

## Evaluating release alternatives for a long-lived bird species under uncertainty about long-term demographic rates

Clinton T. Moore · Sarah J. Converse ·  
Martin J. Folk · Michael C. Runge ·  
Stephen A. Nesbitt

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**Abstract** The release of animals to reestablish an extirpated population is a decision problem that is often attended by considerable uncertainty about the probability of success. Annual releases of captive-reared juvenile Whooping Cranes (*Grus americana*) were begun in 1993 in central Florida, USA, to establish a breeding, non-migratory population. Over a 12-year period, 286 birds were released, but by 2004, the introduced flock had produced only four wild-fledged birds. Consequently, releases were halted over managers' concerns about the performance of the released flock and uncertainty about the efficacy of further releases. We used data on marked, released birds to develop predictive models for addressing whether releases should be resumed, and if so, under what schedule. To examine the outcome of different release scenarios, we simulated the survival and productivity of individual female birds under a baseline model that recognized age and breeding-class structure and which incorporated empirically estimated

stochastic elements. As data on wild-fledged birds from captive-reared parents were sparse, a key uncertainty that confronts release decision-making is whether captive-reared birds and their offspring share the same vital rates. Therefore, we used data on the only population of wild Whooping Cranes in existence to construct two alternatives to the baseline model. The probability of population persistence was highly sensitive to the choice of these three models. Under the baseline model, extirpation of the population was nearly certain under any scenario of resumed releases. In contrast, the model based on estimates from wild birds projected a high probability of persistence under any release scenario, including cessation of releases. Therefore, belief in either of these models suggests that further releases are an ineffective use of resources. In the third model, which simulated a population Allee effect, population persistence was sensitive to the release decision: high persistence probability was achieved only through the release of more birds, whereas extirpation was highly probable with cessation of releases. Despite substantial investment of time and effort in the release program, evidence collected to date does not favor one model over another; therefore, any decision about further releases must be made under considerable biological uncertainty. However, given an assignment of credibility weight to each model, a best, informed decision about releases can be made under uncertainty. Furthermore, if managers can periodically revisit the release decision and collect monitoring data to further inform the models, then managers have a basis for confronting uncertainty and adaptively managing releases through time.

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C. T. Moore (✉)  
USGS Patuxent Wildlife Research Center,  
Warnell School of Forestry and Natural Resources,  
University of Georgia, 180 E Green St, Athens, GA 30602, USA  
e-mail: cmoore@warnell.uga.edu

S. J. Converse · M. C. Runge  
USGS Patuxent Wildlife Research Center,  
12100 Beech Forest Rd, Laurel, MD 20708, USA

M. J. Folk  
Florida Fish and Wildlife Conservation Commission,  
1475 Regal Ct, Kissimmee, FL 34744, USA

S. A. Nesbitt  
Florida Fish and Wildlife Conservation Commission,  
4005 S Main St, Gainesville, FL 32601, USA

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## Introduction

The release of individual organisms that have been either raised in captivity or translocated from a wild population is a common strategy for reestablishing an extirpated plant or animal population (Falk 1992; Wilson and Stanley Price 1994). A population is successfully established when it is capable of replacing itself over some long time frame, i.e., when a sustained growth rate  $\geq 1.0$  is achieved in the population (Pavlik 1994).

However, release programs are typically expensive to start and sustain (Kleiman 1989). To a management agency attempting to restore a population, it is wasteful of resources to continue releasing organisms beyond the point in time where it becomes apparent that either (1) the population is self-sustaining (Armstrong and Ewen 2001; Schaub et al. 2009; Wakamiya and Roy 2009) or (2) the population is simply incapable of self-sustenance, despite any future stream of releases. The management agency would therefore like to discontinue releases when either of these scenarios becomes evident.

For some organisms, these decision points may be quickly and confidently determined, but for other organisms—particularly those that are long-lived, have delayed reproduction and low rates of productivity, or have life history characteristics that expose them to a diversity of reproductive challenges and survival hazards—questions about the release process (how many individuals to release each year, whether to abandon releases) are harder to answer. In such cases, population viability analysis (PVA) may be used to guide release decision-making (Akçakaya et al. 1995; Sarrazin and Legendre 2000; Bell et al. 2003; Slotta-Bachmayr et al. 2004; Schaub et al. 2009; Wakamiya and Roy 2009). A PVA synthesizes current knowledge about a species' life history and uses iterative simulation to project consequences of alternative management decisions in a context of unpredictable environmental and demographic stochastic effects on survival and productivity (Gilpin and Soulé 1986; Menges 1991; Akçakaya and Sjögren-Gulve 2000). The typical output of a PVA model is an estimate of the probability of population persistence (or extinction), according to some threshold definition of persistence over a specified time frame (Akçakaya and Sjögren-Gulve 2000).

One key challenge in the construction of a PVA is the credible representation of different sources of process variation in survival and reproduction. Some sources of variation may be reasoned to affect all individuals equally (e.g., wide-scale environmental effects); others derive from membership in a demographic group (e.g., sex/age class, reproductive status, release cohort); still others are due to inherent differences among individuals (Menges 1992). Furthermore, when population data are used to parameterize

a PVA, the separation of process variation from sampling error is crucial for making an inference about population growth (Clark and Bjørnstad 2004). Failure to take into account important sources of process variability in a PVA overestimates population persistence (Melbourne and Hastings 2008), with the possible consequence of sub-optimal management decision-making.

Another challenge in the use of a PVA for decision-making is the fact that traditional PVA models have no means to formally accommodate biological uncertainty in a decision analytic context. Bayesian PVA, in which the population simulation is conducted under parameter values drawn repeatedly from their posterior distributions, has been proposed when estimation uncertainty attends PVA model parameters (Wade 2002).

However, the structure or parameterization of the model may be so uncertain that multiple plausible models could be easily and justifiably proposed, and there seems to be no consensus as to how to arrive at a decision under such uncertainty. Several ad hoc approaches have been used. One approach involves choosing a single model based on a superior goodness-of-fit statistical test or information criterion result, but this approach is not so much a way to resolve uncertainty as an attempt to sidestep it. That is, by choosing one model, all of the belief is placed on that model, when a model fit result might only suggest a relative placement of weight. This can have very undesirable consequences for decision-making (Pascual et al. 1997; Runge and Johnson 2002). When competing models are recognized, a common argument is that a PVA is nevertheless useful and sufficiently robust for a comparative ranking of management alternatives (Beissinger and Westphal 1998; Akçakaya and Sjögren-Gulve 2000), and simulation studies support this assertion (McCarthy et al. 2003). Alternatively, one can select the single model that represents the “worst-case scenario” and use the model in a decision analysis to manage against the undesired outcome (Akçakaya and Sjögren-Gulve 2000; Taylor et al. 2002). However, either approach (comparative ranking or worst-case modeling) is unhelpful if there exist multiple objectives of management to be formally considered (e.g., minimization of a cost function) or if models project profoundly different outcomes of the decision. Last, one can use model-averaging techniques that generate predictions on the basis of empirically determined model weights, but this requires relevant data. In many reintroduction settings for endangered species, high biological uncertainty is the rule rather than the exception, and in some cases, no relevant data will be available with which to address model uncertainty (for example, anticipated future changes in key demographic parameters that cannot be detected with the available dataset). Tools that more directly confront uncertainty are needed to guide managers in these situations.

