

MODELING EXTINCTION IN PERIODIC ENVIRONMENTS: EVERGLADES WATER LEVELS AND SNAIL KITE POPULATION VIABILITY¹

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Abstract. The effects of periodic environmental fluctuations on population viability are examined based on the use of environmental states. The approach is applied to the Florida population of the Snail Kite, an endangered wetland hawk that feeds almost solely on one species of snail. A preliminary assessment based on stochastic population fluctuations indicated that populations became viable when initial size surpassed 300 individuals. However, changes in population size between consecutive years, nesting success, and the length of the breeding season were all highly and positively related to water level and rainfall characteristics, which are highly periodic. Low water conditions cause Snail Kites to disperse and result in low recruitment, increased adult mortality, and population declines. The effects of cyclic drought were explored using stage-based life tables for three different water conditions or environmental states (drought, lag years following drought, and high years). Population sizes predicted by the model were closely associated with actual kite population counts. Deterministic projections indicated that kite populations would increase when intervals between droughts exceeded 3.3 yr, but stochastic simulations found that populations did not become viable unless intervals exceeded 4.3 yr. The model was sensitive to estimates of survivorship. The use of the environmental state approach is compared to standard techniques for population viability analyses (PVA), and the implications of the model for Everglades water management are discussed.

Key words: Everglades; extinction models; periodic environments; population viability analysis; Snail Kites; water management.

INTRODUCTION

Population viability analysis (PVA) has developed as a tool to assess the likely effects of different management options on extinction (Shaffer 1981, 1990, Gilpin and Soulé 1986, Soulé 1987). In demographic approaches to PVA, populations are projected into the future using means and variances for demographic parameters and sometimes a minimum viable population is determined (Burgman et al. 1988, Boyce 1992). Most applications of this technique are based on the assumption that demographic rates, and the environmental factors that affect them, fluctuate stochastically (Menges 1990, 1992, Boyce 1992). Also known as "environmental stochasticity," this form of uncertainty can have important effects on population viability (Shaffer 1987, Lande 1988, 1993).

Not all environmental or climatic fluctuations are unpredictable or stochastic, and many can occur in a periodic or cyclic fashion (Colwell 1974, Stearns 1981, Burroughs 1992, Beissinger and Gibbs 1993). MacArthur (1968) was one of the first to recognize the implications of periodic environments for the selection of demographic characteristics and its effects on population growth. More recently, demographers have explored the effects of cyclic environments on the am-

plitude and phase of population oscillations (Gourley and Lawrence 1977, Tuljapurkar 1985, 1989, Caswell 1989). Population growth rates are increased by environmental fluctuations with periods of about one generation length, and decreased by fluctuations with much shorter or longer periods (Tuljapurkar 1985). Furthermore, the time to extinction can be quite sensitive to environmental autocorrelation (Tuljapurkar and Orzak 1980). Population persistence times are smaller with serial correlation in environmental variation than with stochastic variation (Goodman 1987).

Despite the importance of these findings, remarkably little consideration has been given to the significance of periodic environments on modeling extinction processes with PVA. Two general approaches have been used by mathematical demographers in developing models for variable environments. In the "element selection method," demographic values for the elements of a single Leslie-Leftkovitch matrix are randomly chosen from a probability distribution for each step of the projection (Burgman et al. 1993). This is the standard approach to modeling populations in stochastic environments, and is modified for periodic environments by covarying the selection of elements with an environmental autocorrelation function or by adding a matrix with the amplitudes of the variation in demographic parameters determined from Fourier decomposition of environmental data (Tuljapurkar 1985, Caswell 1989).

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In the second approach, periodic environments have been modeled by representing cycle stages with separate matrices of vital rates and repeatedly multiplying the matrices in cyclic order (Skellam 1967, Namboodiri 1969, Cohen 1976, 1979*a, b*). This is analogous to choosing matrices based on partitioning the effects on demography of discrete environmental conditions or "environmental states" in the terminology of Colwell (1974). Although this approach has been called the "matrix selection method" (Burgman et al. 1993), a more descriptive label would be the "environmental state method" because it directly relates the definition of matrices to the cycle conditions it was meant to model and the methods used to quantify environmental periodicity or predictability (Colwell 1974, Stearns 1981, Beissinger and Gibbs 1993). In short-term projections (<10 yr), the matrix element method yields a wider range of possible population trajectories than the environmental state method, but in long-term projections (>50 yr) the distribution of population sizes is more variable with the environmental state method (Burgman et al. 1993).

Here I show how to apply the environmental state method for modeling populations in periodically fluctuating environments to PVA management situations. This approach has rarely been applied to the management of small populations (Gilpin 1989, Soulé 1989, Burgman et al. 1993), although it has occasionally been used to explore the implications of environmental variation on population dynamics (e.g., Bierzychudek 1982, Cohen et al. 1983, Caswell 1989). I apply these ideas to the Snail Kite (*Rostrhamus sociabilis*), a highly specialized hawk that feeds almost only on one species of freshwater snail (Plate 1; Snyder and Snyder 1969, Beissinger 1990, Beissinger et al. 1994). Although common throughout much of the Neotropics (Beissinger 1988), the Florida subpopulation is listed by the U.S. government as an Endangered Species. I first conduct a preliminary viability assessment for the Snail Kite based solely on stochastic population fluctuations. Then I examine the effects of rainfall and water levels on kite numbers, and show that stochastic models will be unreliable because of the periodic occurrence of drought (Beissinger 1986), which results in poor food supplies, low nesting success, and population declines (Beissinger and Takekawa 1983, Beissinger 1986, Takekawa and Beissinger 1989, Snyder et al. 1989*a*). Finally, I develop a PVA based on the occurrence of environmental states to explore the effects of periodic environments on population viability.

A PRELIMINARY ASSESSMENT OF KITE POPULATION VIABILITY

Methods

During the past two decades, annual censuses of total Snail Kite numbers in Florida have been made (Sykes 1979, 1983, J. A. Rodgers et al. 1988 and *unpublished*

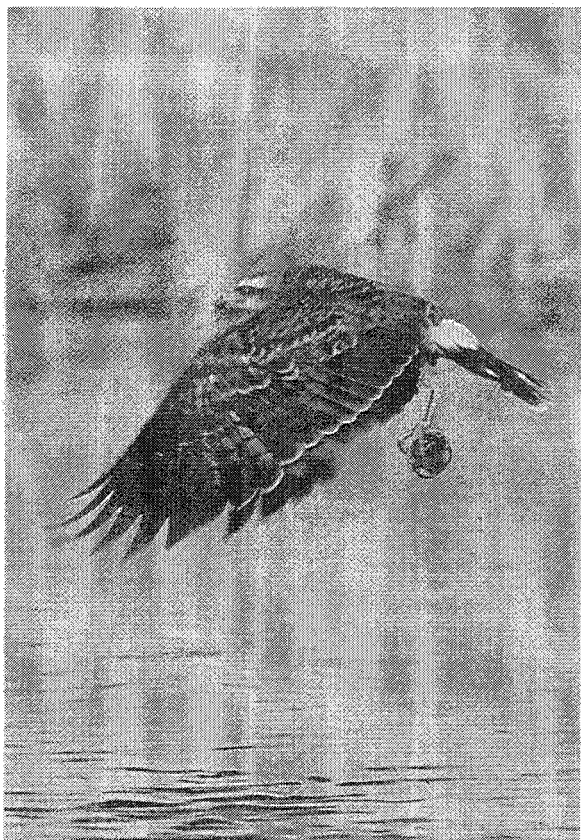


PLATE 1. Female Snail Kite (*Rostrhamus sociabilis*) in the Florida Everglades carrying an apple snail (*Pomacea dolioles*), on which it feeds almost exclusively. Photograph by Noel F. R. Snyder.

