecting density dependence.

Limitations of the randomization test

There are a number of factors that should be considered while interpreting results from the randomization test. I should remark, however, that none of them seem to create systematic biases that would invalidate the procedure.

Measurement errors

Errors of measurement are known to bias the slope of the regression line between d_t and X_t Maelzer

1970; Kuno 1971; Royama 1977). However, such a departure will be present in the slope calculated from the original sequence of X_t, *and* in the slopes obtained from permuted series of X_t. As the randomization test is based on the comparison of b_0 with the distribution of b values computed by permutation, the test results should be relatively insensitive to sampling error. In fact, if we assume that errors of measurement are comparable among X_t values, then the overall variance of X_t (ϵ) amounts simply to the sum of the true variance and the sampling variance. As shown by Pollard *et al.* (1987), the randomization test is not affected by differing values of ϵ, except that high overall variance makes the detection of density dependence more difficult.

Serial correlation in ϵ

An assumption of the randomization test is that ϵ_t be a sequence of independent normally distributed variates, representing the stochasticity element of the system. However, ϵ_t may be subject to serial dependence if, for example,

$$\epsilon_{t+1} = \theta\epsilon_t + \mu_t$$

where $\theta(<1)$ is the serial correlation constant and μ_t a sequence of independent normally distributed variates. Maelzer (1970) showed that any serial correlation in ϵ_t, and by extension in d_t, biases the regression slope b because changes in X_t no longer follow a first-order autocorrelation model, but instead follow a second-order autocorrelation model (Royama 1977; Reddingius 1990). However, the deviation of b from the true slope β is a function of the sign of the serial correlation parameter (θ); negative values of θ decrease b whereas positive values increase b. A carryover effect of environmental influences, if occurring at all in ungulates (Picton 1984; Messier 1991a), should be associated with positive values of θ. Thus, following a severe winter the rate-of-increase one year later should be somewhat lower than it would have been if the winter had been average. The net result of serial correlation among ϵ_t should, therefore, positively bias b calculated from the original sequence of X_t, but not b values computed from permuted sequences of X_t (because here the serial correlation among ϵ_t vanishes). The above argument suggests that the randomization test would underrate the intensity of density dependence if serial correlation occurs. However, a rejection of H_0 would reinforce the conclusion that density dependent mechanisms actually operate.

Time delay

Often, the rate of population growth at time t is dependent not only on current population size (X_t), but also on some previous population size (X_{t-1}, X_{t-2}, etc.). In these circumstances, fluctuations in animal numbers are not a realization of a piece of first-order Markov chain (Reddingius 1971). The implications of population models that follow a second or upper order process, on the sensitivity of the randomization test, have not been evaluated. Second order process, where d_t is a function of X_t and X_{t-1}, often exhibit cyclic fluctuations in numbers (Royama 1977). This implies that plots of d_t on X_t will be characterised by ellipsoidal (counterclockwise) patterns with various degrees of compression towards the major axis (May *et al.* 1974). Thus, we can safely generalise that the presence of a time delay would restrict the applications of the randomization test because of a poorly defined relationship between d_t and X_t (Itô 1972; Royama 1977; Hanski and Woiwod 1991).

Table 1. Results of the randomization and the permutation test using three statistics (T), when applied to caribou census data of Fig. 4. T were (1) the product-moment correlation coefficient (r_{dx}) and (2) the slope (b) of the regression line between population size ($\log_e$-values, X_t) and the exponential rates of growth ($d_t = X_{t+1} - X_t$), and (3) the logarithmic range (L) of X_t values ($X_{max} - X_{min}$). Results include the observed statistic values ($T = r_0$, b_0, and L_0) calculated from the original sequence of X_t values, and the mean statistic values of 500 permutated series of d_t. The estimate of P is also given, i.e., the chance to refute H_0 (density independence hypothesis) while H_0 is actually true.