We consider the problem of releasing Whooping Cranes (*Grus americana*) to establish a population in Florida, USA. The Whooping Crane is a critically endangered North American bird. Approximately 500 individuals are estimated to exist worldwide (T. Stehn, U.S. Fish and Wildlife Service, unpublished report, September 2008), with about one quarter of the global population held in breeding facilities. International management of the species is guided by the Whooping Crane Recovery Plan, which calls for the establishment of one to two self-sustaining breeding populations to augment the sole wild population that migrates between Canada and the USA. A reintroduction effort began in 1993 with the release of Whooping Crane chicks to establish a non-migratory flock in Florida. A second reintroduction effort was started in 2001 to establish a Wisconsin–Florida migratory flock; in this effort, chicks imprinted on an ultralight aircraft are led on their initial migratory path.

Decision-making about releases in both efforts is hampered greatly by the fact that Whooping Cranes are long-lived birds with delayed age to reproduction ( $\geq 4$  years) and low rates of productivity (on average,  $< 1$  fledglings per pair annually in the wild population). Released birds for both projects come from captive populations, and it is not well known how vital rates for such birds differ from their wild counterparts or from their own wild-fledged offspring.

The Florida Fish and Wildlife Conservation Commission (FWC) released Whooping Cranes annually from 1993 to 2004. By 2004, and after the release of 286 birds, the flock had produced only four wild-fledged birds (through 2009, an additional 6 chicks have been produced). The release program was suspended in 2004 because of managers' concerns of high adult mortality and low productivity of released birds. We therefore undertook a modeling effort to address the question of whether releases should be resumed, and if so, in what pattern and intensity through time. This work follows an effort to estimate hierarchical components of survival and productivity in the population (Moore et al. in preparation) and precedes an effort to formally consider the population viability model in the context of other objectives in a multi-stakeholder structured decision analysis (Converse et al. in preparation).

Our work had three objectives. First, we wanted to build a baseline PVA model that incorporated empirically estimated sources of process variance at several meaningful hierarchical levels and that accounted for uncertainty in these estimates to project population outcomes under alternative release scenarios. Second, we wanted to construct plausible alternatives to this baseline model to express uncertainty about underlying biological mechanisms. Third, we wanted to evaluate the best release scenario for achieving the greatest projected probability of population establishment conditional on model choice, and

we wanted to illustrate an approach for finding the single, best release scenario under uncertainty about the predictive accuracy of each of the competing models.

## Methods

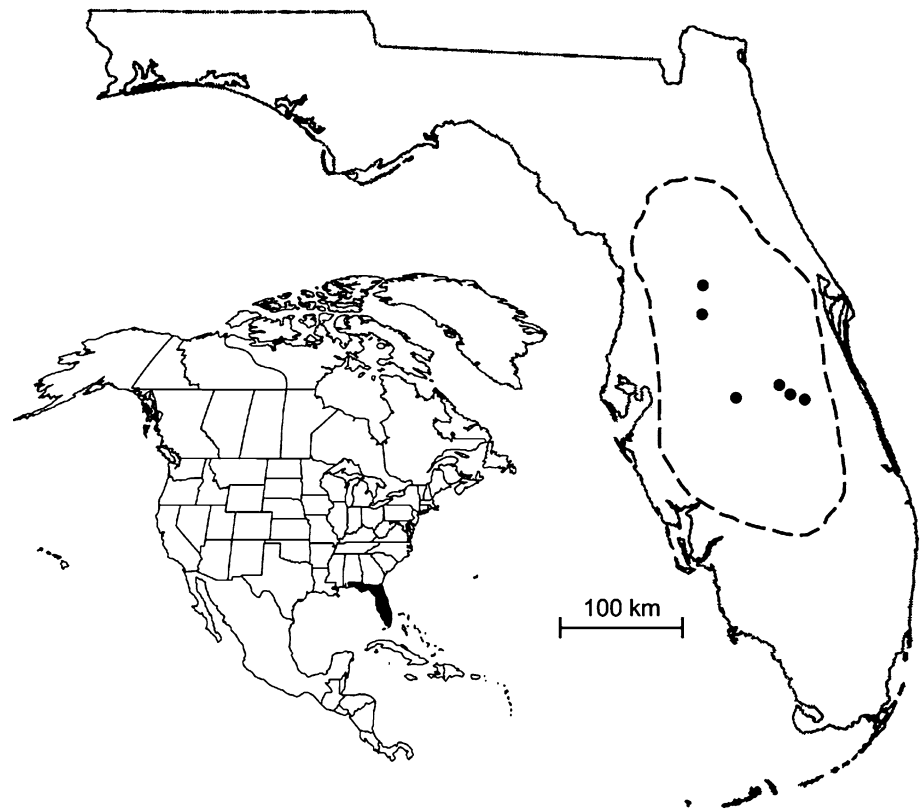
### Data collection

Between 1993 and 2004, 286 captive-reared Whooping Cranes were released annually in batches (“release cohorts”) of 1–14 (mode = 8) birds at a time, two to seven times per year at locations in central Florida (Fig. 1). Each cohort comprised birds drawn from different captive rearing facilities and was assembled with an approximately equal representation of sexes. Nearly all of the birds were released as chicks ( $< 1$  year of age); a few (5%) were released as 1 year olds. Birds were hatched and raised in captivity at the USGS Patuxent Wildlife Research Center (Laurel, Maryland, USA; 66%), the International Crane Foundation (Baraboo, Wisconsin, USA; 27%), and other zoological facilities (7%). Upon arrival in Florida, birds were held approximately 2 weeks in an acclimation pen; at release, each bird was equipped with a radio transmitter, a numbered leg band, and a unique combination of colored leg bands. Releases occurred in the cooler months (October–April), often at a different location each year and sometimes at multiple locations within a year.

A series of health checks on each bird during the acclimation period yielded data on bird weight and other physiological measurements just prior to release. After release, field biologists attempted to detect each bird's unique radio transmission on a weekly basis and determine whether the radio was transmitting in “mortality mode,” an indication of the bird's death or detachment of the transmitter. If the signal indicated mortality, a search was made for the carcass and, if found, the biologist attempted to determine the cause of death. If the transmitter separated, or if the transmission signal failed, biologists attempted to locate the bird by searching at sites known to be used by the bird or its associates, capture it, and affix a new transmitter. If the bird had not been located within 6 months of its signal loss, it was assumed to have exited the population, either through death or permanent emigration from the region (e.g., 9 of 16 birds that dispersed from Florida did not return; Folk et al. 2008). Thus, in our survival rate modeling (see below), “survival” refers to the joint probability of surviving and remaining in the region.

During weekly searches for birds, biologists recorded reproductive behaviors, including formation/dissolution of pair bonds, pair membership, nesting activity, and productivity. The fate of each egg produced was followed through incubation, hatching, and rearing. Chicks that

**Fig. 1** Reintroduction area (dashed region) and release locations (filled circles) of 286 captive-reared Whooping Cranes (*Grus americana*) released between 1993 and 2004 in Florida, USA



fledged (became independent of parental care and attention) were captured, marked, fitted with a radio transmitter, and released. Wild-fledged (WF) birds were then monitored in the same manner as captive-reared (CR) birds.