data). Although these counts are fraught with problems of inaccuracy (Rodgers et al. 1988), they are nevertheless useful indicators of the relative magnitude of kite population changes from year to year. The mean and variance of the annual percentage change in population size give an approximation of the mean and variance of the geometric rate of increase or lambda (λ). The percentage change in population size is a particularly useful measure, since it incorporates the two main sources of uncertainty that affect population viability (e.g., environmental and catastrophic stochasticity; Shaffer 1987), if the period of census is sufficiently long (Pimm 1991). However, this approach will probably underestimate the important effects that demographic and genetic stochasticity exert on extinction rates when population sizes are small (<50 individuals) if census numbers never reach those thresholds. Thus, a more valid measure of risk may be the probability of populations reaching a very small size (e.g., 25 birds), called "quasiextinction" (Ginsburg et al. 1982).

To explore population viability, I stochastically simulated kite populations using a random walk model (Feller 1968, Burgman et al. 1993, Folley 1994). Random walk models view population growth as a one-dimensional diffusion process that is analogous to the

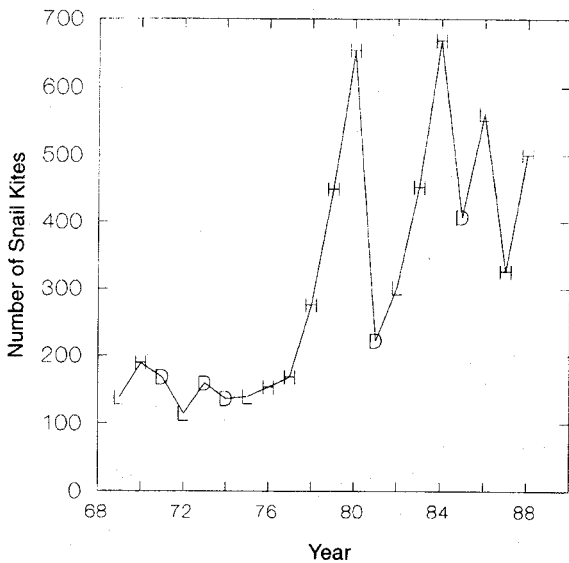


FIG. 1. Annual census counts of the Florida Snail Kite population conducted at the end of each year just prior to the onset of the next breeding season. Water level conditions (D = drought year, L = lag year, and H = high water year) used in the definition of environmental states are shown. They reflect conditions during the breeding season preceding the census. Data were taken for 1969–1980 from Sykes (1983), for 1981 from Beissinger (1984, 1986), and for 1982–1988 from J. A. Rodgers et al. (1988, unpublished data).

Brownian motion of a particle along a gradient whose force is measured by lambda. In this model, population size N_t grows annually by:

$$(N_{t+1}) = N_t G,$$

where G , for growth, is a random number with a mean of lambda and a standard deviation equal to the standard deviation of lambda. The mean and standard deviation of the annual percentage change in kite numbers were used for estimates of lambda and the standard deviation of lambda, respectively. A similar approach has been used to solve analytically for the expected (mean) time to extinction using diffusion analysis (Lande 1993, Folley 1994). The estimate of a mean time to extinction is greatly affected by the underlying highly skewed distribution of extinction times (Pimm et al. 1993) and does not provide a probabilistic estimate of the risk of extinction that can be easily interpreted in relation to management decisions. Thus, it is much less useful to managers than probabilistic estimates of the likelihood of extinction. No carrying capacity or upper boundary to population growth was included in the model because Snail Kites are not territorial, there is no evidence of density dependence on reproduction or survival, and the choice of an upper boundary would have been completely arbitrary. This allowed simulated populations to grow to large sizes unlikely to occur in Florida, resulted in conservative extinction estimates, and has been suggested for similar situations (Ginzburg et al. 1990).

Twenty years of census data from 1969 to 1989 (Fig. 1) were used to calculate a mean, variance, minimum, and maximum for the annual percentage change in population size. During this period, kite populations fluctuated between 114 and 668 individuals, and on average (± 1 SD) increased by $13 \pm 38\%$ annually. In the simulation, populations with initial sizes between 150 and 330 birds were allowed to increase or decrease by choosing a random number for the annual percentage change based on the descriptive statistics above, assuming a normal distribution truncated at the observed range (-66% to 64% change). Simulations were conducted using Lotus 1-2-3 (1989) and @Risk (Palisade 1991) for 50 and 100 yr time intervals. One thousand replications were completed for each initial population size. Viable populations were defined as those that exceeded extinction or quasiextinction levels during 95% of the replications.

Results

The probability of extinction and quasiextinction declined slowly as the initial population size of kites increased (Fig. 2). Quasiextinction rates generally exceeded 5% until initial population size surpassed 300 individuals. At first glance, 300 birds seems a rather small number for a viable population, and the probabilities of extinction in this analysis appear to be low (Fig. 2). These results were most likely due to the fact that the kite population increased during the period of census by an average of 13% annually. The increase in Florida kite numbers was due to a number of con-

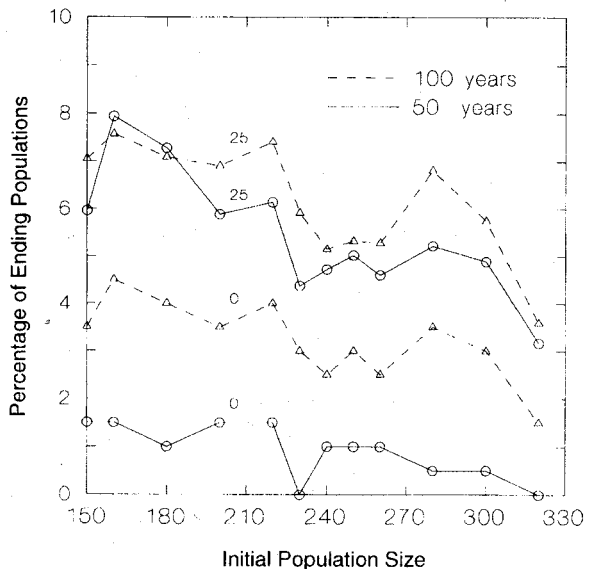


FIG. 2. A preliminary viability analysis for the Florida Snail Kite showing the effects of initial population size on extinction (0) and quasiextinction (<25 individuals). Stochastic simulations of 1000 replications of kite populations were projected for 50 or 100 yr using the mean and standard deviation of the annual percentage change in kite census numbers.