	Randomization test						Permutation test		
	($T = r_{dx}$)			($T = b$)			($T = L$)		
Caribou herd	r_0	$\bar{r}$	P	b_0	$\bar{b}$	P	L_0	$\bar{L}$	P
Pukaskwa	0.589	0.415	0.06	-0.6741	-0.3530	0.03	0.949	1.436	0.03
Avalon	0.422	0.228	0.14	-0.0551	-0.0067	0.09	4.400	4.400	1.00
Example	0.762	0.197	® 0.01	-0.1299	-0.0119	® 0.01	1.354	1.361	0.77

Linear model

Pollard *et al.* (1987) developed their statistical procedure with the assumption that the relationship between d_t and X_t is linear. However, I suspect, without presenting a proof, that the randomization test can be applied on the basis of a curvilinear model when inspection of residuals along the regression line reveals a poor fit (e.g., Pukaskwa herd, Fig. 5). As for the linear model, r_{dx} of the curvilinear regression model (more appropriately R_{dx}) calculated from the original sequence of X_t, can be compared with R values obtained from permuted sequences of d_t. Here, the hypothesis of density independence should imply that all correlation constants (β_1, β_2, etc.) equal zero, assuming infinite sample sizes. For example, applying a quadratic model to the Pukaskwa data (Fig. 5) appreciably improves the fit (R_{dx} = 0.82, compared to 0.59 for the linear model), with a rejection of H_0 at $P < 0.01$.

Final remarks

Density dependence is achieved by a complex of factors whose collective action creates bounded population fluctuations (Berryman *et al.* 1987; Berryman 1991; DeAngelis and Waterhouse 1987). The question is not whether density dependence exists, for without it, the recognised persistence of most natural populations would be inexplicable (Royama 1977). Rather, the goal is to assess (1) in what range of densities do feedback mechanisms operate, and (2) what are the population processes involved? Any test of density dependence based on a series of census data cannot address the later question. For example, the abrupt decline in the rate-of-increase of the Pukaskwa herd at elevated densities (Fig. 5) may be due to food competition, emigration, or some form of interaction between the two factors. An appropriate test, however, would differentiate between a period of unlimited growth and a period during which mechanisms of population regulation are instrumental in stabilizing numbers.

Unlimited growth, often associated with a given range of densities, does not imply that prevailing population processes are largely density-uninfluenced. It is important to stress that two density-influenced factors may have antagonistic actions on population growth. For example, at Isle Royale, wolf predation and food competition exert opposite influences on moose during periods of moderate density (Messier 1991a). The net effect of two population processes with opposite actions is to make the rate-of-increase largely insensitive to changes in density (i.e., weak density dependence), a type of interaction associated with the unnecessary concept of "density-vague" population regulation (Strong 1984, 1986).

Some ecologists object to the notion of "equilibrium" that underlies most tests of density dependence (Wolda 1989). A long-term equilibrium density is simply a mathematical abstraction illustrating the fact that a population trajectory over time would tend to converge toward that equilibrium (Berryman 1991). The modern view of population dynamics recognises the lability of equilibrium points due to stochastic effects, and the fact that equilibria can be unstable or multiple (DeAngelis and Waterhouse 1987; Berryman *et al.* 1987; Sinclair 1989). In that perspective, one of the basic questions in studies of population dynamics is not simply to determine whether the density of animals is regulated or not, but to assess the relative importance of density-dependent and density-independent processes in changes of population size over time (Schaefer and Messier 1991).

Acknowledgements

The Natural Sciences and Engineering Research Council of Canada supported my work through a University Research Fellowship and an operating grant for computer analyses. B. R. Neal and J. A. Virgl provided critical comments on the manuscript.

References

Albon, S. D., Clutton-Brock, T. H. and Guinness, F. E. 1987. Early development and population dynamics in red deer. II. Density-independent effects and cohort variation. – *Journal of Animal Ecology.* 56: 69 – 81.

Bergerud, A. T. 1971. The population dynamics of Newfoundland caribou. – *Wildlife Monograph.* No. 25.