#### General model framework

We built an age- and breeding stage-structured model framework around which the two major phases of our work, the statistical estimation and the population simulation phases, were organized (Table 1, Fig. 2). The framework focused on the female segment of the Whooping Crane population. We justified this focus because our empirical estimates of breeding class transition and productivity (see “Parameter estimation” section below) implicitly incorporated effects caused by any sex ratio variation that occurred during the release program, and our assumption was that such variation would continue into the future, with unchanged effects on productivity. Survival and the initiation of reproductive behavior in Whooping Cranes are both closely tied to age; therefore, the framework allowed for different survival among five discrete age classes (ages 0, 1, 2, 3, 4+ years; defined as number of whole years since July 1 of hatch year, the approximate fledging date) and, similarly, for the transition into first breeding status (initiation of pair-bonding). Once a female enters breeding status, her breeding experience, rather than age, may be a better predictor of her

survival and productivity, as this change in status appears to initiate a life-long change in behaviors (S.A. Nesbitt, FWC, unpublished data). Therefore, our framework recognized three sequential breeding classes, each with a unique survival rate, rate of productivity, and probability of transition into the next higher class: (1) paired females (or unpaired females with a previous history of pairing) lacking a previous history of nestling production (class P); (2) paired or unpaired females with previous production of nestlings but no previous history of fledgling production (class N); (3) paired or unpaired females with previous production of fledglings (class F). Wild-fledged females were assumed to follow the same scheme of model transitions as captive-reared females, but these transitions were governed by potentially different rates of survival, productivity, and breeding class transitions: as will be seen later, competing hypotheses about the degree of similarity of parameters in the WF and CR segments represented biological uncertainty that strongly influenced predicted outcomes.

#### Parameter estimation

We estimated parameters of age-specific survival, breeding class transition, and productivity rate for the CR population segment in hierarchical linear-logit models. The hierarchical approach permitted separate estimation of parameters related to the sampling of birds (observation error) from

**Table 1** Parametric structure of a population simulation model for Whooping Cranes (*Grus americana*) reintroduced in Florida, USA

Parameter Group	Age Classes (Never Paired Birds)					Breeding Classes		
	0	1	2	3	4+	P	N	F
Annual survival								
Mean rate	$\varphi_0$	$\varphi_1$	$\varphi_2$	$\varphi_3$	$\varphi_{4+}$	$\varphi_P$	$\varphi_N$	$\varphi_F$
Cohort effect	$\sigma^2_{C0}$	$\sigma^2_{C1}$	←————— $\sigma^2_{C2+}$ —————→					
Bird effect	$\sigma^2_{B0}$	$\sigma^2_{B1}$	←————— $\sigma^2_{B2+}$ —————→					
Time effect	←————— $\sigma^2_T$ —————→							
Transition into Paired (P) breeding class								
Mean rate		$\Psi_{UP}^{(1)}$	$\Psi_{UP}^{(2)}$	$\Psi_{UP}^{(3)}$	$\Psi_{UP}^{(4+)}$			
Bird effect		←————— $\sigma^2_{PB}$ —————→						
Time effect		←————— $\sigma^2_{PT}$ —————→						
Transition into Nestling (N) breeding class								
Mean rate						$\Psi_{PN}$		
Bird effect						$\sigma^2_{PNB}$		
Transition into Fledgling (F) breeding class (= rate of fledgling production)								
Mean rate						$\Psi_{PF}$	$\Psi_{NF}$	$\Psi_{FF}$
Bird effect						$\sigma^2_{PFB}$		

Mean rates of survival ( $\varphi_i$ ) and breeding class transitions ( $\psi_{ij}$ ) are augmented by random effects ( $\sigma_i^2$ ) attributed to time, the bird's release cohort, or the bird itself (parameter subscripts and superscripts refer to age classes, breeding classes, or variation sources as described in the text). Estimates for all parameters were obtained from data on 286 captive-reared Whooping Cranes released between 1993 and 2004 under a hierarchical Bayesian statistical model employing the same structure

<sup>a</sup> P, Paired females (or unpaired females with a previous history of pairing) lacking a previous history of nestling production; N, paired or unpaired females with previous production of nestlings but no previous history of fledgling production; F, paired or unpaired females with previous production of fledglings

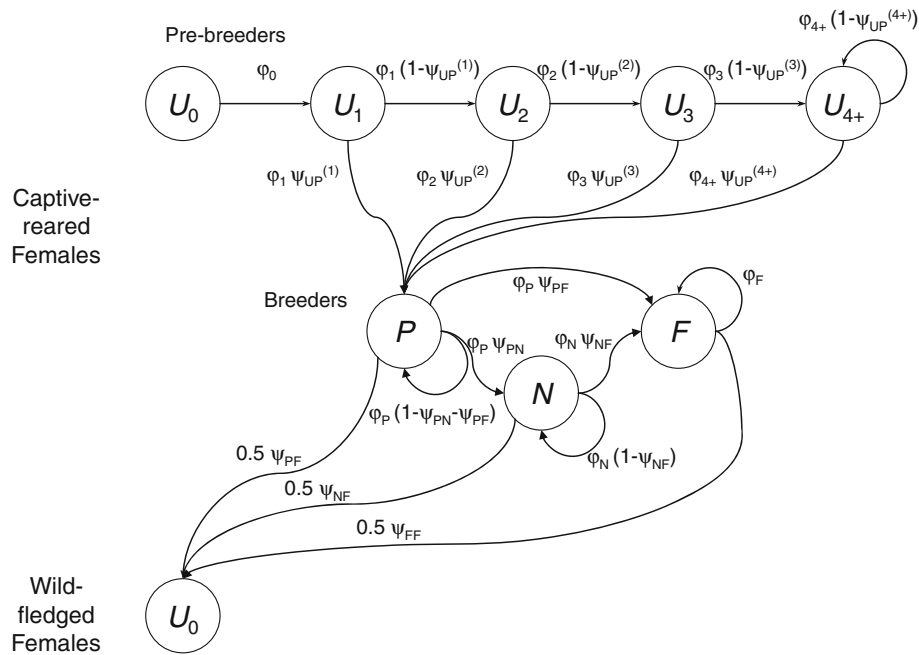
those related to process variation (Clark and Bjørnstad 2004). We used data on CR birds collected through June 2007. The models and estimation procedure are briefly presented below and in Appendix; a full description is provided elsewhere (Moore et al. in preparation).

*Survival estimation*

To make more efficient use of available telemetry data for survival estimation, we fit a model to data from both sexes of CR birds; however, through use of an additional model parameter for a sex-related survival effect, we were able to isolate and retrieve female-specific survival estimates for later use in the population simulation phase of our work.

We divided the 1993–2007 data period into quarters of a year (January–March, April–June, etc.), and we estimated the probability of survival in each quarter as a function of fixed effects (intercept, sex) and random effects (age/stage, time, release cohort, individual). We modeled the set of age class and breeding class-specific survival means ( $\varphi_i$ ) as a random effect with values drawn from a zero-centered normal distribution with variance parameter  $\sigma_G^2$ . Time was a random effect assumed to arise from a zero-centered normal distribution with variance  $\sigma_T^2$ ; thus, time had a uniform effect on the survival of all birds alive in any particular portion of the year (Table 1).

We included in the model of survival a random effect of cohort membership for each individual. Some characteristics



**Fig. 2** Female-based model for projecting dynamics of the Florida non-migratory Whooping Crane population through time. Birds released ( $U_0$ ) into the population survive annually into successive age classes of unpaired birds ( $U_1$ ,  $U_2$ ,  $U_3$ ,  $U_{4+}$ ), and unpaired birds may themselves survive and become paired ( $P$ ). Paired birds may then survive and produce no young, nestling(s) that do not fledge, or fledgling(s). Likewise, birds that have ever produced only nestlings ( $N$ ) may become fledgling producers ( $F$ ). All fledglings produced by

any class of breeder become the 0 age class of the wild-fledged segment. Symbols along arrows represent the mean survival and transition rates displayed in Table 1. Subscript pairs  $ij$  represent transitions from class  $i$  to class  $j$ . Pathways within the wild-fledged segment (not shown) are identical to the captive-reared segment; however, rates of transition among classes may differ between the two segments according to the hypothesized model

of the release cohort (composition and social structure, release location, circumstances of the acclimation and release) could be assumed to affect survival in a consistent way for all birds in that cohort. It may also be reasonable to assume that such effects diminish with time among the surviving birds. Therefore, we modeled the cohort random effect interactive with time using three zero-centered normal distributions. Through a bird's first year of life, the cohort random effect was assumed to arise from a distribution with variance  $\sigma_{C0}^2$ ; in its second year, the effect was assumed to arise from a distribution with variance  $\sigma_{C1}^2$ ; beyond its second year, the effect was assumed to arise from a distribution with variance  $\sigma_{C2+}^2$  (Table 1).

