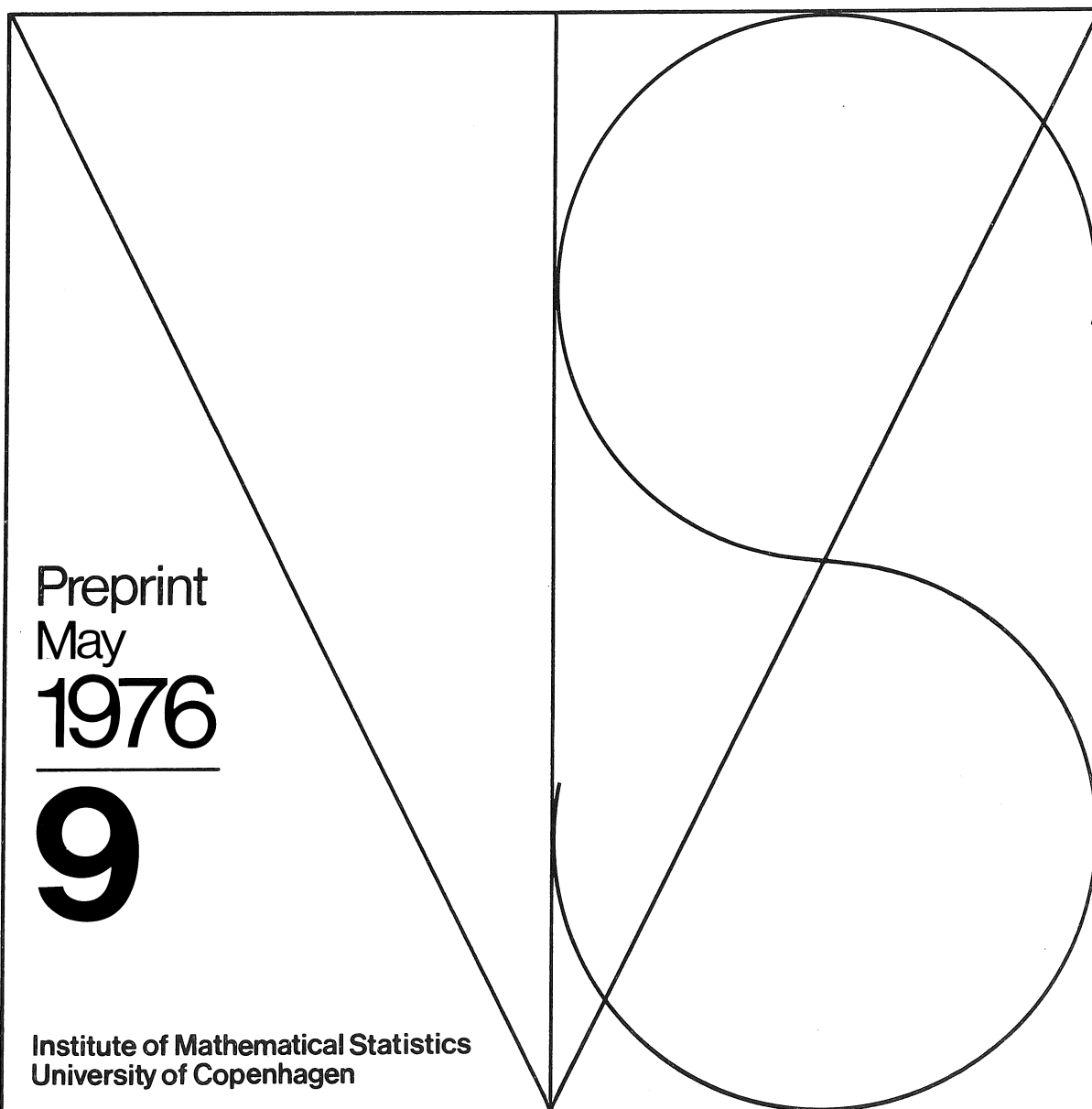Niels Keiding

Population Growth and Branching Processes in Random Environments

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POPULATION GROWT AND

BRANCHING PROCESSES

IN RANDOM ENVIRONMENTS

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Some stochastic generalizations of classical single-species population growth models are discussed from the viewpoint of branching processes with random environments. The basic theme is the interplay between environmental and sampling ("demographic") variability. Although the former will presumably most often dominate, it is possible in some cases to obtain a balance. This leads to the study of some diffusion processes from which earlier models are obtained by specialization. Two examples are presented in order to indicate some of the difficulties around direct empirical use of the models.