Bergerud, A. T. 1980. A review of the population dynamics of caribou and wild reindeer in North America. – In: Reimers, E., Gaare, E. and Skjenneberg, S. (eds.), *Proceedings of the 2nd International Reindeer/Caribou Symposium. Trondheim, Norway.* Direktoratet for vilt og ferskvannsfisk: 556 – 581.

Bergerud, A. T. 1983. The natural population control of caribou. – In: Bunnell, F. L., Eastman, D. S. and Peek, J. M. (eds.), *Symposium on natural regulation of wildlife populations. Forest, Wildlife and Range Experiment Station, University of Idaho, Moscow. Proceedings No. 14:* 14–61.

Bergerud, A. T. 1989. *The abundance, distribution and behaviour of caribou in Pukaskwa National Park, 1972–89.* Canada, Min. of Environment, Pukaskwa National Park.

Bergerud, A. T. and Ballard, W. B. 1988. Wolf predation on caribou: the Nelchina herd case history, a different interpretation. – *Journal of Wildlife Management.* 52: 344 – 357.

rgerud, A. T., Noland, M. J., Curnew, K. and Mercer, V. E. 1983. Growth of the Avalon Peninsula, Newfondland caribou herd. – *Journal of Wildlife Manage-ient.* 47: 989 – 998.

rryman, A. A. 1991. Stabilization or regulation: what t all means! – *Oecologia* 86: 140 – 143.

rryman, A. A., Stenseth, N. C. and Isaev, A. S. 1987. Natural regulation of herbivorous forest insect populations. – *Oecologia.* 71: 174 – 184.

ulmer, M. G. 1975. The statistical analysis of density dependence. – *Biometrics.* 31: 901 – 911.

aughley, G. 1977. *Analysis of vertebrate populations.* John Wiley and Sons, New York.

lutton-Brock, T. H., Major, M. and **Guinness, F. E.** 1985. Population regulation in male and female red deer. – *Journal of Animal Ecology.* 54: 831 – 846.

lutton-Brock, T. H., Major, M., Albon, S. D. and **Guinness, F. E.** 1987. Early development and population dynamics in red deer. I. Density-dependent effects on juvenile survival. – *Journal of Animal Ecology.* 56: 53 – 67.

eAngelis, D. L. and **Waterhouse, J. C.** 1987. Equilibrium and nonequilibrium concepts in ecological models. – *Ecological Monographs.* 57: 1 – 21.

Fowler, C. W. 1987. A review of density dependence in populations of large mammals. – In: Genoways, H. H., (ed.), *Current Mammalogy. Vol. 1.* Plenum Press, New York: 401 – 441.

Freeland, W. J. and **Choquenot, D.** 1990. Determinants of herbivore carrying capacity: plants, nutrients, and *Equus asinus* in northern Australia. – *Ecology.* 71: 589 – 597.

Gaston, K. J. and **Lawton, J. H.** 1987. A test of statistical techniques for detecting density dependence in sequential censuses of animal populations. – *Oecologia.* 74: 404 – 410.

Hanski, I. and **Woiwod. I.** 1991. Delayed density-dependence. – *Nature.* 350: 28.

Itô, Y. 1972. On the methods for determining density-dependence by means of regression. – *Oecologia.* 10: 347 – 372.

Krebs, J. R. 1970. Regulation of numbers in the great tit (Aves: Passeriformes). – *Journal of Zoology.* London. 162: 317 – 333.

Kuno, E. 1971. Sampling error as a misleading artifact in "key factor analysis". – *Research in Population Ecology.* 13: 28 – 45.

Leader-Williams, N. 1980. Population dynamics and mortality of reindeer introduced into South Georgia. – *Journal of Wildlife Management.* 44: 640 – 657.

Macnab, J. 1985. Carrying capacity and related slippery shibboleths. – *Wildlife Society Bulletin.* 13: 403 – 410.

Maelzer, D. A. 1970. The regression on log N_{n+1} on N_n as a test of density dependence: an exercise with computer-constructed density-independent populations. – *Ecology.* 51: 810 – 822.