Lastly, we included an individual, bird-level random effect in the model of survival. A bird's specific genetic makeup, its rearing conditions, or its unique behavior in the wild could all influence survival in a way that is distinct from other birds. Furthermore, if a bird's individual experiences prior to and immediately following release are large components of this effect, then the bird random effect could be reasoned to diminish with time as those experiences become farther removed with survival of the bird. Therefore, we modeled the bird-level random effect interactive with time, as we did for the cohort effect. That is, we assumed that the bird random effect arose from zero-

centered normal distributions with variance parameters  $\sigma_{B0}^2$ ,  $\sigma_{B1}^2$ , and  $\sigma_{B2+}^2$  corresponding to the first, second, and post-second years of life, respectively (Table 1). Interactive parameters for the bird- and cohort-level random effects allow demographic variability to change as a function of time since release. This might be reflected as a short-term period of high population loss immediately after release, as has been observed in other populations of released birds (Sarrazin and Legendre 2000; Le Gouar et al. 2008).

#### Estimation of productivity and breeding class transition probabilities

Captive-reared female Whooping Cranes infrequently produced nestlings in the same year they first pair-bonded (4 of 11 nestling-producing females). Thus, our model framework portrayed the more common occurrence of a female first spending  $\geq 1$  years in breeding class P before ever producing nestlings (transition into breeding class N) or fledglings (transition into class F).

We modeled productivity and breeding class transitions in a group of sub-models. First, for all females surviving to age 2 years, we built a sub-model to estimate the probability of transition from never-paired into newly-paired



status as a function of age class membership in the previous breeding season ( $\psi_{UP}^{(i)}$ ; probability of entering class P at given age  $i = 1, 2, 3,$  or  $4+$  in the previous year). Because annual environmental or demographic conditions may affect the initiation of pairing for all birds in a year, the sub-model also contained a random effect due to year (zero-centered normal distribution, variance  $\sigma_{PT}^2$ ). Finally, we included an individual bird random effect (zero-centered normal distribution, variance  $\sigma_{PB}^2$ ) to model bird-to-bird variability in this transition probability (Table 1).

Next, we developed a sub-model that predicted the probability of production of a female's first nestling ( $\psi_{PN}$ ; transition into breeding class N) or first fledgling ( $\psi_{PF}$ ; transition into class F) given that she had ever paired as of the previous year. Because we had fewer data to work with (analyses were restricted to females in breeding class P each year), we did not include a temporal random component in the sub-model; however, we did include bird-level random effects (zero-centered and normally-distributed) with variances  $\sigma_{PNB}^2$  and  $\sigma_{PFB}^2$  for the class N and class F transitions, respectively (Table 1). No Florida bird has ever produced more than a single fledgling in a breeding season; thus, the transition rate  $\psi_{PF}$  also serves as the estimated productivity rate (male or female offspring) for a class P female.

Last, we developed two sub-models that predicted the probability of first production of a fledgling by a female currently in breeding class N ( $\psi_{NF}$ ) and the probability of subsequent production of a fledgling by a female currently in breeding class F ( $\psi_{FF}$ ). Because data were very sparse for both sub-models (analyses were restricted to females having ever produced nestlings only, or to fledglings, respectively), we estimated a simple mean and variance for both parameters and did not consider contributing random effects (Table 1). For the same reason stated above, the transition rate parameters  $\psi_{NF}$  and  $\psi_{FF}$  also serve as the estimated rates of productivity for class N and class F females, respectively.

For each of the estimation models and sub-models here described, we used Markov-chain Monte Carlo (MCMC) sampling in the software WinBUGS (Gilks et al. 1994) to compute posterior probability distributions for all model parameters (Moore et al. in preparation). Mean effects in all models were sampled from vague normal prior distributions with mean 0 and variance  $\geq 1,000$ . Random effect variances ( $\sigma_i^2$ ) in all models were drawn as precision values (i.e.,  $1/\sigma_i^2$ ) from vague gamma distributions with mean 1 and variance  $\geq 500$ . We derived posterior distributions from three MCMC chains, gathering 1,000,000 samples from each chain following a burn-in run of 40,000 samples, and we examined the chains to confirm their convergence. To reduce the effects of serial autocorrelation, we “thinned” each chain by eliminating all but every 100th sample.

Combining the thinned chains thus yielded a final set of 30,000 samples to define the posterior distribution.

### Construction of the baseline PVA model

Using estimated posterior distributions of all the effects described above (age- and breeding class-specific survival rates  $\phi_i$ , transition probabilities into and among breeding classes  $\psi_{ij}$ , random effect variances for survival and transition probabilities  $\sigma_i^2$ ; see note in Appendix), we constructed an individual-based PVA model for the female segment of the Florida population. Given an initial population of females of known age and breeding class structure and known birth source (CR or WF), the model advanced each bird through annual stochastic processes of survival, entry into the paired breeding class, transition among breeding classes, and production of fledglings. Because the model used an annual time step, we estimated annual survival rates (and their corresponding posterior distributions) by multiplying appropriate sets of quarterly survival parameters within the MCMC sampling runs. To distinguish this model from alternative models later described, we termed this the “Baseline” model, or model  $M_{Base}$ .

Model  $M_{Base}$  was structured in two nested iterative loops. The outermost loop (“sampling” loop) drew values of model parameters from their posterior distributions; thus, different draws of values within this loop reflected uncertainty due to model parameter estimation (Wade 2002). For a given draw of parameter values in a sampling iteration, control passed to a “replication” loop, in which the model simulation was run multiple times over a fixed time horizon. The parameter values defined probability distributions from which random effects were drawn and assigned to individual birds and time periods in the simulation. Hence, this loop reflected stochastic environmental and demographic uncertainty in the survival and productivity processes.

A replication iteration was initialized with each bird in the starting population (time 0) assigned a complement of nine random effects: (1) three age-specific individual random effects for survival (from the zero-centered normal distributions indexed by  $\sigma_{Bi}^2$ ,  $i = 0, 1, 2+$ ); (2) 3 age-specific cohort-level random effects for survival (from the normal distributions indexed by  $\sigma_{Ci}^2$ ,  $i = 0, 1, 2+$ ); (3) an individual random effect for the probability of transition into the paired breeding class (from the normal distribution indexed by  $\sigma_{PB}^2$ ); (4) individual random effects for the probability of transition from the paired class into classes N and F (from the normal distributions indexed by  $\sigma_{PNB}^2$  and  $\sigma_{PFB}^2$ ). Because the cohort-level random effect for survival applied only to released birds, we fixed  $\sigma_{Ci}^2 = 0$  for WF birds. Within the annual time steps of the simulation, as new birds were added to the population either through

releases or successful fledging, a complement of random effects was drawn for each bird. Each bird retained its assigned random effects as long as it persisted within the simulation. We prevented any bird from surviving indefinitely in the simulation by incrementally reducing its survival rate each year after age 15 years (the length of our study) to 0 by age 30 years, which is the approximate midpoint of the maximum life span assumed for wild birds (23 years; Binkley and Miller 1980) and the age of the oldest known individual (38 years; Patuxent Wildlife Research Center captive rearing facility).