1. INTRODUCTION

The influence of randomly varying environments on the qualitative conclusions

of simple models in population dynamics has lately been studied by a number

of authors. We want in this paper to add some comments to this literature by

making explicit the connection to recent developments in the theory of bran-

ching processes. This approach emphasizes the interplay between environmental

and sampling (or "demographic") variability. The main conclusion is that if

these variations are of about the same magnitude per individual per time unit,

then the environmental variations will dominate in large populations, that is,

sampling variation is unimportant except as regards questions of extinction.

However, in some cases the environmental fluctuations may be assumed small so

that a balance may be obtained. It is indicated how diffusion processes may

then be obtained as approximations for large populations.

Section 2 treats the simple (Malthusian) case of unrestricted exponential

growth, with comments on age-dependent vital rates and various stochastic

models. A more detailed review was given by Keiding (1975).

The case of finite carrying capacity is studied in Section 3, via the traditional (Verhulst) logistic law and some related stochastic models, although the warnings sounded already by Feller (1939) about the arbitrariness of this approach may be more relevant than ever in the face of the current elaborate generalizations.

Although the prime purpose of this work is in obtaining qualitative conclusions we briefly sketch in Section 4 two sets of data where the question of random environmental variation seems essential to the description. These examples are not supposed to prove or disprove the models but rather to indicate how and where difficulties regarding empirical inference with such models may arise.

As a final note we should point out that there exists a large body of work on random temporal variations of the parameters of models in population genetics. Some references were given by Keiding (1975) but we shall not comment further upon this literature here.

2. UNRESTRICTED GROWTH

The simple deterministic Malthusian growth

$$(2.1) \qquad\qquad N_t = N_0 \, e^{rt}$$

may be derived from a number of increasingly complex deterministic and stochastic models. These were partly reviewed by Keiding (1975) and we shall be satisfied with a few brief remarks here. Of course, (2.1) is the solution of the differential equation $dN_t/dt = r \, N_t$, which will apply for a population where all individuals have age-independent instantaneous birth and death rates b and d with $b - d = r$. The generalization to age-dependent birth and death rates b_x and d_x dates back from the beginning of this century, see e.g. Pollard (1973, Chapter 3). In this case (2.1) holds provided the initial age

distribution is <u>stable</u>, that is, given by a density proportional to

$$e^{-rx - \int_0^x d_y dy}$$

where now r is given as the unique real solution to

$$I(r) = \int_0^\infty e^{-rx} b_x e^{-\int_0^x d_y dy} dx = 1$$

A simple stochastic model incorporating sampling variations is the linear birth-and-death process with birth and death intensities $\lambda_i = i \lambda$, $\mu_i = i \mu$. Here

$$E(X_t \mid X_0) = X_0 e^{(\lambda - \mu)t}$$

giving average Malthusian growth with $r = \lambda - \mu$. The combined effects of age-structure and sampling variations may be analyzed in a so-called age-dependent birth-and-death process (see e.g. the review by Keiding and Hoem (1976)) or via the more general branching processes reviewed by Jagers (1975) and Mode (1975). The result is that given that the average initial age distribution is of the stable form, the expected population size at time t is given by (2.1).

There are several possible approaches to the problem of incorporating random environmental variation, that is, stochastic fluctuations in the growth rate.