TABLE 1. Spearman rank correlations between annual measures of Snail Kite demography in Florida and annual water level or rainfall characteristics at Lake Okeechobee (Lake) and State Water Conservation Area 3A (CA3A). Demographic characteristics include the percentage change in total Snail Kite numbers from year to year (population change), the percentage of nests that were successful (nesting success), and the length of the breeding season in weeks. *N* is the number of years.

| Everglades | Annual statistic | Snail Kite population change (<i>N</i> = 19) | | Snail Kite productivity | | | |
|-------------|------------------|---|--------|----------------------------------|--------|----------------------------------|-------|
| | | Lake | CA3A | Nesting success (<i>N</i> = 14) | | Breeding season (<i>N</i> = 13) | |
| | | Lake | CA3A | Lake | CA3A | Lake | CA3A |
| Water level | Mean | 0.59** | 0.63** | 0.66** | 0.60* | 0.42† | 0.26 |
| | Minimum | 0.66** | 0.62** | 0.80*** | 0.70** | 0.47† | 0.25 |
| | Maximum | 0.58** | 0.27 | 0.29 | -0.01 | 0.49* | -0.04 |
| | Winter | 0.32† | 0.49* | 0.36 | 0.53* | 0.17 | 0.21 |
| | Spring | 0.58** | 0.60** | 0.73** | 0.65** | 0.44† | 0.21 |
| | Summer | 0.74*** | 0.40† | 0.24 | 0.02 | 0.50* | 0.10 |
| Rainfall | Total | 0.79*** | 0.43* | 0.58* | 0.53* | 0.34 | -0.01 |
| | Minimum | 0.27 | 0.38† | -0.04 | 0.30 | 0.52* | 0.47† |
| | Maximum | 0.15 | 0.05 | 0.15 | 0.02 | -0.45† | -0.32 |
| | Winter | 0.59** | 0.37† | 0.82*** | 0.46† | 0.23 | -0.02 |
| | Spring | 0.33† | 0.29 | 0.28 | 0.38† | -0.16 | 0.04 |
| | Summer | 0.19 | 0.05 | -0.10 | 0.29 | 0.20 | 0.31 |

† $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

secutive high water years in the late 1970s and mid-1980s (Fig. 1). Even though the population sometimes experienced large declines under drought conditions (Beissinger 1986), it was also capable of large increases under good conditions (Snyder et al. 1989a).

Two factors may make the results in Fig. 2 misleading. First, both the rates of annual population decline and growth used in this analysis may be overestimated because of biases inherent to the annual kite census procedure (Rodgers et al. 1988). More importantly, annual changes in population size were likely to have been greatly affected by water levels and their management during the period of study. Everglades water management regimes have undergone many changes in the past three decades and will continue to be adaptively managed in the future. Because of the potential importance of water levels to kite population viability, below I empirically examine the relationship between kite population dynamics, demography, and environmental conditions in detail.

RELATIONSHIPS BETWEEN SNAIL KITE NUMBERS, DEMOGRAPHY, AND ENVIRONMENTAL CONDITIONS

Methods

I compared kite population dynamics and demography to water levels and rainfall in the main portion of the kite's range in southern Florida (Beissinger and Takekawa 1983, Sykes 1983). Rainfall and water level records were obtained from the South Florida Water Management District and the U.S. Army Corp of Engineers for Lake Okeechobee and State Water Conservation Area 3A (CA3A). Environmental conditions for Lake Okeechobee (Glades, Hendry, and Okeechobee counties) were represented by the average of three locations. Conditions for CA3A (Dade and Broward

counties) were represented by data from gage 3-28 in the southeastern portion of CA3A. This site is in the midst of the area most heavily used by kites from 1970 to 1990 (Sykes 1983, Beissinger 1986, Bennetts et al. 1988) and conditions at this location are representative of the southern end of CA3A (C. White, *personal communication*). Since kites initiate nests from November through August (Snyder et al. 1989a), environmental data were grouped from October through September the following year to yield annual means, totals, minima, and maxima that reflected the nesting season preceding the annual November kite census. In addition, seasonal conditions were estimated from water level or rainfall statistics for: (1) winter (October–February), when nesting is first initiated; (2) spring (March–June), the height of the nesting season and often the driest period; and (3) summer (July–September), when rainfall usually reaches its peak and breeding tapers off (Snyder et al. 1989a). Spearman rank correlations (Sokal and Rohlf 1981) were calculated between totals for these seasonal categories and the annual percentage change in kite numbers using kite censuses conducted during the November following the nesting season. Environmental conditions were also correlated with the percentage of kite nests that were successful and the duration in weeks of the kite breeding season (Snyder et al. 1989a).

Results

Changes in the Florida Snail Kite population size between consecutive years were highly and positively related to water level and rainfall characteristics at both Lake Okeechobee and CA3A (Table 1). Strong relationships were found between the percentage of population change, and the monthly average and annual minimum water levels and total annual rainfall at both

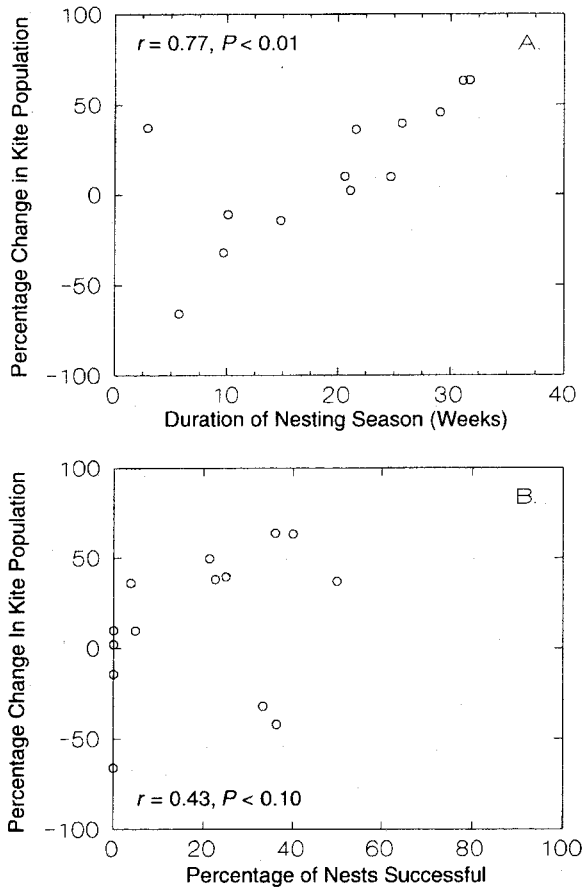


FIG. 3. The relationship between the annual percentage change in kite population size, and (A) the length of the breeding season and (B) the productivity of nests. Spearman rank correlations are given for each.

locations. Kite population change in Florida was strongly related to maximum annual water levels at Lake Okeechobee but not at CA3A, which has less topographic variation and dries out more frequently than the lake. Winter rainfall levels at both the lake and CA3A were good predictors of annual kite population change. Spring and summer water levels at Lake Okeechobee were most strongly related to changes in population size, whereas at CA3A winter and spring water levels were better predictors of population change. Similar relationships between water level, rainfall, and annual percentage change in population size were obtained when environmental characteristics were correlated with changes in the number of kites using each area in a particular year. But sample sizes were much smaller because areas were not used by kites each year, and the percentage change in numbers fluctuated much more greatly (Rodgers et al. 1988) because kites moved across the Florida landscape between these and other areas (Sykes 1979, Beissinger and Takekawa 1983, Takekawa and Beissinger 1989). It is important to note that the percentage change in the Florida kite population was not related to environmental conditions

at the time of the annual census (November) in CA3A (water level: $r = 0.14$, $P > 0.50$; rainfall: $r = 0.11$, $P > 0.50$). However, it was related to water level ($r = 0.62$, $P < 0.01$), but not rainfall ($r = 0.10$, $P > 0.50$), at Lake Okeechobee.