In combination with the age- and breeding class-specific mean effects, the assignment of random effects resulted in bird-specific probabilities of survival, breeding class transition, and fledgling production for the simulation. Furthermore, because of random effects induced by time (variances  $\sigma_T^2$  and  $\sigma_{PT}^2$ ), these probabilities also varied year to year within the simulation. The simulation moved the population forward from 1 year to the next, with stochastic births, deaths, and breeding class transitions determined by draws from Bernoulli distributions indexed by this full set of probabilities.

#### Alternatives to the baseline model

A key uncertainty that influences predicted outcomes of bird releases is the extent to which the demographic performance of wild-fledged birds reflects that of their captive-reared parents. This is an important source of uncertainty because the performance of wild-fledged birds has often been observed to exceed that of captive-reared birds (Buner and Schaub 2008; Heath et al. 2008; Roche et al. 2008). Because the Florida population has seen too few wild-fledged birds to make reliable inferences (only two of the wild-fledged females had entered breeding states at the time parameter estimation was completed), decision-making about releases should be considered in the light of plausible alternative hypotheses (Williams et al. 2002). We constructed two alternatives to the model  $M_{Base}$  using sets of available parameter estimates. The three models all simulated individual female birds in the population and projected them through time in response to hypothesized survival and productivity rates and periodic releases of captive-reared chicks. The models differed in how vital rates for the CR and WF segments of the population resembled or differed from each other. In all three models, survival and productivity parameters estimated solely from the CR segment of the population were assumed to apply to simulated CR birds (i.e., we assumed that the demographic rates of CR birds would continue at rates observed between 1993 and 2007). In the Baseline model, these estimated rates were assumed to also apply to simulated WF birds.

In an alternative model (model “ $M_{Wild}$ ”), survival and productivity rates of the WF segment were assumed to more closely correspond to those of the only wild flock in existence, the Aransas-Wood Buffalo (ARWB) migratory flock. Thus, estimated rates for that population (Link et al. 2003) were applied to simulated WF birds. We applied the estimated overall survival rate from their work (0.91; model CAAE) to all age and breeding classes of WF birds in place of survival rates estimated from CR females (0.66–0.82 for unpaired birds, 0.79–0.94 for birds in breeding classes). Link et al. (2003) also provided information on year-to-year variability in survival rate as well as estimation uncertainty; therefore, the survival rate applied to WF birds varied from year to year and among simulation runs (to account for estimation uncertainty). For productivity, we assumed that CR and WF birds shared a common rate of transition into the breeder classes (i.e., probability that an unpaired female forms her first pair bond). However, we applied the ARWB estimate of average per-breeder productivity rate (0.33; 1938–2001 period) to WF birds in place of the three breeding class-specific productivity rates estimated from the CR data (0.05, 0.0, and 0.36 for classes P, N, and F, respectively). As we did for the survival rate parameter, we incorporated the annual stochastic variation and parameter estimation uncertainty (provided by Link et al. 2003) in our simulations of recruitment rate; thus recruitment rate for WF birds varied among years and simulation runs.

A third model form considered an Allee-type effect (model “ $M_{Allee}$ ”) in which individual fitness increased upon the population reaching a “critical mass” of individuals. Allee effects may be expected in small, establishing populations (Courchamp et al. 1999; Stephens and Sutherland 1999) and may arise through a variety of mechanisms, including the reduced availability of mates, obfuscation of behavioral cues among potential breeders or foraging birds, or diversion of energies into sentinel and predator avoidance behaviors (Courchamp et al. 1999; Stephens et al. 1999). Model  $M_{Allee}$  does not propose a specific mechanism; it simply suggests that a threshold density of breeders must be reached before the productivity rate is enhanced. Under model  $M_{Allee}$ , the survival portion was kept exactly the same as that in model  $M_{Wild}$ . However, the productivity rate applied to simulated WF birds depended on a population size condition. When the number of breeding-age females (all females  $\geq 2$  years, from both CR and WF segments) exceeded a fixed threshold size ( $B_T$ ), the ARWB productivity rate was assumed to apply to simulated wild-fledged breeding-class birds. Otherwise, simulated WF birds received the productivity rate estimate derived from CR birds. By varying the value of  $B_T$ , the model could be made equal to model  $M_{Wild}$  ( $B_T = 0$ ) or could be made



approximately equal to model  $M_{\text{Base}}$  ( $B_T \rightarrow \infty$ ) (but with the higher ARWB survival rate applied to the WF birds).

The model set thus portrayed a plausible range of population response consistent with profound uncertainty about the performance of WF birds; i.e., their performance is similar to that of CR birds (model  $M_{\text{Base}}$ ), resembles that of the ARWB flock, always (model  $M_{\text{Wild}}$ ), or resembles ARWB performance only when number of breeding-age females exceeds some size threshold (model  $M_{\text{Allee}}$ ).

### Model predictive performance

We derived a measure of predictive performance for models  $M_{\text{Base}}$  and  $M_{\text{Wild}}$  by using each model to re-play the exact sequence of bird releases over the period 1993–2004 to predict the population structure of females as of 2008. We ran each model  $n = 100,000$  times to generate a multivariate posterior distribution of 2008 population structure predictions, and we assessed each distribution against the known 2008 population structure. For each distribution, we found the center point using a minimum-volume ellipsoid estimator (MVE subroutine in SAS Proc IML v9.1; SAS Institute 2004), and we computed the distance of each point in the distribution from the center. We also computed the distance of the observed 2008 population structure from the center point, and we ranked all  $n + 1$  distances. We interpreted predictive performance for each model as  $1 - r_{2008}/(n + 1)$ , where  $r_{2008}$  is the ranked distance for the 2008 observation. This quantity reflects the distance of the observed 2008 population structure from the edge of the distribution, relative to distance from the center to the edge. The measure was scaled from 0 to 1, with the respective extremes reflecting poor (e.g., the 2008 observed structure lying beyond all model predictions) or excellent performance (e.g., the 2008 observation exactly coinciding with the distribution center point). Because models  $M_{\text{Wild}}$  and  $M_{\text{Allee}}$  are distinguished only in the rate of productivity of wild-fledged birds, and because only two female WF birds had entered a breeding class (class P) by 2008, a comparison of the predictive performance of models  $M_{\text{Allee}}$  and  $M_{\text{Wild}}$  was not possible. Model  $M_{\text{Allee}}$  makes predictions about outcomes that are plausible but have not yet occurred; therefore, its predictions can be assessed only with the passage of time.

### Decision alternatives

For each competing PVA model, we investigated population outcomes under 29 alternative fixed schedules of bird release that differed in duration, magnitude, frequency, and temporal delay. Combinations of the number of cohorts released per year (1, 2, or 3 cohorts per year; 4 females per cohort), the number of years of release (5, 10, 15, or

20 years), and the number of years to delay the start of the release schedule (1 or 11 years) resulted in 24 alternative release schedules. Four additional options employed the release of birds in alternate years, in combinations of one or two cohorts per year over 10- or 20-year time frames (all with a 1-year delay in the start of the schedule). Finally, as the 29th alternative, we included the option of no further releases. The set of schedules was designed to address other objectives of the release program; those objectives and design rationale are discussed in detail elsewhere (Converse et al. in preparation). However, all options were within the operational scope, ability, and resource constraints of the FWC.