Manly, B. F. J. 1977. The determination of key factors from life table data. – *Oecologia.* 31: 111 – 117.

May, R. M., Conway, G. R., Hassell, M. P. and **Southwood, T. R. E.** 1974. Time delays, density-dependence and single-species oscillations. – *Journal of Animal Ecology.* 43: 747 – 770.

Mercer, E., Mahoney, S., Curnew, K. and **Finlay, C.** 1985. Distribution and abundance of insular Newfoundland caribou and the effects of human activities. – *Proceedings of the North American Caribou Workshop* 2: 15 – 32.

Messier, F. 1989. Toward understanding the relationship between wolf predation and moose density in southwestern Québec. – In: Seip D., Pettigrew, S. and Archibald, R. (eds.), *Wolf-prey dynamics and management. B. C. Ministry of Environment, Wildl. Working Rep. No. 40:* 13 – 25.

Messier, F. 1991a. The significance of limiting and regulating factors on the demography of moose and white-tailed deer. – *Journal of Animal Ecology.* 60: 377 – 393.

Messier, F. 1991b. On the concepts of population limitation and population regulation as applied to caribou demography. – In: Butler, C. E. and Mahoney, S. P., (eds.), *Proceedings of the Fourth North American Caribou Workshop.* St. John's, Newfoundland: 260 – 277.

Messier, F. and **Crête, M.** 1984. Body condition and population regulation by food resources in moose. – *Oecologia.* 65: 44 – 50.

Messier, F. and **Crête, M.** 1985. Moose-wolf dynamics and the natural regulation of moose population. – *Oecologia.* 65: 503 – 512.

Messier, F., Huot, J., Le Henaff, D. and **Luttich, S.** 1988. Demography of the George River caribou herd: evidence of population regulation by forage exploitation and range expansion. – *Arctic.* 41: 279 – 287.

Morris, R. F. 1959. Single-factor analysis in population dynamics. – *Ecology.* 40: 580 – 588.

Morris, R. F. 1963. Predictive equations based on key-factors. – *Memoirs of the Entomological Society of Canada.* 32: 16 – 21.

Picton, H. D. 1984. Climate and the prediction of reproduction of three ungulate species. – *Journal of Applied Ecology.* 21: 869 – 879.

Podoler, H. and **Rogers, D.** 1975. A new method for identification of key factors from life-table data. – *Journal of Animal Ecology.* 44: 85 – 114.

Pollard, E., Lakhani, K. H. and **Rothery, P.** 1987. The detection of density-dependence from a series of annual censuses. – *Ecology.* 68: 2046 – 2055.

Reddingius, J. 1971. Gambling for existence. A discussion of some theoretical problems in animal population ecology. – *Acta Biother.* 20 (Suppl.): 1 – 208.

Reddingius, J. 1990. Models for testing: a secondary note. – *Oecologia.* 83: 50 – 52.

Reddingius, J. and **den Boer, P. J.** 1989. On the stabilization of animal numbers. Problems of testing. 1. Power estimates and estimation errors. – *Oecologia.* 78: 1 – 8.

Royama, T. 1977. Population persistence and density dependence. – *Ecological Monographs.* 47: 1 – 35.

Sauer, J. R. and Boyce M. S. 1983. Density dependence and survival of elk in northwestern Wyoming. – *Journal of Wildlife Management.* 47: 31 – 37.

Shaefer, J. A. and Messier, F. 1991. The implications of environmental variability on caribou demography: theoretical considerations. – *Proceedings of the Fifth North American Caribou Workshop, Yellowknife, N.W.T., 19–21 march 1991.*

Siegel, S. and Castellan, N. J. 1988. *Nonparametric statistic for the behavioral sciences.* McGraw-Hill Book Company, New York.

Sinclair, A. R. E. 1973. Regulation and population models for a tropical ruminant. – *East African Wildlife Journal.* 11: 307 – 316.