Water level and rainfall characteristics were highly related to measures of kite productivity (Table 1). Strong positive relationships were found between nesting success and average monthly and minimum annual water levels, and total annual rainfall at both locations. Winter rainfall and water conditions in the following spring were most strongly related to nesting success. The duration of the kite nesting season was correlated with average monthly and monthly minimum and maximum water levels at the lake but not at CA3A. Summer water conditions most influenced the duration of the nesting season. The length of the nesting season was positively related to minimum monthly rainfall at both locations (Table 1), indicating that low rainfall levels may result in a cessation of nesting.

Annual change in kite population size was strongly correlated with the length of the breeding season but was only weakly related to nesting success (Fig. 3). Nesting success in this species is generally low, exceeding 40% only during the best years (Snyder et al. 1989a). During low water years, few nests are attempted and most fail. Low nesting success appears to be offset by the chance to attempt several nests and raise multiple broods during high water years. Nest initiations can span a period of 6–7 mo if water conditions are favorable and most kites probably make multiple nesting attempts (Snyder et al. 1989a). Thus, it is not surprising that kite population trends are more closely related to the duration of the nesting season, which is highly variable, than to nesting success, which is generally low (Fig. 3). When used together in a multiple regression to predict the percentage change in kite population size, the duration of the breeding season ($T = 3.7$, $P < 0.006$) and nesting success ($T = 2.9$, $P < 0.02$) account for 74% of the variation ($r = 0.86$, $N = 11$, $P < 0.005$).

Annual changes in kite population size also reflect the effects of water conditions on annual survivorship, but survivorship has been less well studied (Beissinger 1986, Snyder et al. 1989a). High annual survival (>90%) of both fledglings and adults appeared to be typical of years with favorable water conditions, whereas low postfledging survival occurred during dry years. Judging from the data of Sykes (1979, 1983), Beissinger (1986), and Snyder et al. (1989a), most adult mortality probably occurred in drought years and was quite likely caused by starvation and the dangers imposed by drought-related dispersal (Beissinger and Takekawa 1983, Takekawa and Beissinger 1989).

MODELING EFFECTS OF WATER LEVEL PERIODICITY ON KITE VIABILITY

The state-based approach for modeling variable environments

Since water levels strongly affect kite demography, the preliminary viability analysis (Fig. 2), or any other

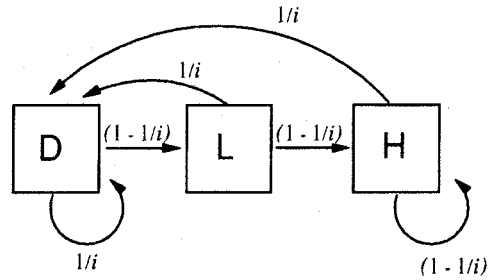
projection of population trend and viability, is likely to be affected by the relative frequency of low and high water conditions during the period of study. In the Everglades, low water conditions or dry-downs (also called "drought") occur periodically with a strong 5–7 yr cycle (Beissinger 1986). The periodicity of dry-downs has become shorter during the past century, from an interval between dry-downs of ≥ 10 yr to 4–5 yr (Beissinger 1986). These changes in "drought" frequency could have been induced by natural changes in rainfall patterns, such as a decline in the frequency of hurricanes, or by the combined effects of the massive drainage of the Everglades region, increased water demands of growing urban areas in southern Florida, and water management practices (Shih 1983, Beissinger 1986).

The cyclic occurrence of water levels suggests that standard population viability analyses based on stochastic variation of average demographic rates (Shaffer 1981, Burgman et al. 1988, Boyce 1992) would not capture the dynamics of kite population fluctuations (Tuljapurkar 1985). Instead, the effects of cyclic drought on population viability can be explored by examining how drought periodicity affects population viability. The advantage of this approach is that, rather than estimating the viability of a kite population that will be greatly affected by water management decisions, the effects of water management can be examined by determining the minimum periodicity of dry-downs that would allow kite populations to persist.

The environmental state method allows just such a question to be answered. To investigate how environmental variability affects population persistence, a time-varying model based on the probabilistic occurrence of environmental states is used (Fig. 4). Environmental states represent discrete sets of environmental conditions that affect demography. The number of possible environments can be few (e.g., "good" and "bad" states) or many (Cohen 1976, Tuljapurkar 1989), but the former is most likely in PVA applications where the effects of management options are being evaluated. For each environmental state, age- or stage-based estimates of vital rates and their variances are used to construct the Leslie-Leftkovich matrix to model the demographic life cycle (Fig. 4). This acts to partition the variance in annual demographic rates among environmental states, and tends to reduce the variation within states.

To analyze population dynamics, the environmental state method requires a three-step process (Cohen 1979b, Caswell 1989). First, a model describing the temporal variation in environment states must be developed (Fig. 4). Temporal variation in environments can be modeled based on one of several probabilistic processes (e.g., aperiodic, deterministically periodic, or stochastically periodic) for the occurrence of environmental states (Caswell 1989, Tuljapurkar 1989). Then this model, often in the form of an environmental tran-

A. Environmental States Cycle



B. Demographic Life Cycle

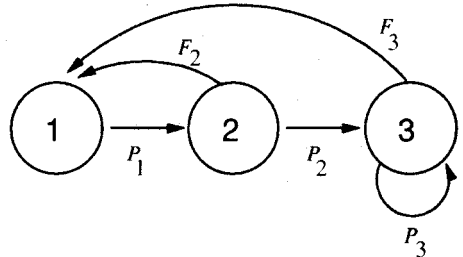


FIG. 4. Schematic representation of the environmental state approach to population viability analysis (PVA). Demographic processes, represented by the life cycle graph for the Snail Kite (B), take place within the cycle of fluctuating environmental states (A). The life cycle must be projected for the same time interval as is used in the environmental state cycle, so that the sequence of environments can control the choice of potential values for vital rates (i.e., matrices). (A) Environmental states, shown by squares, are discrete sets of environmental conditions that affect demography. Transition probabilities among environmental states can be assigned for the projection interval (typically 1 yr). In this paper, the sequence and occurrence of three environmental states (D = drought, L = lag years following drought, H = high water years preceded by continuous flooding) is determined by transition probabilities related to the number of years between droughts (i) or the probability of the occurrence of drought in any given year ($1/i$). (B) Life cycle diagram for the Snail Kite based on three stage classes (1 = fledgling or age 0–1; 2 = subadult or age 1–2; and 3 = adult or >2 yr of age). Demographic rates (P = annual survival and F = fecundity) are estimated for each stage class and each environmental state.

sition matrix, is used to determine the sequence of environmental states and hence the Markov chain of projection matrices. Finally, the demographic projections are made based on the occurrence of vital rates dictated by the sequence of environmental states (Fig. 4).