Several authors, including Cappocelli and Ricciardi (1974) and Tuckwell (1974) suggested adding a white noise term to the basic differential equation of the <u>deterministic</u> model, thus converting it into the stochastic differential equation

$$(2.2) \qquad dN_t/dt = (r + \varepsilon) N_t$$

with ε = white noise with variance ω^2. A basic problem is how to interpret the right hand side of this equation. According to the so-called Ito Calculus, the

solution of (2.2) is a diffusion process with infinitesimal mean and variance αx and $\omega^2 x^2$ whereas the so-called Stratonovich calculus yields the solution as the diffusion with parameters $(\alpha + \omega^2/2)x$ and $\omega^2 x^2$. The resulting <u>expected</u> population sizes at time t (conditional on the population size at time 0) are, respectively

$$N_0 e^{\alpha t} \quad \text{and} \quad N_0 e^{(\alpha + \omega^2/2)t}$$

whereas the <u>median</u> population sizes are

$$N_0 e^{(\alpha - \omega^2/2)t} \quad \text{resp.} \quad N_0 e^{\alpha t}.$$

It may be seen that $P\{0 < N_t < \infty\} = 1$ for all t and that the following extinction/explosion criteria hold (limits are almost sure).

Ito   Stratonovich

$\alpha > \dfrac{\omega^2}{2}$ $\alpha > 0$ $N_t \to \infty$

$\alpha = \dfrac{\omega^2}{2}$ $\alpha = 0$ N_t fluctuates, $\liminf N_t = 0$, $\limsup N_t = \infty$

$\alpha < \dfrac{\omega^2}{2}$ $\alpha < 0$ $N_t \to 0$ (but $N_t > 0$).

For further details concerning the alternative stochastic integration calculi we refer to Goel and Richter-Dyn (1974), Feldman and Roughgarden (1975) and their references to the theoretical literature.

It is also possible to interpret the growth parameters of the stochastic models as being themselves random in a similar fashion as in the theory of doubly stochastic Poisson processes. For Markov branching processes (including the linear birth-and-death process discussed above) this was done by Kaplan (1973). Keiding (1975) pointed out that if the net growth rate $\rho = E(\lambda - \mu) > 0$ and provided the stochastic process specifying the random birth and death rates λ and μ satisfies certain mixing conditions, then the distribution of the

normalized population size $(X_t e^{-\rho t})^{t^{-\frac{1}{2}}}$ is asymptotically that of $U e^V$ where

U and V are independent, $U = I\{X_t \neq 0\}$ and V is normal with zero mean and

variance specified only by the environmental variations. This is one mathematical version of the conventional wisdom that environmental variation outweighs sampling variation (except as regards extinction), cf. May (1973).

To arrive at a more general diffusion process, Keiding (1975) suggested the following approximation scheme, starting from a discrete-time branching process with random environments (BPRE), cf. Athreya and Karlin (1971).

Let, for each k, $Z_0(k), Z_1(k), \ldots$ be a BPRE with initial population size $Z_0(k) = k$. Assume that the environments are independent and identically distributed and let $\ell_i(k)$ be the conditional expected offspring per individual given the i'th environment. We then assume

$$E(\ell_i(k)) = 1 + \alpha/k + o(k^{-1})$$

$$Var(\ell_i(k)) = \omega^2/k + o(k^{-1})$$

and finally that τ^2, the average reproduction variance per individual, is constant. Then as $n \to \infty$, the process $Y_t(n) = Z_{[nt]}(n)/n$ will converge in distribution to a diffusion with parameters αx and $\tau^2 x + \omega^2 x^2$. Details including a complete diffusion-theoretical boundary classification were given by Keiding (1975). For $\tau^2 = 0$, the diffusion process corresponds to the Ito solution above, and an important effect of $\tau^2 > 0$ is that the _asymptotic attraction_ of the state 0 is replaced by _absorption_, or in other words: extinction in finite time is possible if and only if sampling variation is included in the model. We notice also that the diffusion approximation generalizes a classical result due to Feller (1951) who assumed constant environment ($\omega^2 = 0$).

