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Ten-year Periodicity in Whooping Crane Census

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Although the Whooping Crane (*Grus americana*) has received more public interest than perhaps any other endangered species in North America, amazingly little is known of the factors influencing its demography and population dynamics. A reasonably accurate census of the endangered Whooping Crane population overwintering at Aransas National Wildlife Refuge, Texas has been recorded since 1938, affording a 46-yr time series (Miller et al. 1974, Binkley and Miller 1983). Here we report the discovery of a previously unreported 10-yr periodicity in this time series.

In April, cranes migrate north to nesting grounds in Wood Buffalo National Park, N.W.T., Canada. Complete nesting surveys are available only since 1970, although counts of juvenile-plumaged birds are available from Aransas for all years (Binkley and Miller 1983). Mortality rates have been estimated by Binkley and Miller (1980, 1983). The population experienced a per capita growth rate of 0.02 for the period 1938–1956, and 0.04 since 1957 (Binkley and Miller 1983).

Taking square roots of population sizes to homogenize variance (cf. Anderson 1977—a necessary step overlooked by Miller et al. 1974), the time series was detrended separately for the two growth periods defined by Binkley and Miller (1983) by calculating residuals from least-squares linear regression (similar results may be obtained by second-order differencing). The resulting stationary time series was examined for periodicity by plotting the sample autocorrelation function (Box and Jenkins 1970) illustrated in Fig. 1 and by calculating a periodogram (Fig. 2) using fast Fourier transform procedures outlined by Bloomfield (1976). Both approaches indicated a strong periodic pattern with period length of approximately 10 yr. Although statistical inference procedures for autocorrelation and periodogram peaks are only approximate (Shimshoni 1971, Bloomfield 1976), in both cases the significance probabilities for 10-yr periodicity were quite small ($P < 0.001$).

The periodic pattern is particularly apparent after removing high-frequency "flutter" by calculating a 3-yr moving average (although a moving average is not necessary to demonstrate the patterns we describe). In Fig. 3 we illustrate a least-squares regression fit to the periodic model:

$$X(t) = 0.0013 + 0.826 \cos \omega t - 0.291 \sin \omega t + \epsilon,$$

where $X(t)$ is the moving average of the detrended square root of population size, ω is $2\pi/(\text{period length} = 10)$, and ϵ is an error term. Nearly ⅔ of the variance in the detrended time series is attributable to this 10-yr harmonic ($R^2 = 64.7\%$, df = 41, $P < 0.001$).

Although Binkley and Miller (1983) ascribe periodic fluctuations in the Whooping Crane population to variation in recruitment, our results are inconsistent and suggest that variation in mortality also must be important. Recruitment of juvenile-plumage cranes into the Aransas Refuge counts varied considerably among years but did not possess significant periodicity. Furthermore, we found no significant correlation between rate of recruitment and the detrended square root of Whooping Crane census ($R^2 = 0.059$, df = 44, $P > 0.1$). We further note that recruitment of young into the Aransas census is confounded by mortality of chicks on nesting grounds because chicks are not counted until they reach the Aransas area in late autumn.

Recruitment is thought to vary as a function of water levels on nesting grounds (Kuyt et al. 1981), which also may influence vulnerability of cranes to predation because terrestrial predators can better penetrate nesting areas in years of low water levels. Also, during drought conditions, crane families presumably range farther to find suitable wetland feed-

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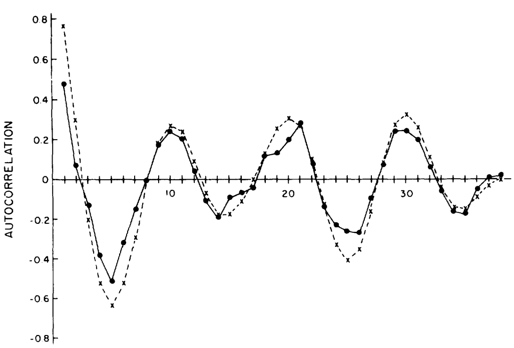

Fig. 1. Autocorrelation of detrended square root (●), and of 3-yr moving average of detrended square root (X) of Whoopinig Crane census.

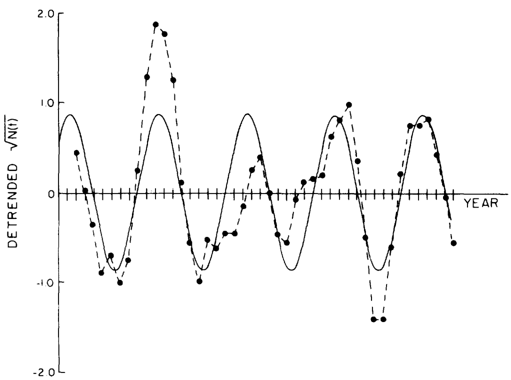

Fig. 3. Periodic regression of 3-yr moving average of detrended square root of Whooping Crane census.

ing sites and consequently are more likely to encounter terrestrial predators (Kuyt et al. 1981). However, we found no significant ($P > 0.1$) correlation between breeding season precipitation and the square root of detrended crane fluctuations or between a 3-yr moving average of breeding season precipitation and the square root of detrended crane counts.