### Simulation of release schedules

From a common population starting point in 2008 (13 CR females in 3 breeding classes, 4 WF females in 2 age classes and 1 breeding class), we simulated the response of the population to each release schedule. We assumed that each cohort release introduces four female CR chicks (and the same number of male chicks) into the population, which approximates the 1993–2004 releases. We simulated each schedule 10,000 times under each alternative model. Under model  $M_{\text{Allee}}$ , we conducted simulations for each of eight different settings of the  $B_T$  parameter: 5, 10, 15, 20, 25, 30, 40, and 50 females. All simulations were conducted over a fixed 131-year time frame (a point 100 years beyond the latest possible release under any schedule) or were stopped at an earlier time point if the population had grown very large ( $>1,000$  females). In each simulation, we computed the population trend (simple linear regression of untransformed population size) over the final 20 years of the simulation. Thus, for each set of simulations for a given model and release schedule, we took the proportion of simulations that yielded a positive trend as the posterior probability of population increase.

## Results

Over the period 1993–2004, 286 birds (135 females) were released. As of mid-year 2007, the cut-off date for statistical analyses, all but 33 had died or permanently emigrated from the region. Of the causes of death that could be determined, most were attributed to predation or power line collisions (M.J. Folk, FWC, unpublished data). Of 61 released females surviving to age 2 years, 38 subsequently formed pair bonds by 2007, and of these, four produced nine fledglings.

The measures of predictive performance for models  $M_{\text{Base}}$  and  $M_{\text{Wild}}$  were 0.485 and 0.517, respectively; thus, the 2008 population observation was well within the

**Table 2** Simulation outcomes (proportion of simulations yielding positive population growth) for alternative release strategies (delay until first release, duration of releases, numbers of cohorts released/ year) under alternative models of population growth of Whooping Cranes reintroduced in Florida, USA

Release strategy			Model $M_{Wild}^a$	Model $M_{Allee}^b$								Model $M_{Base}$
Delay (years)	Duration (years)	Cohorts		$B_T = 5$	$B_T = 10$	$B_T = 15$	$B_T = 20$	$B_T = 25$	$B_T = 30$	$B_T = 40$	$B_T = 50$	
	0	0	0.900	0.759	0.422	0.097	0.004	0.001	0.001	0.001	0.001	0.002
1	5	1	0.907	0.813	0.601	0.311	0.070	0.009	0.002	0.001	0.001	0.002
1	5	2	0.916	0.841	0.677	0.439	0.189	0.055	0.013	0.002	0.001	0.001
1	5	3	0.911	0.857	0.727	0.533	0.303	0.136	0.045	0.004	0.001	0.002
1	10	1	0.915	0.851	0.714	0.481	0.175	0.032	0.006	0.001	0.001	0.002
1	10	2	0.923	0.875	0.777	0.636	0.424	0.226	0.086	0.007	0.002	0.002
1	10	3	0.935	0.896	0.816	0.696	0.543	0.380	0.232	0.057	0.008	0.001
1	15	1	0.921	0.866	0.771	0.587	0.246	0.061	0.014	0.002	0.002	0.001
1	15	2	0.932	0.897	0.833	0.727	0.561	0.369	0.187	0.028	0.005	0.002
1	15	3	0.938	0.912	0.861	0.786	0.671	0.551	0.407	0.155	0.037	0.002
1	20	1	0.926	0.884	0.810	0.658	0.303	0.086	0.017	0.002	0.002	0.002
1	20	2	0.937	0.916	0.864	0.794	0.667	0.486	0.282	0.050	0.010	0.002
1	20	3	0.951	0.930	0.889	0.843	0.756	0.662	0.550	0.259	0.087	0.002
11	5	1	0.907	0.835	0.558	0.150	0.010	0.003	0.001	0.002	0.002	0.003
11	5	2	0.911	0.855	0.640	0.254	0.047	0.010	0.005	0.003	0.003	0.006
11	5	3	0.924	0.858	0.680	0.345	0.112	0.038	0.011	0.003	0.002	0.004
11	10	1	0.916	0.857	0.625	0.204	0.021	0.008	0.005	0.006	0.006	0.015
11	10	2	0.921	0.875	0.724	0.395	0.134	0.046	0.017	0.003	0.002	0.003
11	10	3	0.936	0.893	0.766	0.512	0.276	0.154	0.068	0.014	0.003	0.002
11	15	1	0.921	0.873	0.664	0.251	0.039	0.009	0.004	0.002	0.002	0.004
11	15	2	0.935	0.893	0.776	0.494	0.236	0.107	0.043	0.010	0.002	0.001
11	15	3	0.944	0.913	0.821	0.623	0.425	0.274	0.163	0.046	0.014	0.001
11	20	1	0.922	0.883	0.712	0.286	0.059	0.014	0.005	0.002	0.001	0.002
11	20	2	0.940	0.912	0.810	0.590	0.346	0.186	0.088	0.017	0.005	0.002
11	20	3	0.948	0.927	0.858	0.703	0.540	0.405	0.281	0.104	0.036	0.001
1	10 (AY) <sup>c</sup>	1	0.904	0.818	0.628	0.321	0.054	0.005	0.001	0.002	0.002	0.001
1	10 (AY)	2	0.914	0.844	0.712	0.477	0.184	0.040	0.007	0.001	0.001	0.001
1	20 (AY)	1	0.911	0.862	0.721	0.396	0.073	0.009	0.003	0.001	0.001	0.001
1	20 (AY)	2	0.927	0.886	0.812	0.661	0.326	0.099	0.023	0.002	0.001	0.002

<sup>a</sup> Model  $M_{Wild}$  hypothesizes that survival and productivity rates of the wild-fledged segment more closely correspond to those of the only wild flock in existence, the Aransas-Wood Buffalo migratory flock

<sup>b</sup> Model  $M_{Allee}$  hypothesizes increased productivity when number of females  $\geq 2$  years in the population passes a threshold ( $B_T$ )

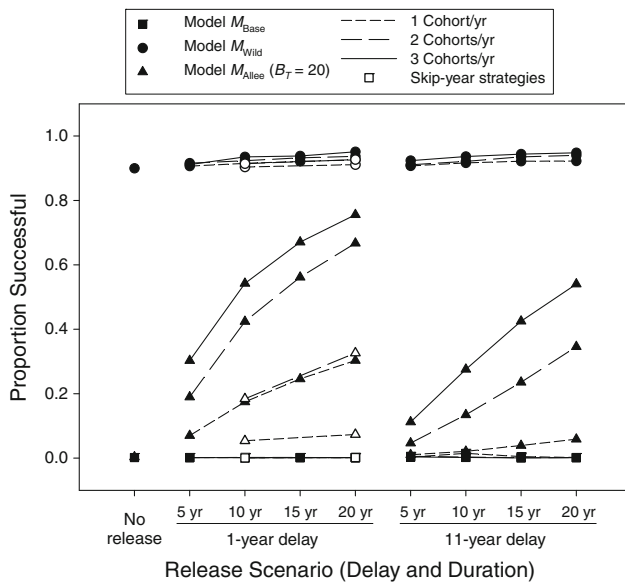
<sup>c</sup> AY, Releases in alternate years during the 10- or 20-year period

prediction range of both models. The slightly greater value for model  $M_{Wild}$  is consistent with very limited ( $n = 9$  WF birds) empirical evidence (Moore et al. in preparation) of greater annual survival in WF than in CR birds. The inability for the 2008 observation to further discriminate these two models is explained by the considerable degree of parametric uncertainty that attends the model estimates and the stochasticity in the simulation.

Simulation outcomes (proportion of simulations with positive population growth) exhibited two clear patterns

(Table 2; Fig. 3). First, outcomes were extremely sensitive to choice of the model. Under model  $M_{Base}$ , all release schedules yield nearly 0 chance of successful population establishment, whereas under model  $M_{Wild}$ , prospects for establishment are excellent ( $\geq 0.90$ ) under any release schedule, including the option of no further releases. Furthermore, the outcomes are sensitive to the choice of the value of  $B_T$  in model  $M_{Allee}$ .