3. FINITE CARRYING CAPACITY

The simplest and most commonly studied mathematical description of growth under limited resources is the logistic (Verhulst) model given by the differential equation

$$(3.1) \qquad dN_t/dt = r\, N_t (1 - N_t/K)$$

with solution

$$N_t = \frac{N_0\, K}{N_0 + (K - N_0)\, e^{-rt}}$$

The number of possible micromodels generalizing this basic deterministic relation is considerably larger than for the Malthusian growth model discussed above. Various birth-and-death processes have thus been proposed by Feller (1939) (see also Kendall (1949)), Bartlett (1960), and Prendiville (see e.g. Iosifescu and Taŭtu (1973)).

We shall here consider some discrete-time stochastic processes motivated by generalizations of the simple branching process reproduction scheme. Although we shall as usual use the "discrete generation" terminology, some of the results may have a more natural interpretation for time-equidistant sampling of populations with overlapping generations.

Retaining the assumption of independence of reproducing individuals, there are basically two ways of letting the density influence the growth structure: either the offspring size of each reproducing individual may be depressed under crowding or the number of reproducing individuals may be dependent on the population size. It is tempting to interpret the first of these schemes as "regulation of survival" and the second as "regulation of recruitment" although the concepts of "reproducing individuals" and "offspring size" are defined relative to the census scheme, in particular the age at which individuals are counted.

The details of these models are as follows. Working with branching process approximations to the general stochastic epidemic, Becker (1976) suggested a modification modelling density-dependent growth. Let the distribution of the offspring of each individual in a generation of size x have mean r g(x) with g(x) = max{1 - x/K,0} and some variance $\sigma^2(x)$ where one choice is $\sigma^2(x)$ constant but a more realistic one, compatible with the Poisson distribution, may be $\sigma^2(x) = \sigma^2 g(x)$.

On the other hand Sevast'yanov and Zubkov (1974) defined the so-called ϕ-branching processes by assuming that the offspring distribution is constant but that the number of (independently) reproducing individuals in a generation of size x is some function $\phi(x)$ of x, where the case $\phi(x) = x$ corresponds to the simple Galton-Watson process and $\phi(x) = a + x$ (a an integer) to a Galton-Watson process with immigration. This scheme was generalized to random ϕ by Yanev (1975).

It is possible to arrive at similar diffusion approximations for the later stages of the development of large populations as in Section 2 by appropriate choices of the parameters in these models. We proceed to show one such construction in detail and add some remarks on other possible schemes.

Consider a branching process with offspring distributions depending on the current (random) environment as well as on the size of the current generation.

The environments are assumed to vary independently with time-homogeneous distributions. The conditional mean $\ell(x)$ given the environment and the size x of the previous generation is

$$\ell(x) = 1 + m(1 - x/K).$$

Assume that the carrying capacity K is constant but that the growth rate m depends on the environment (but not on x).

To arrive at an approximating diffusion we study a series $\{Z_n(j), n = 0,1,2,...\}$, $j = 1,2,...$ of these processes with $Z_0(j) = j$ and associated carrying capacities jK. Let E_j and Var_j refer to the j'th process and assume that (in analogy with Section 2)

$$E_j(1 + m) = 1 + \alpha/j + o(j^{-1})$$

$$Var_j(1 + m) = \omega^2/j + o(j^{-1}) \quad .$$

Finally the average offspring variance τ^2 is assumed constant.