Wolves (*Canis lupus*) are known predators of Whooping Cranes (Kuyt et al. 1981), killing at least 4 birds in the summer of 1983 (Rod Drewien pers. comm.). These recent observations of mammalian predation on cranes may be of particular interest given the 10-yr periodicity known to occur in several species of potential predators, particularly wolf, lynx (*Lynx canadensis*), and red fox (*Vulpes vulpes*; Bulmer 1974, Finerty 1980). In fact, Wood Buffalo National Park is near the epicenter of periodicity for the well-known lynx-hare cycle (Elton and Nicholson 1942, Finerty 1980, Smith and Davis 1981). Although we cannot yet identify the mechanism generating periodicity, we are fascinated by the precise prediction of a 10-yr cycle for Whooping Cranes by population-cycle allometry (Peterson et al. 1984).

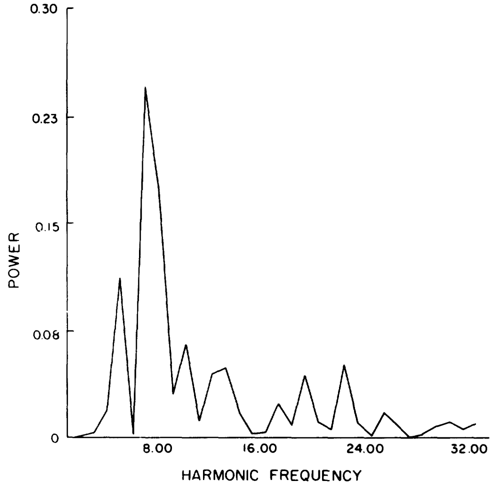

Fig. 2. Fast Fourier transform periodogram of detrended square root of Whooping Crane population size. Peak in relative power occurs at a harmonic corresponding to a 10-yr cycle.

Given no changes in environmental regimen from that existing since 1957, or in periodicity since 1938, we may use the time series to forecast the future population size of Whooping Cranes, using the econometric ARIMA model with periodic differencing (Pankratz 1983, Vandaele 1983). We identified an appropriate ARIMA model following the procedure of inspecting residual autocorrelation and partial autocorrelation functions as outlined by Bowerman and O'Connell (1979). The best model was determined to be a first-order moving-average process model at both primary and periodic (seasonal) levels, often written

$$\text{ARIMA}(0,1,1)(0,1,1)_{10}.$$

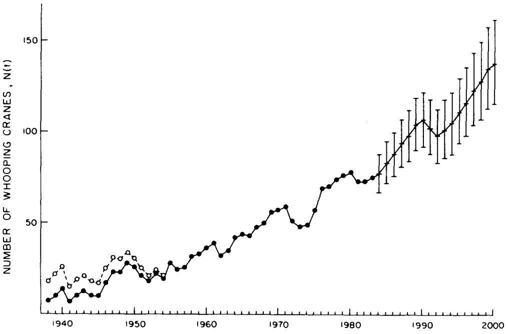

Fig. 4. ARIMA model population forecasts for the Aransas-Wood Buffalo population of Whooping Cranes to year 2000. Years 1938-1956 have been adjusted to the same mean growth rate as 1957-1984; original observations are represented by open circles. Vertical bars are 95% confidence intervals.

We used standard iterative procedures to fit the model

$$\sqrt{N(t)} - 2\sqrt{N(t-1)} + \sqrt{N(t-10)} = a(t) - 0.707\ a(t-1) - 0.799\ a(t-10),$$

where $N(t)$ is population size at time t (with adjusted growth rate for 1938-1956) and $a(t)$ is white noise (totally random variance). This model leaves a residual mean square of only 0.09, and acceptance is justified by a Box-Pierce Chi-square statistic calculated from autocorrelation of residuals [$Q = 8.652 < \chi^2$ (10 df) $= 18.307$].

Forecasts of square roots of population size, $\sqrt{\hat{N}(t)}$, are calculated

$$\sqrt{\hat{N}(t)} = \sqrt{N(t-1)} + \sqrt{N(t-10)} - \sqrt{N(t-11)} - 0.799\ a(t-10) - 0.707\ a(t-1) + 0.565\ a(t-11)$$

(Pankratz 1983). Because forecasts were calculated on square roots of population size, squares of these forecasts will be biased underestimates of true forecasts (Nelson 1973). Correction for bias is accomplished by

$$E[N(t)] = \left[\sqrt{\hat{N}(t)}\right]^2 + s^2,$$

where s^2 is the residual mean square. The 95% confidence limits on forecasts shown in Fig. 4 were corrected in the same way, but bias was small, being considerably less than one bird in all years.

The U.S. Fish and Wildlife Service-Canadian Wildlife Service management objective of 40 nesting pairs for the Aransas-Wood Buffalo population (Whooping Crane Recovery Team 1980) should be reached approximately in year 2000, given an average 57% of nonjuvenile-plumage birds breeding. This, of course, assumes no changes in the ecology or management of the population over the next 16 yr. In spite of periodic dips in population size projected at approximately 10-yr intervals, forecasted populations of Whooping Cranes are encouraging. Additionally, potential success of a recent program to employ Sandhill Cranes (*Grus canadensis*) as foster parents at Gray's Lake National Wildlife Refuge, Idaho, may enhance our ability to secure future success of Whooping Cranes in North America (Drewien and Bizeau 1978). Nevertheless, our observations on periodic depression in Whooping Crane population growth suggest practical importance for improved understanding of the 10-yr cycle phenomenon, which has fascinated but eluded population biologists for decades (Finerty 1980).

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