Second, whereas the outcome is not sensitive to the release schedule under either model  $M_{Base}$  or  $M_{Wild}$ , the



**Fig. 3** Simulation outcomes (proportion of simulations yielding positive population growth) for alternative release strategies under three alternative models of population growth for the Florida non-migratory Whooping Crane population. Time delay until the first release and duration of release are displayed on the horizontal axis. Outcomes are plotted for one (short dashes), two (medium dashes), or three (solid line) cohorts per year under model  $M_{Base}$  (squares), model  $M_{Wild}$  (circles), and case  $B_T = 20$  of model  $M_{Allee}$  (triangles). Under models  $M_{Base}$  or  $M_{Wild}$ , the outcome is insensitive to the decision, resulting either in extirpation (model  $M_{Base}$ ) or establishment (model  $M_{Wild}$ ) in every case. Under model  $M_{Allee}$ , the outcome is highly sensitive to the release decision, and the response pattern reveals greater probability of success with intensive release activity that occurs earlier and persists longer. For a description of the model, see text

outcome is highly sensitive to the decision for different values of  $B_T$  in model  $M_{Allee}$  (Table 2; Fig. 3). That is, under the Allee model, decisions that result in release of more birds over time are far more likely to establish a population than those that release fewer.

**Discussion**

All population viability models make predictions of population persistence attended by uncertainty. Our work explicitly accounted for at least four sources of uncertainty (Regan et al. 2002), two of which are aleatory, including process variability and demographic stochasticity, and two of which are epistemic, including parametric uncertainty and model (structural) uncertainty.

Aleatory uncertainties arise through environmental and demographic stochastic effects that are expressed through the model. In many PVA applications, such effects may be attributed to a few specific causes and thus modeled explicitly. In contrast, our approach used empirically

estimated random effects from survival and reproductive data on marked birds to integrate a broad suite of stochastic influences that would have been difficult to estimate directly or even to identify. Thus, although it was not possible for us to directly estimate effects due to environmental conditions, habitat, characteristics of the individual bird (genetics, physiological condition, rearing environment, behavior, etc.), its interactions with other birds, and countless other factors, we were able to infer their aggregative influence on bird survival and productivity.

To directly account for parametric uncertainty in predictions of management outcome, we conducted the PVA by sampling from estimated posterior distributions of the model parameters (Wade 2002). Finally, we accounted for structural (model) uncertainty, in which population mechanisms are uncertain or in dispute. Structural uncertainty implies that population response to a proposed action may be consistent with any of several competing hypotheses. Few wild-fledged birds have been produced in Florida, and the oldest have only recently attained breeding age. Thus, for Whooping Cranes released in Florida, the key structural uncertainty is whether survival and reproductive performance of WF birds is similar to that of their CR parents. In fact, based on other bird reintroduction case studies, captive-rearing effects that reduce the demographic performance of first-generation birds as compared to their wild-reared offspring may well exist (Buner and Schaub 2008; Heath et al. 2008; Roche et al. 2008).

Therefore, we expressed structural uncertainty through a set of models that made different predictions about WF performance, and all were based on empirical observations of birds in the wild. Model  $M_{Base}$  predicts that WF performance is identical to that observed in the CR segment, whereas model  $M_{Wild}$  predicts performance is similar to that observed in the wild ARWB migratory flock. Model  $M_{Allee}$  suggests a conditional application of the preceding models in which the WF segment exhibits ARWB-like performance only when a population threshold is reached. Although we have no evidence that a demographic Allee effect occurs in this population, its behavior and predictions were intermediate between models  $M_{Base}$  and  $M_{Wild}$ ; thus, inclusion of this model seemed compelling and justifiable. Furthermore, Allee effects are thought to be a serious potential impediment for reintroduction programs (Stephens and Sutherland 1999; Deredec and Courchamp 2007). Although positive associations between number released and reintroduction success have been well documented (Wolf et al. 1996; Fischer and Lindenmayer 2000), empirical evidence of causative Allee effects in reintroduction programs remains scarce (Deredec and Courchamp 2007).

The estimated probability of population persistence varied over the range 0.001–0.951 among models in the

model set: the population persists or is extirpated according to the model selected and the action chosen (Table 2). For either model  $M_{\text{Base}}$  or  $M_{\text{Wild}}$ , the population outcome is nearly insensitive to the choice of release schedule. Under model  $M_{\text{Base}}$ , extirpation is essentially guaranteed regardless of action taken, whereas under model  $M_{\text{Wild}}$ , any release schedule, including that of no further releases, results in a very high probability of population persistence. Assuming that the cost of each decision is a co-consideration, and that the objective of management is a specific balance between likelihood of population restoration and cost of the action, then discontinuing releases will almost certainly be the optimal decision if either model  $M_{\text{Base}}$  or model  $M_{\text{Wild}}$  is the most appropriate model.

In contrast, under model  $M_{\text{Allee}}$ , population responses are sensitive to the release decision for settings of the Allee threshold between 10–40 adult females. A threshold of 20 birds elicits the greatest range in the probability of persistence response, ranging from 0.004 if no more birds are released, to 0.756 under the most intensive and immediate schedule of releases (Table 2; Fig. 3). Depending on the specific balance between cost and population restoration objectives, some form of bird release is likely to be the optimal decision under this model and for a range of threshold settings.

By re-playing the 1993–2004 history of releases and generating predictions of population outcome as of 2008, we were able to assess the predictive performance of models  $M_{\text{Base}}$  and  $M_{\text{Wild}}$ . Despite the intensity, duration, and expense of the reintroduction effort, and despite the stark differences in model structure and the divergent nature of their projections, evidence of the superiority of one model over another remains equivocal. This outcome reflects the great degree of predictive noise in each model and, more importantly, the scarcity of data in the population segment (WF birds) that would help to distinguish these models. Thus, 15 years after the first release, practically no confident statement can be made about the long-term persistence of the population. Therefore, without other information, the choice of a decision action is challenging because system uncertainty remains quite high.

Yet, natural resource management decisions must be made, whether or not structural uncertainty impedes the decision. When structural uncertainty is profound, as it is in our study, we propose a strategy that assigns a credibility weight to each model and then selects an optimal action based on maximizing an appropriate model-averaged objective; for example, population recovery balanced against implementation cost. Credibility weights could be empirically derived (e.g., through a re-scaling of predictive performance measures), but they are often subjective assignments. As such, without other evidence, we could

arbitrarily assign equal weight to each of the PVA models that we simulated, or we could rely on subjective judgments by a panel of experts in crane population biology. Converse et al. (in preparation) describe the use of an expert elicitation process to derive credibility weights for this problem.

If the release decision can be periodically revisited in the future, and if monitoring can be continued to further assess these alternative models (Ewen and Armstrong 2007), then we have a basis for iteratively adjusting model credibility weights through time using Bayes' formula (Williams et al. 2002). In this way, uncertainty about the process is iteratively reduced through time, and management thus adapts to this evolution of knowledge (Sarrazin and Barbault 1996; Palmer et al. 2006).

## Conclusion

We have demonstrated how four forms of uncertainty can be incorporated into PVA models used to project the outcome of reintroduction scenarios. Empirical estimates of random effects in survival and productivity processes, recovered through hierarchical Bayesian modeling approaches, can be used in a PVA model to represent forms of process variance and demographic stochasticity. Parametric uncertainty can be addressed through a PVA that samples from posterior distributions of model parameters. Finally, uncertainty about key biological processes may induce two or more plausible, competing PVA models, and a best decision with respect to all models can be identified when measures of model credibility can be obtained either empirically or through expert judgment. If the decision can be periodically revisited, and if data are available to continually inform the models, then there exists a means to adaptively manage the resource in response to updated knowledge.