Then, letting $Y_t(n) = Z_{[nt]}(n)/n$, one obtains to the first approximation

$$E_n(Y_{t+\frac{1}{n}}(n) - Y_t(n) \mid Y_t(n) = y)$$

$$= \frac{1}{n} E_n(Z_{[nt+1]}(n) \mid Z_{[nt]}(n) = ny) - y$$

$$= \frac{1}{n}\left[1 + \frac{\alpha}{n}(1 - \frac{ny}{nK})\right] ny - y = \frac{1}{n}(\alpha y - \frac{\alpha y^2}{K})$$

and

$$Var_n(Y_{t+\frac{1}{n}}(n) - Y_t(n) \mid Y_t(n) = y)$$

$$= \frac{1}{n^2} E_n[Var\{Z_{[nt+1]}(n) \mid Z_{[nt]}(n) = ny, nt'th\ environment\}]$$

$$+ \frac{1}{n^2} Var_n[E\{Z_{[nt+1]}(n) \mid Z_{[nt]}(n) = ny, nt'th\ environment\}]$$

$$= \frac{1}{n^2} ny\tau^2 + \frac{1}{n^2} \frac{\omega^2}{n}(1 - \frac{ny}{nK})^2 n^2y^2$$

$$= \frac{1}{n}(\tau^2 y + \omega^2 y^2(1 - y/K)^2).$$

From standard diffusion approximation theory (e.g. Kurtz (1975)) it will then follow that under suitable moment conditions $Y_t(n)$ will converge in distri-

bution to a diffusion X_t with infinitesimal mean and variance $\alpha x(1 - x/K)$ and $\tau^2 x + \omega^2 x^2 (1 - x/K)^2$.

For this diffusion, the boundary 0 is <u>exit</u> if the sampling variance $\tau^2 > 0$, otherwise <u>natural</u>. If $\tau^2 > 0$, the upper boundary is ∞ and <u>natural</u>, if $\tau^2 = 0$, the infinitesimal variance is 0 at K and both 0 and K are <u>natural</u> boundaries.

These facts may be summarized as follows. When there is sampling variation $(\tau^2 > 0)$, environmental fluctuation in the growth rate $(\omega^2 > 0)$ and finite regulation term $(K < \infty)$, then the population will fluctuate over $(0, \infty)$ but is certain to go extinct sooner or later. However, this situation changes qualitatively if $\tau^2 = 0$, $\omega^2 = 0$, or $K \to \infty$.

Thus if there is no sampling variation $(\tau^2 = 0)$, the population will stay within $(0, K)$ and never go extinct. If $K \leq \omega^2/2$, however, the population size will converge to 0, otherwise there will exist a stationary distribution. The properties of the diffusion process when $K \to \infty$ were discussed in Section 2. Notice in particular that when $K = \infty$, the process need not go extinct when $\tau^2 > 0$ (it will have a positive probability of growing indefinitely if $\alpha > \omega^2/2$) and a stationary distribution will never exist for $\tau^2 = 0$.

Special cases of the diffusion process have been considered earlier. The model with $\tau^2 = 0$ is the Ito solution of a stochastic differential equation model analyzed by Levins (1969), May (1973), Tuckwell (1974), Goel and Richter-Dyn (1974) and Feldman and Roughgarden (1975). A different approach is due to Kiester and Barakat (1974). The model with no environmental variation $(\omega^2 = 0)$ may be seen as a possibly more satisfactory alternative to the mixed deterministic-stochastic model describing random variation "in the death of adults" proposed by Levins (1969) and further discussed by Tuckwell (1974) and Goel and Richter-Dyn (1974).

Notice that if the average offspring variance had been chosen as

$\tau^2 \max[(1 - x/jK), 0]$ (such as discussed above) instead of constant we would

have obtained an infinitesimal variance term of $\tau^2 x(1 - x/K) + \omega^2 x^2 (1 - x/K)^2$

and the process would have been confined to $[0, K]$ even when $\tau^2 > 0$. This

diffusion has been studied in connection with population genetics, see Kimura

(1962), cf. the discussion by Jensen (1973) and the review by Karlin and

Levikson (1974).

The above derivation assumed a randomly varying growth rate but a constant

regulation term. Fluctuations in the regulation term could also have been

studied within this framework but we shall rather indicate how one might

proceed from Yanev's generalization of Sevast'yanov and Zubkov's ϕ-branching

process. Assume that given the environment, the average number $\phi(x)$ of indi-

viduals that are allowed to reproduce in a generation of size x is given by

$\phi(x) = x - mx^2/K$ and that each of these have an average offspring of $1 + m$.