Thus, in the environmental state method the sequence of environments controls the choice of matrices and potential values for vital rates. If this sequence has some underlying periodicity, the sequence of vital rates used in the model will occur with this periodicity, rather than purely stochastically as would be typical of standard PVA models. Whereas changes in the sequence of environmental states does not affect estimators of

TABLE 2. Vital rates used for three different environmental states in the deterministic and stochastic simulations of the Florida Snail Kite population. Environmental states are defined by water conditions during the current and previous year. Nest success is the proportion of nests fledging young. Fledglings are 0–1 yr old, subadults are 1–2 yr old, and adults are >2 yr old.

| Environmental state | Age class | Nesting success | | | Proportion Nesting | Nesting attempts per year | Annual survival | | |
|---------------------|-----------|-----------------|------|-----------|--------------------|---------------------------|-----------------|------|-----------|
| | | Mean* | SD | Range | | | Mean | SD | Range |
| Drought year | Fledgling | 0.00 | 0.00 | 0.00–0.00 | 0.00 | 0.00 | 0.50 | 0.10 | 0.30–0.80 |
| | Subadult | 0.03 | 0.10 | 0.00–0.25 | 0.15 | 1.00 | 0.60 | 0.10 | 0.40–0.90 |
| | Adult | 0.03 | 0.10 | 0.00–0.25 | 0.15 | 1.00 | 0.60 | 0.10 | 0.40–0.90 |
| Lag year | Fledgling | 0.00 | 0.00 | 0.00–0.00 | 0.00 | 0.00 | 0.85 | 0.03 | 0.75–0.92 |
| | Subadult | 0.16 | 0.10 | 0.04–0.33 | 0.15 | 1.00 | 0.90 | 0.03 | 0.80–0.95 |
| | Adult | 0.16 | 0.10 | 0.04–0.33 | 0.80 | 1.50 | 0.90 | 0.03 | 0.80–0.95 |
| High year | Fledgling | 0.00 | 0.00 | 0.00–0.00 | 0.00 | 0.00 | 0.90 | 0.03 | 0.80–0.95 |
| | Subadult | 0.30 | 0.10 | 0.10–0.40 | 0.25 | 1.00 | 0.95 | 0.03 | 0.85–0.98 |
| | Adult | 0.30 | 0.10 | 0.10–0.40 | 1.00 | 2.20 | 0.95 | 0.03 | 0.85–0.98 |

population growth in cyclic environments (Cohen 1979a, b, Caswell 1989), the results may be sensitive to noncyclic permutations that change the order of occurrence of environmental states (Caswell 1989) and to the absence of transitions from one environmental state to another.

Defining environmental states and estimating model parameters

I developed an exploratory model of the Florida kite population using stage-based life tables (Lefkovich 1965, Caswell 1989) for three different water conditions or environmental "states" (Fig. 4). The bases for classifying environmental conditions into states were the movements of kites in response to water levels (Beissinger and Takekawa 1983, Takekawa and Beissinger 1989) and the ensuing effects on recruitment and survival (Table 1, Fig. 3). Environmental states were classified, based on current and past water levels (Fig. 4), as high water years, drought or low water years, and lag years that follow drought (Snyder et al. 1989a). During high water years, kites were primarily found in a few large wetland tracts (Sykes 1979, 1983, Rodgers et al. 1988) where nesting success and survivorship were high (Beissinger 1986, Snyder et al. 1989a). These areas dried-out during drought years, and the birds dispersed across the peninsula in search of food, using small marshes, canals in urban areas, agricultural fields or any refugia with water remaining (Beissinger and Takekawa 1983, Takekawa and Beissinger 1989). During drought years, adult mortality increased, few nests were attempted, and nest success was low (Beissinger 1986, Snyder et al. 1989a). Following drought, most kites returned to the large wetland tracts, which had been reflooded. Survivorship increased but the effects of low water conditions, often accompanied by fire, on snail populations were sometimes manifested during the following or lag year, which reduced reproductive success (Snyder et al. 1989a).

Environmental states are clearly reflected in the annual changes in kite numbers (Fig. 1). Population in-

creases were generally associated with high water and lag conditions, and population declines were associated with drought years ($\chi^2 = 7.67$, $df = 2$, $P = 0.022$).

Vital rates were estimated for Snail Kites under each environmental state (Table 2) for three age classes to use in deterministic and stochastic population projections (Fig. 4) parameterized for a prebreeding census (Noon and Sauer 1992). Fledglings (0–1 yr old), subadults (1–2 yr old), and adults (>2 yr old) were differentiated mainly on the basis of reproductive rates (Snyder et al. 1989a). A finer age-structured model was not feasible due to small sample sizes of age-specific demographic data. Fecundity was modeled as the product of the proportion of nests that fledged young (nesting success), the number of young that fledged per successful nest, the proportion of the population that nested, and the number of nesting attempts per year. Sex ratio was assumed to be 1:1. For each environmental state, estimates of mean nesting success were taken from Snyder et al. (1989a), and ranges and standard deviations were calculated from their data. Nesting success was assumed to be the same for adults and subadults since no differences were found (Snyder et al. 1989a). During a drought only 15% of the population attempted to nest once during a short breeding season, whereas nearly all adults attempted to nest on average 2.7 times under the best conditions during a high water year (Beissinger 1986, Snyder et al. 1989a). I assigned a more conservative value of 2.2 nesting attempts per year for high water years. I estimated that 25% of the subadults bred annually based on data in Snyder et al. (1989a). Subadults were assumed to breed once annually, since most nested relatively late in the breeding season (Snyder et al. 1989a). During lag water years, both the proportion of birds nesting and the nesting attempts per year were reduced compared to high water years, because breeding seasons tended to be shorter and not all kites had returned to primary nesting areas (Beissinger and Takekawa 1983, Beissinger 1986, Snyder et al. 1989a, Takekawa and Beissinger 1989).

Survivorship during high water years was estimated

at 95%, projected from studies of a small number of banded and telemetered adults (Snyder et al. 1989a) and subadults (Snyder et al. 1989b). During lag years survivorship was estimated as slightly lower (90%) based on the survival of kites that were radio-tagged near the end of a drought after many had already dispersed from drying wetlands to Lake Okeechobee (Snyder et al. 1989b), a refugium that remained partly flooded throughout the drought (Beissinger and Takekawa 1983). Survival during drought years was given a value of 60%, the average percentage change in the population during drought years after 1973 when kites began to use CA3A in large numbers. This estimate assumes that little or no recruitment occurred during drought years and that most birds had returned to wetlands where they were censused during the following winter. Because variation in the percentage change in the kite population was high during droughts and since droughts vary greatly in their intensity, the range and variation of annual survival during droughts was greater than for other environmental states. Fledglings were assumed to survive slightly less well than adults. Annual variation in survivorship was assumed to be normally distributed.