Sinclair, A. R. E. 1989. Population regulation in animals. – In: Cherrett, J. M., (ed.), *Ecological concepts. Blackwell Scient. Publ, Oxford: 197 – 241.*

Skogland, T. 1985. The effects of density-dependent resource limitations on the demography of wild reindeer. – *Journal of Animal Ecology.* 54: 359 – 374.

Skogland, T. 1986. Density dependent food limitation and maximal production in wild reindeer herds. – *Journal of Wildlife Management.* 50: 314 – 319.

Skogland, T. 1990. Density dependence in a fluctuating wild reindeer herd; maternal vs. offspring effects. – *Oecologia.* 84: 442 – 450.

Slade, N. A. 1977. Statistical detection of density dependence from a series of sequential censuses. – *Ecology.* 58: 1094 – 1102.

Sokal, R. R. and Rohlf, F. J. 1981. *Biometry. Second ed.* W. H. Freeman and Company, New York.

St. Amant, J. L. S. 1970. The detection of regulation in animal populations. – *Ecology.* 51: 823 – 828.

Strong, D. R. 1984. Density-vague ecology and liberal population regulation in insects. – In: Price, P. W., Slobodchikoff, C. N. and Gaud, W. S., (eds.), *A new ecology: novel approaches to interactive systems.* John Wiley and Sons, New York: 313 – 327.

Strong, D. R. 1986. Density-vague population change. – *Trends Ecol. Evol.* 1: 39 – 42.

Van Ballenberghe, V. 1985. Wolf predation on caribou: the Nelchina herd case history. – *Journal of Wildlife Management.* 49: 711 – 720.

Varley, G. C. and Gradwell, G. R. 1960. Key factors in population studies. – *Journal of Animal Ecology.* 29: 399 – 401.

Varley, G. C. and Gradwell, G. R. 1963. Predatory insects as density dependent mortality factors. – *Proceedings of the Sixteenth International Congress of Zoology.* 1: 240.

Varley, G. C., Gradwell, G. R. and Hassell, M. P. 1973. *Insect population ecology: an analytical approach.* Blackwell, Oxford.

Vickery, W. L. and Nudds, T. D. 1984. Detection of density-dependent effects in annual duck censuses. – *Ecology.* 65: 96 – 104.

Watson, A. 1970. Territorial and reproductive behaviour of red grouse. – *Journal of Reproduction and Fertility Supplement.* 11: 3 – 14.

Wolda, H. 1989. The equilibrium concept and density dependence tests: what does it all mean? – *Oecologia.* 81: 430 – 432.

Appendix I

Summary of caribou census data for the Pukaskwa herd in Ontario (Bergerud 1989, A. T. Bergerud pers. comm.) and the Avalon herd in Newfoundland (Bergerud 1971, Bergerud *et al.* 1983, Mercer *et al.* 1985, and S. Mahoney pers. comm.). Data for a hypothetical example mimicking an expanding herd are also summarized.

Pukaskwa		Avalon		Example	
N	Year	*N*	Year	*N*	Year
15	1972	71	1956	10.0	1
15	1973	86	1957	12.1	2
15	1974	111	1958	13.4	3
18	1975	206	1959	16.6	4
22	1976	350	1961	18.3	5
22	1977	409	1962	19.4	6
26	1978	508	1964	23.4	7
31	1979	518	1965	24.7	8
20	1980	650	1966	26.5	9
28	1981	720	1967	26.8	10
17	1982	1050#	1970	26.9	11
22	1983	1500#	1975	30.3	12
26	1984	2050#	1977	32.4	13
22	1985	3000	1979	32.1	14
24	1986	5099	1984	34.0	15
30	1987	5782	1990	36.9	16
12	1988			35.3	17
14	1989			35.7	18
20	1991			37.5	19
				37.9	20
				38.8	21

Estimated from Fig. 2 of Bergerud *et al.* 1983.

Printed from manuscript after editorial review.

Printed from manuscript after editorial review.