Consider a similar series of processes $\{X_n(j)\}$ as above but assume now that

in the j'th process m is constant $= \alpha/j$ (although a randomly varying m could

also be easily handled), that K is random with

and

$$E_j \left(\frac{1}{K}\right) = \frac{1}{j\kappa} + o\left(\frac{1}{j}\right)$$

$$\text{Var}_j \left(\frac{1}{K}\right) = \frac{\theta^2}{j} + o\left(\frac{1}{j}\right) \quad ,$$

and that the offspring variance τ^2 is constant. Then $Z_{[nt]}(n)/n$ will converge

in distribution to a diffusion with infinitesimal parameters $\alpha x(1 - x/\kappa)$ and

$\tau^2 x + \theta^2 x^4$. This again is a generalization of processes considered earlier

by the above mentioned authors.

4. EXAMPLES

The purpose of this section is to present two empirical examples of situations where consideration of environmental stochasticity seems unavoidable. In particular we want to indicate that a definite identification of a random component as environmental (as opposed to measurement error, or intrinsic sampling variation) will sometimes be rather difficult.

Example 1. Growth of human placenta during pregnancy.

In an effort to set up a scheme for early detection of abnormal pregnancies Winkel et.al. (1976) assumed that the plasma progesterone concentration (PPC) is proportional to the size of the placenta, at least from the 12th to 36th weeks of pregnancy. Fig.1 shows on a logarithmic scale the results of weekly measurements of PPC from the 12th to 31st week of pregnancy for one woman. S.L. Lauritzen, in his statistical appendix to the above mentioned paper, suggested using a diffusion model for unrestricted growth such as described in Section 2. Clearly, sampling variation may be disregarded for the large population of progesterone producing placenta cells. Assume that mesurement errors may be disregarded as well.   The log(PPC) may then be interpreted as obtained by equidistant sampling from a Wiener process, that is, distributed as a homogeneous process with independent normal increments. For the woman of Fig. 1, the mean and variance of the weekly increments were 0.0302 and 0.0009, respectively.

The question of the role of measurement uncertainty was approached by Lauritzen by computing the autocorrelation coefficients of the observed increments. If measurement errors were unimportant, all autocorrelations should be zero whereas one would expect a negative first order autocorrelation R_1 otherwise. The observed R_1 was .01, thus indicating that the variation in the data of Fig. 1 around the straight line could be ascribed wholly to environmental variations in the growth rate of the placenta.
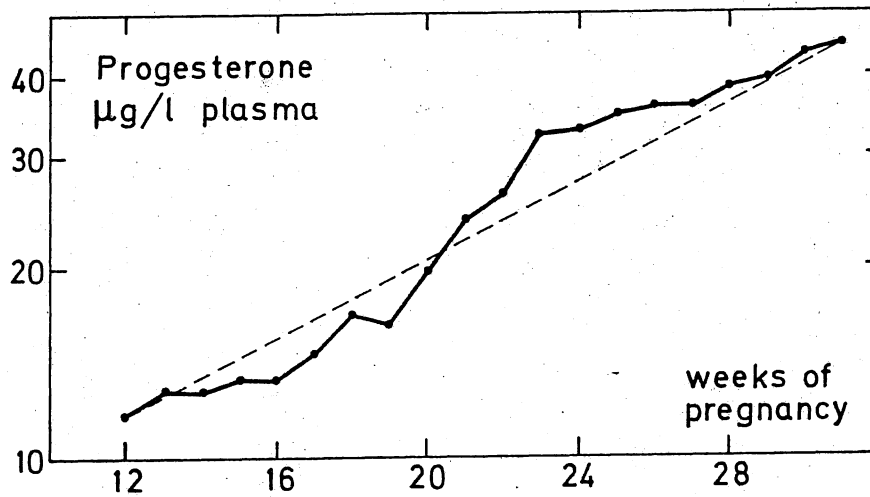

Fig. 1 The plasma progesterone concentration for a pregnant woman.