The occurrence and sequence of environmental states was chosen based on the environmental state cycle in Fig. 4. The interval between droughts (i) determined both the cyclic occurrence of environmental states and the probability of drought occurring in a given year ($1/i$). Thus, environmental states followed an i -yr cycle, which can also be seen by taking the eigenvalues of the transition matrix for the environmental states in Fig. 4 (S. L. Pimm, *personal communication*). Results will be affected by the absence of transitions between certain states, which do not occur by model definition (i.e., lag to lag, and drought to high). Not all such transitions are logically possible (i.e., lag to lag) or biologically likely (i.e., drought to high).

Deterministic and stochastic simulations were performed to examine how drought intervals affect kite population viability. I investigated both deterministic and stochastic drought intervals. For all simulations, initial population size was set at the preliminary viability estimate of 300 birds. In deterministic simulations, populations were projected for different fixed intervals between droughts using deterministic demographic rates for each environmental state (Table 2). Populations were projected for ≈ 20 yr or until a drought-flood cycle had been completed. In stochastic simulations, demographic rates were allowed to vary stochastically for each environmental state (Table 2). However, the interval between droughts was varied either deterministically ("perfectly periodic") or stochastically ("stochastically periodic"): these two classifications would be equivalent to deterministic periodic environments and stochastic homogeneous environments, respectively, in the terminology of Caswell (1989: 197). In the latter model, the likelihood of a

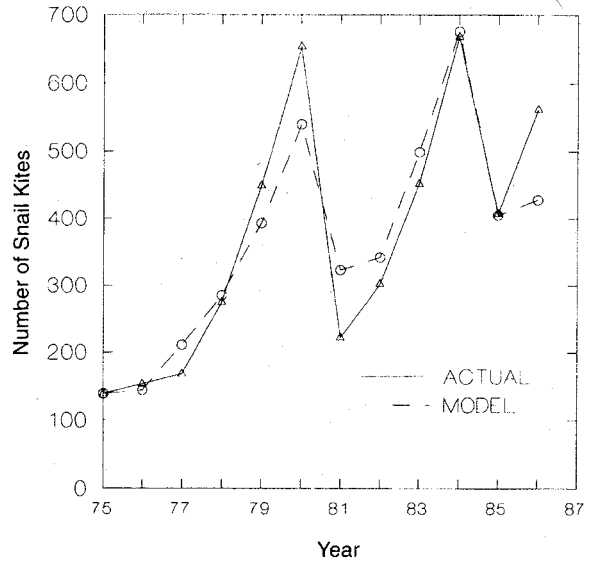


FIG. 5. The relationship between the number of Snail Kites censused in Florida and the number predicted based only on demographic parameters for the environmental states associated with actual water conditions. Only years when field studies were conducted were used.

drought occurring in a given year was determined by generating a random number from a binomial distribution based on the annual drought probability (i) for a given drought interval (Fig. 4). Perfectly periodic dry-downs might occur in wetlands where water levels were completely controlled by management operations (e.g., reservoirs). In nature, however, droughts occur with an average periodicity that includes some degree of stochastic variation or unpredictability in the time between successive droughts (Beissinger 1986). Also, the Everglades are too large for water levels to be managed completely independent of variation in rainfall. Thus, the stochastically periodic model would be more likely to apply to the Everglades. No carrying capacity or density functions were used in the simulations for reasons given earlier (also see Ginzburg et al. 1990).

Results

I compared the relationship between the number of kites predicted by the environmental state model and actual census data (Fig. 5). The predicted population size was based only on demographic parameters associated with actual water conditions (environmental states). These parameters were estimated independently from the population counts with one exception, i.e., the survival rate during droughts for which I used the average population decline during droughts (see *Defining environmental states and . . . above*). Actual kite numbers and the population size predicted by the model were closely associated (Fig. 5). Although the model captures the dynamics of the system, it may underestimate population highs and lows, which is likely to result in conservative estimates of extinction proba-

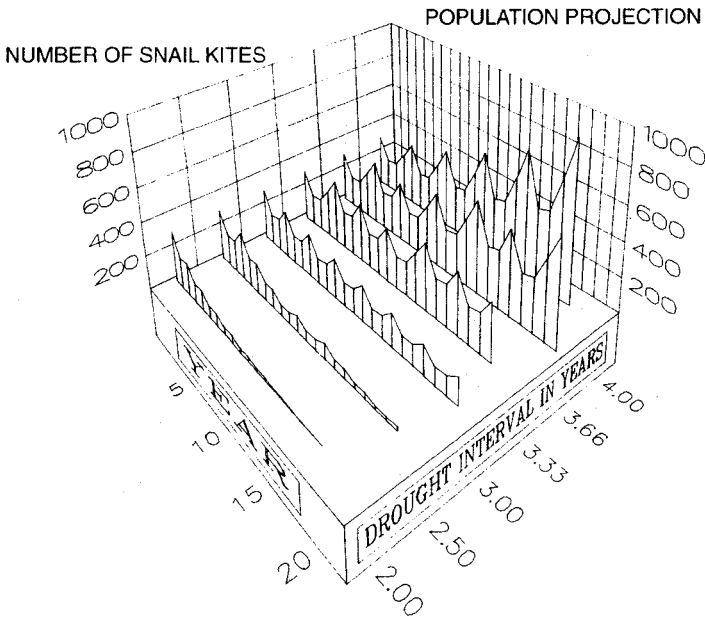


FIG. 6. Deterministic simulations showing the effects of the interval between dry-down or drought events on Snail Kite populations. A drought interval (i) of 3.0 yr is equal to three droughts in 9 yr or a probability of the occurrence of drought in a year of 0.33; an interval of 3.33 yr is equal to three droughts in 10 yr or an annual probability of occurrence of 0.30; and so on. Initial populations of 300 birds were projected for 20 yr or until the end of a drought-flood cycle.

bilities. However, this comparison cannot serve to validate the accuracy of model predictions. Validation would require comparing predicted population sizes from both the environmental state model and standard stochastic population projections to an independent time series of census counts, but insufficient data prevented this analysis.

The interval between droughts strongly affected kite population trends. In deterministic simulations, populations declined if drought occurred more frequently than once every 3.33 yr and increased when the interval between droughts reached or exceeded this frequency (Fig. 6). Sensitivity analysis suggested that reproductive parameters, which have been well studied (Snyder et al. 1989a), had the least effect on simulation outcomes (Table 3). Only changes in adult reproductive

capacity during high water years affected the results. Survivorship, however, had very important effects (Table 3). The model was most sensitive to changes in adult survivorship during drought and lag years. Subadult survivorship during droughts and fledgling survival during high years also had important effects.