On the basis of the analysis, Winkel et.al. suggested a new monitoring scheme, where each woman is used "as her own control" in place of the conventional population reference intervals commonly used in clinical medicine.

Example 2. The whooping crane population of North America.

The whooping crane is an extremely rare migratory bird with breeding area in Wood Buffalo Park, Northwest Territories, Canada, and wintering grounds in Aransas National Wildlife Refuge, Texas, USA. Miller et.al. (1974) report the annual counts from 1938 - 1972 of whooping cranes arriving at Aransas in the fall. The birds born the previous spring have a different plumage and are referred to as "young", the rest are called "adults" even though they probably do not reproduce at least during their first three years of life. See Table 1. Fig. 2 is a graph on a logarithmic scale of the total number of birds. Some of the early counts are known to be incomplete, particularly those of 1938 and 1945 where the total number of birds was less than the number of adults the following year.

Table 1. Adult and young whooping
cranes counted at Aransas Natio-
nal Wildlife Refuge from 1938 to
1972

| Year	Adult	Young	Total
1938	10	4	14
1939	16	6	22
1940	21	5	26
1941	13	2	15
1942	15	4	19
1943	16	5	21
1944	15	3	18
1945	14	3	17
1946	22	3	25
1947	25	6	31
1948	27	3	30
1949	30	4	34
1950	26	5	31
1951	20	5	25
1952	19	2	21
1953	21	3	24
1954	21	0	21
1955	20	8	28
1956	22	2	24
1957	22	4	26
1958	23	9	32
1959	31	2	33
1960	30	6	36
1961	33	5	38
1962	32	0	32
1963	26	7	33
1964	32	10	42
1965	36	8	44
1966	38	5	43
1967	39	9	48
1968	44	6	50
1969	48	8	56
1970	51	6	57
1971	51	5	56
1972	46	5	51
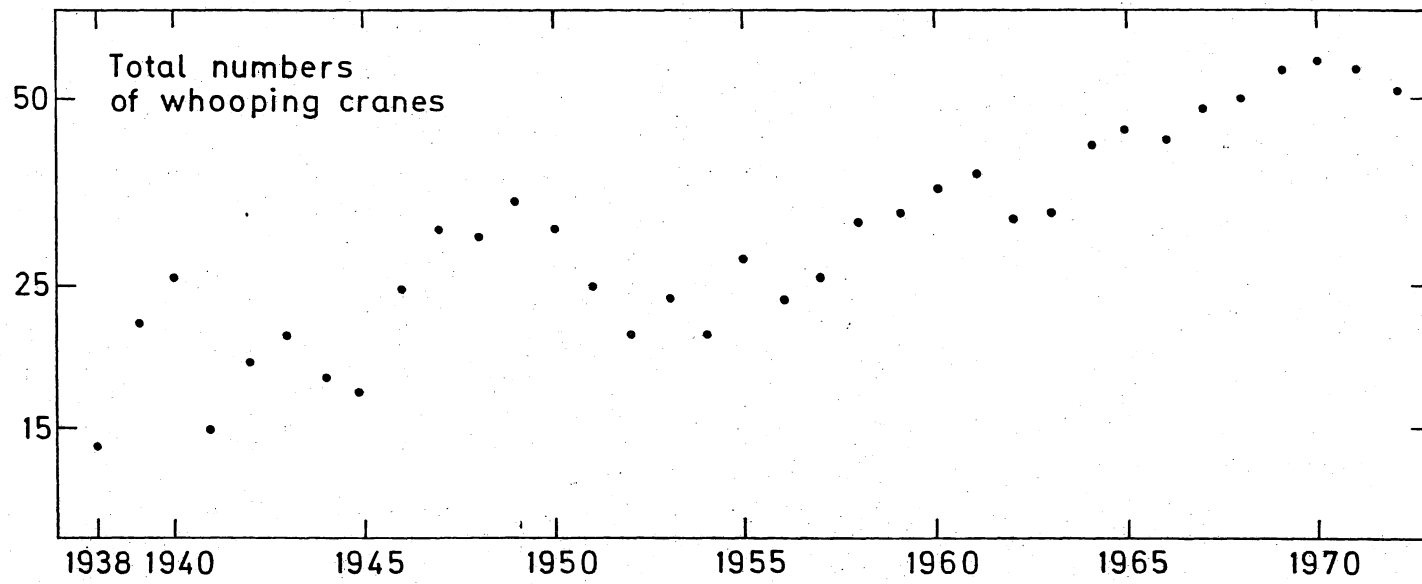
Fig. 2 Numbers of whooping cranes arriving at Aransas National Wildlife Refuge.