Stochastic simulations indicated that viable kite populations required long hydroperiods, and were more strongly influenced by stochastically periodic than perfectly periodic drought intervals (Figs. 7 and 8). Kite populations did not reach a 95% likelihood of persistence for 50 or 100 yr when periodic drought occurred at variable intervals until the average interval between droughts exceeded 4.3 yr (Fig. 8). When drought occurred at fixed intervals, only a 3.3-yr or 3.6-yr interval was required for viable populations at 50 and 100 yr, respectively. This difference occurs because under variable intervals there is a chance that several drought years may happen sequentially, which may greatly decrease the population. However, under variable intervals kites also had a greater likelihood of reaching higher numbers (Fig. 7), because continuous high water conditions could occur, which would allow populations to increase greatly. The "boom" and "bust" nature of kite population dynamics is reflected in the shape of the cumulative probability function of ending population size for stochastically periodic droughts (Fig. 7). Although perfectly periodic droughts resulted in viable populations at shorter intervals than stochastic droughts, they increased the risk of extinction when dry-downs occurred at very short intervals (Fig. 8).

Because results from previous models were most affected by survivorship estimates (Table 3), a sensitivity analysis for the stochastic simulations was performed by changing annual adult survivorship. Such changes

TABLE 3. Sensitivity analyses for the deterministic projection of the effects of drought intervals on Snail Kite population trends (Fig. 5). Each demographic parameter was increased and decreased by 10% for drought intervals of 3.0 and 3.33 yr. The average percentage change in final population sizes are shown. Because changes in the number of nesting attempts per year, proportion of birds breeding, nesting success, and number fledging per nest had the same effect on final population size, they were grouped together as reproductive parameters. See Table 2 and *Modelling effects of water level . . . : Defining environmental states and . . .* for the definitions of environmental states.

| Demographic parameter | Age class | Environmental state | | | | | |
|-----------------------|-----------|---------------------|------|-----|------|------|------|
| | | Drought | | Lag | | High | |
| | | 3.0 | 3.33 | 3.0 | 3.33 | 3.0 | 3.33 |
| Reproduction | Subadult | 0 | 0 | 0 | 0 | 0 | 1 |
| | Adult | 0 | 0 | 6 | 7 | 25 | 26 |
| Survival | Fledgling | 0 | 0 | 6 | 8 | 26 | 27 |
| | Subadult | 27 | 21 | 0 | 0 | 5 | 8 |
| | Adult | 54 | 43 | 70 | 58 | 26 | 30 |

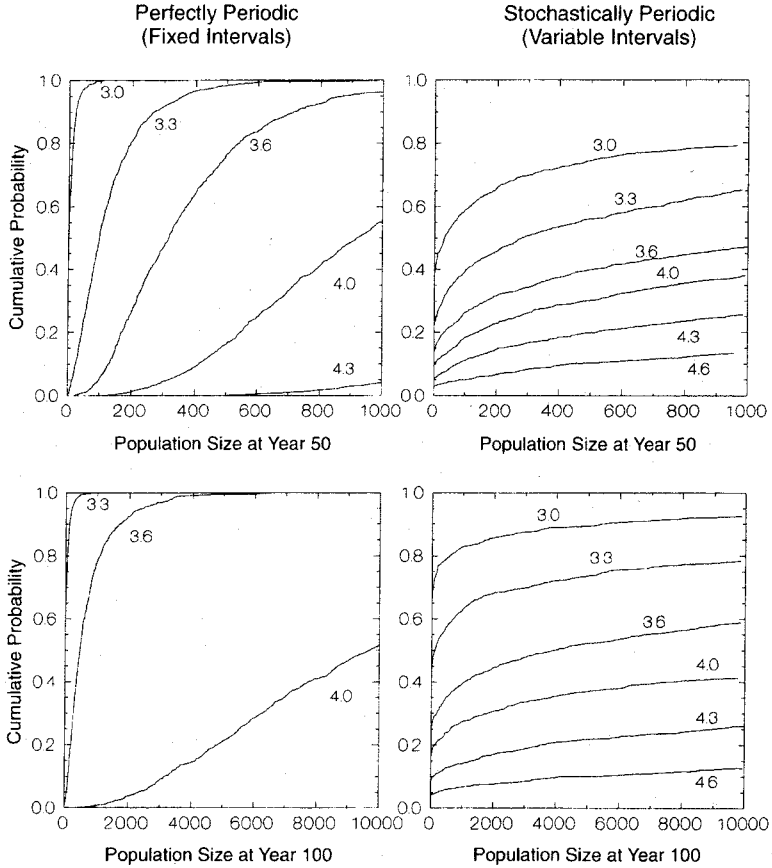


Fig. 7. Results from stochastic simulations of the effects of drought intervals on Snail Kite populations. The interval between droughts was allowed to vary at either fixed intervals ("perfectly periodic") or at variable intervals ("stochastically periodic"). Cumulative probability functions for the ending population size at 50 and 100 yr are shown based on 1000 replications each beginning with 300 individuals.

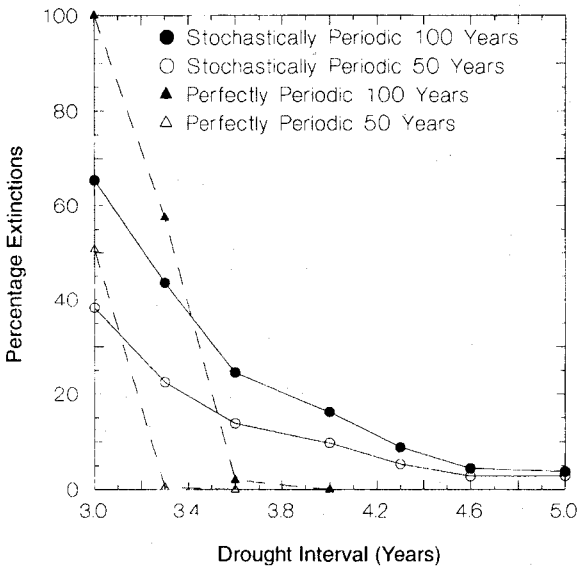


Fig. 8. Results from stochastic simulations in Fig. 7 for the effects of drought intervals on the viability of Snail Kite populations. See legend in Fig. 7 for details.

generally shifted the average interval between droughts that is required for a viable kite population by 1 yr. When annual adult survivorship during drought conditions was changed by adding 0.1, viable populations required an average interval of only 3.6 yr rather than 4.6 yr between dry-downs. However, when survivorship during lag or high years was changed by subtracting 0.1, viable populations were reached at 5.3-yr and 5.6-yr intervals for 50 and 100 yr, respectively, instead of at 4.6-yr intervals.

DISCUSSION

PVA is a relatively new management tool that is usually based on annual random fluctuations in demographic characteristics due to environmental stochasticity (Shaffer 1981, 1990, Gilpin and Soulé 1986, Boyce 1992). However, environmental variation can exhibit long-term cycles that directly affect demography and population fluctuations (Stearns 1981, Beissinger 1986, Witteman et al. 1990, Krukonis and Schaffer 1991, Burroughs 1992, Beissinger and Gibbs 1993). For example, El Niño events may occur with periodic-

ities of ≈ 3 yr, varying from 2 to 10 yr between events (Quinn et al. 1978, Philander 1983, Fei-Fei et al. 1994, Tziperman et al. 1994), and can have strong effects on the fecundity and survivorship (Boag and Grant 1984, Schreiber and Schreiber 1984, 1989, Gibbs and Grant 1987a, b). Standard stochastic projections of populations (Burgman et al. 1988, Boyce 1992) based on annual means and variances for demographic rates incorporate both long-term periodicity and short-term fluctuations. Such projections would likely result in inaccurate estimates of extinction probabilities (Tuljapurkar and Orzack 1980, Tuljapurkar 1985).