Miller et.al. applied a simple (linear) birth-and-death process to describe the growth and used this as a basis for predictions regarding future population size. It seems in fact obvious that at least initially the sampling ("demo-graphic") variation should be taken into account for this small population so that some stochastic model should be applied.

As noticed by Miller et.al., several of the conditions for the simple birth-and-death process were obviously not met. Let us first notice that under that model, the average number of births, and hence of surviving young birds arri-ving in Aransas in the fall should be proportional to the total number of birds the previous year. But the observed number of surviving young depends very little on the number of birds the year before. A simple regression analysis for the whole period gives

no. surviving young = 3.0 + .06 (no. birds last year)

showing a positive but insignificant dependence (t = 1.7, d.f. = 32).

This fact as well as the detailed study by Novakowski (1966) of the breeding area suggests that the recruitment is only slightly dependent on population size.

Table 2. Observed and fitted Poisson distri-
bution of surviving young whooping cranes
reaching Aransas 1938 - 1972.

No. of young cranes	Obs.	Exp.
0 - 2	6	5.0
3	5	5.3
4	4	6.4
5	8	6.1
6	5	4.9
7 -	7	7.3

Mean 4.8, Variance 5.9 $\chi^2 = 1.72$, d.f. = 5.

Still working in simple models assuming constant environment, one might then attempt a birth-immigration-death (BID) process, see. e.g. Bailey (1964), interpreting immigration as the population – independent recruitment. It may be noticed (Table 2) that the distribution of births may be fitted nicely by a Poisson distribution consistent with a BID process with zero birth rate, a so-called immigration-death (ID) process. In the BID process one could estimate the rates .06, 3.0, (from the regression) and .12 (the traditional occurrence/exposure rate), and this gives that the process approaches a stationary negative binomial distribution with mean 3.0/(.12 – .06) = 50. For the ID process the rates 4.8 and .12 will imply a stationary Poisson distribution with mean 4.8/.12 = 40. After adding some "initial population size" (interpreted as the population size at the beginning of the present regime) the order of magnitude of the results seems plausible. If applicable, the BID process clearly is a simple alternative stochastic description of density-dependent growth although fixed recruitment becomes inherently meaningless for population sizes approaching zero. An important conclusion is that the predictions made by Miller et al. on the basis of a birth-and-death process seem far too optimistic.

There are of course serious objections to such descriptions which disregards the social structure (including age at sexual maturity, sex differences, etc.) as well as age structure (which Miller et al. suggest might be responsible for some of the early fluctuations). Moreover, the expected population increment from time 0 to time t of the estimated BID process is $50(1 - e^{-.06t})$ which converges far more rapidly towards the stationary value than the observations

will support. In attempting more detailed studies of the fluctuations, it is almost necessary to analyse the annual numbers of deaths. These should be equal to the differences between the total population size one year and the number of adults the next year which do show large fluctuations, in particular in the beginning of the period, but this phenomenon may to a certain extent be explained by incomplete recording.

On the basis of these considerations it seems fairly uncertain whether the whooping crane population at present is growing under effective density regulation or not and the role of random environmental variations is also open to question. At the very least, it is very difficult to predict future population sizes.

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