This paper applies an approach to PVA based on the use of environmental states. Classifying environments into states has been explored by demographers (Cohen 1976, 1979a, b, Tuljapurkar 1985, 1989, Caswell 1989) and used as a method to measure environmental predictability and periodicity (Colwell 1974, Stearns 1981, Beissinger and Gibbs 1993). Here I applied a similar approach as a way to examine the effects of environments and environmental management on population viability. Given the large year-to-year changes in demographic rates under oscillating environmental conditions, accurate measures of demography are often difficult to characterize and may differ radically among cohorts depending on environmental conditions at the time of birth. In such environments, demography may be easier to quantify if the environment can be classified into states on the basis of physical conditions and demographic responses. In addition, the effects of environmental variation on population viability swamp out the effects of demographic stochasticity in cyclic or oscillating environments. The use of environmental states partitions the variance in annual demographic rates among environments. This allows PVA models to be greatly refined and should increase the reliability of their predictions. For example, Bierzychudek (1982) found that the environmental state approach more accurately predicted population growth than the element approach in a study of a forest perennial herb. Classifying environments into states is also useful when environmental patterns are periodic, and there is some contingency or dependency of one state on another (Colwell 1974). Criteria for designating environmental states depend on how environmental fluctuations affect the organism, but should be quantifiable (Stearns 1981, Beissinger and Gibbs 1993).

Many kinds of environmental variation, including aperiodic environments and catastrophes, can be incorporated into the environmental state approach to PVA, depending on how the distribution of transition probabilities for the occurrence of environmental states is defined. In this paper, I modeled periodic environmental variation using time-invariant transition probabilities (i in Fig. 4) for the occurrence of environmental states that was unaffected by the past history of the system, even though I did incorporate past and present water level conditions into the definitions of

environmental states. Caswell (1989) and Tuljapurkar (1989) discuss the properties of and present models for a variety of other patterns of environmental variation, while Colwell (1974), Stearns (1981), and Beissinger and Gibbs (1993) discuss methods for detecting and measuring environmental periodicity and predictability.

The environmental state approach to modeling environmental variation and demography might be useful for other kinds of PVAs. Management decisions that may be modeled by this approach include understanding the effects of fire intervals and intensities on plant persistence, wetland dry-downs and burns for vegetation and waterfowl management, river flow regimes and dam discharges (Gilpin 1989, Soulé 1989), and different land management rotation programs (e.g., logging, mowing). Environmental states may be also useful to examine changes in the frequency of rainfall, severe storms or hurricanes, all of which are thought to be affected by global climate change (Emanuel 1987, Gray 1990, Schneider et al. 1992). The "state-based" approach to PVA is especially useful for examining the effects of management regimes that could occur at either regularly planned (deterministic) or unplanned (stochastic) intervals. For example, deterministic dry-downs resulted in viable kite populations at shorter intervals than stochastic droughts, but they greatly increased the risk of extinction when dry-downs occurred at very short intervals (Fig. 7).

The environmental state approach to PVA has several inherent disadvantages that are also common to traditional PVA approaches. First, using environmental states to classify demography is a data-rich procedure. To develop good fecundity and survival estimates for each environmental state will require at least several years of field data under each environmental condition. Likewise, good PVAs require extensive demographic information. Second, for nearly all PVA models there are insufficient data to test or validate extinction probabilities and the critical choice of the level of environmental variance (Boyce 1992). However, it is possible to test for the effectiveness of state definitions by examining how well environmental conditions alone predict population trends and whether they improve accuracy over stochastic fluctuations. Finally, for state-based models, the definition and categorization of environmental states require that some environmental variable can be measured and its effect on demography be understood.

The particular model developed here for the Snail Kite has two shortcomings. First, the model was sensitive to estimates of survival rates (Table 3), the demographic variable that is least well known for kites (Snyder et al. 1989a). Estimates of survivorship from systematic studies of large numbers of banded and telemetered birds would rectify this problem. Survival during drought conditions had the greatest effects on model outcomes, although the model was nearly as sensitive

to survivorship estimates during years of good water levels (Table 3). Few data currently exist to be confident of the pessimistic and optimistic estimates of survivorship that I used for high water and drought years, respectively.

Second, the model did not include a spatial component that would allow populations in different regions (e.g., the southern Everglades and Lake Okeechobee) to fluctuate somewhat independently in the fashion of a metapopulation. However, it is unlikely that the kite population in Florida is structured as a metapopulation because the birds move fluidly between Lake Okeechobee, the Central Lakes region, and the conservation areas (Sykes 1979, Beissinger and Takekawa 1983, Snyder et al. 1989a, Takekawa and Beissinger 1989). Furthermore, no genetic differences exist between birds nesting in these regions (J. A. Rodgers, *personal communication*). Nevertheless, once the extent and nature of movements of birds between wetland units are better known, spatially explicit models could be developed based on wetland-specific recruitment and survival rates (Snyder et al. 1989a), and immigration and emigration between regions for each environmental state.

Finally, results from this study have implications for Everglades water management. Nesting success, the length of the breeding season, and changes in kite numbers were all highly positively related to water levels (Table 1). It is possible that continued lowering of water levels, due to the demands of an expanding human population in southern Florida or to management activities such as the restoration of Everglades National Park (Walters et al. 1992, Davis and Ogden 1994), may result in dry-downs that are too frequent to maintain viable kite populations (Figs. 6–8). Unfortunately, the 14-yr period of record for hydrological modeling used by the U.S. Army Corps of Engineers to evaluate Everglades management options was too short to determine if this would occur; the difference between a viable and inviable kite population may be the difference between drying 3 times or 4 times during 14 yr. Furthermore, the effect of water management on drought intervals has not even been considered by ecologists in their plans to restore the Everglades (Davis and Ogden 1994). If kites continue to use federally designated Critical Habitat in CA3A, during dry years water deliveries from other areas (Walters et al. 1992) may help to assure that the periodicity of dispersal events or dry-downs regularly exceeds 4 yr. Strong correlations found between environmental conditions at CA3A in winter months and kite population changes the following year (Table 1) suggest that it is possible to predict in early winter which years are likely to need water deliveries in late spring.

Such management would also sustain long hydroperiod marshes, which although once probably an important part of the Everglades (Fennema et al. 1994) have all but disappeared under current water regimes.

A lack of long hydroperiod marshes will likely result in a decline in apple snails (*Pomacea paludosa*) and the many species of fishes, turtles, crocodylians and birds that feed on them (Fogarty and Albury 1967, Snyder and Snyder 1969, 1971, Kushlan 1975, Donnay and Beissinger 1993). Long hydroperiod marshes can act as a buffer to the seasonal variation in Everglades water levels that has increased during the past century (Beissinger 1986). Contrary to popular wisdom (Davis and Ogden 1994), the Everglades is one of the least seasonal wetlands in the Neotropics (Beissinger and Gibbs 1993), and increased seasonality of water levels could be expected to have negative effects on other components of the ecosystem.

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