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**Conflict of interest** The authors declare that they have no conflict of interest.

**Appendix**

The statistical estimation models for survival and breeding class transition are described in the text. The accompanying mathematical descriptions are provided below and are more fully developed in Moore et al. (in preparation). Estimates from the models (Table 3) were used to construct the baseline PVA model.

**Survival estimation**

Each female bird  $j$  released into the wild as part of cohort  $c$  was a member of age or breeding class  $k$  ( $k \in \{0, 1, 2, 3, 4 + , P, N, F\}$ ) in period  $i$  (3-month divisions of the year, starting from January 1993). The number of days that bird  $j$  survived within period  $i$  was assumed to be binomially distributed with probability  $p_{ij}(k, c)^{1/d_i}$  over  $x_{ij}$  exposure days, where period  $i$  is  $d_i$  days in length and  $0 \leq x_{ij} \leq d_i$ .

Quarterly survival probability was modeled as a linear function of a mean (an intercept plus a female fixed effect) and random effects of age/breeding class, time, cohort, and individual:

$$\begin{aligned} \text{logit}(p_{ij}(k, c)) &= \alpha_k^G + \delta_i^T + \delta_{cj}^* \\ &= (\mu_{\text{female}} + \delta_k^G) + \delta_i^T \\ &\quad + (\delta_c^{C0} + \delta_j^{B0})I(\text{age} = 0) \\ &\quad + (\delta_c^{C1} + \delta_j^{B1})I(\text{age} = 1) \\ &\quad + (\delta_c^{C2+} + \delta_j^{B2+})I(\text{age} \geq 2) \end{aligned}$$

where  $\delta_k^G$  is a random effect due to membership in age or breeding class  $k$ ,  $\delta_i^T$  is a random effect due to period  $i$ ,  $\delta_c^{C*}$  are age-class specific random effects due to membership in release cohort  $c$ ,  $\delta_j^{B*}$  are age-class specific random effects due to bird  $j$ , and  $I(z)$  is the indicator function for expression  $z$ . Random effects were modeled as deviates from zero-centered normal distributions with corresponding variance parameters  $\sigma_G^2$ ,  $\sigma_T^2$ ,  $\sigma_{C0}^2$ ,  $\sigma_{C1}^2$ ,  $\sigma_{C2+}^2$ ,  $\sigma_{B0}^2$ ,  $\sigma_{B1}^2$ , and  $\sigma_{B2+}^2$ .

Posterior distributions of annual age and breeding-class specific survival rates ( $\varphi_k$ ) were estimated by summing appropriate terms of the model above, transforming the sum to the probability scale, and multiplying four of the resulting terms together:

$$\varphi_k = \prod_{i=1}^4 \text{logit}^{-1}(\alpha_k^G + \delta_i^T + \delta_{cj}^*)$$

**Estimation of productivity and breeding class transition probabilities**

Transition into breeding class P occurred when a female bird of age  $\geq 2$  years first exhibited pairing behavior. For never-paired bird  $j$  that was age  $k$  ( $k = 1, 2, 3, 4+$ ) in the year previous to  $i$ , we assumed that first pairing occurred as a Bernoulli outcome with probability  $\theta_{ij}^{UP}(k)$ . Transition probability was thus modeled as a linear function of fixed intercept ( $\mu_{UP}$ ) and age-specific ( $\beta_k$ ) effects and of random effects of time ( $\delta_i^{PT}$ ) and bird ( $\delta_j^{PB}$ ):

$$\text{logit}(\theta_{ij}^{UP}(k)) = \mu_{UP} + \beta_k + \delta_i^{PT} + \delta_j^{PB}$$

Random effects were modeled as deviates from zero-centered normal distributions with corresponding variance parameters  $\sigma_{PT}^2$  and  $\sigma_{PB}^2$ . We obtained posterior distributions of annual age-specific transition probability into class P ( $\psi_{UP}^{(k)}$ ) by transformation of the above sum.

Transition from class P into class N occurred when a female produced her first nestling but failed to produce a fledgling. Transition from class P into class F occurred when a female’s first nestling developed into a fledgling (male or female). For bird  $j$  belonging to class P, both events were assumed to occur as Bernoulli outcomes with probabilities  $\theta_j^{PN}$  and  $\theta_j^{PF}$ , respectively. Linear models relating each transition probability to a fixed intercept and a random effect due to bird were:

$$\begin{aligned} \text{logit}(\theta_j^{PN}) &= \mu_{PN} + \delta_j^{PNB} \quad \text{and} \\ \text{logit}(\theta_j^{PF}) &= \mu_{PF} + \delta_j^{PFB} \end{aligned}$$

Random effects were modeled as deviates from zero-centered normal distributions with corresponding variance parameters  $\sigma_{PNB}^2$  and  $\sigma_{PFB}^2$ . We obtained posterior distributions of annual transition probability from class P into classes N ( $\psi_{PN}$ ) or F ( $\psi_{PF}$ ). As no Florida bird has ever produced more than one fledgling in a year,  $\psi_{PF}$  serves as the estimate of productivity for birds in class P.

Transition from class N into class F occurred when a female who had only ever produced a nestling in prior attempts produced her first fledgling (male or female). We assumed that this event was a Bernoulli outcome with probability  $\psi_{NF}$ . Similarly, a bird already in class F produces another fledgling with probability  $\psi_{FF}$ . We modeled each of these probabilities as a simple mean with no random effects:

$$\text{logit}(\psi_{NF}) = \mu_{NF} \quad \text{and} \quad \text{logit}(\psi_{FF}) = \mu_{FF}$$

These probabilities effectively serve as estimates of productivity for birds in class N and F, respectively.



**Table 3** Estimates of age and breeding-class specific mean annual survival rate ( $\varphi_i$ ), mean breeding transition rate ( $\psi_{ij}$ ), and associated random effects ( $\sigma_i$ ) of 286 captive-reared female Whooping Cranes reintroduced in Florida, USA, 1993–2004 (Moore et al. in preparation)

Age/breeding class		Mean	Credible interval <sup>a</sup>	
			Lower	Upper
Annual survival rate				
Means for never-paired birds				
Post-release to Age 1	$\varphi_0$	0.664	0.0	1.0
Age 1	$\varphi_1$	0.672	0.0	0.999
Age 2	$\varphi_2$	0.766	0.469	0.938
Age 3	$\varphi_3$	0.821	0.556	0.955
Age 4+	$\varphi_{4+}$	0.805	0.512	0.948
Means for female breeding classes <sup>b</sup>				
Class P	$\varphi_P$	0.816	0.540	0.952
Class N	$\varphi_N$	0.785	0.454	0.950
Class F	$\varphi_F$	0.936	0.703	1.000
Cohort-level random effects				
To age 1	$\sigma_{C0}$	2.387	1.334	3.965
Age 1	$\sigma_{C1}$	1.580	0.488	2.998
Age 2+	$\sigma_{C2+}$	0.237	0.030	0.657
Bird-level random effects				
To age 1	$\sigma_{B0}$	2.979	1.735	4.595
Age 1	$\sigma_{B1}$	1.666	0.090	3.311
Age 2+	$\sigma_{B2+}$	0.274	0.029	0.952
Time random effect	$\sigma_T$	0.620	0.356	0.922
Annual breeding transition rate				
To paired class from unpaired				
Pr(class P   Age 1 unpaired)	$\psi_{UP}^{(1)}$	0.257	0.005	0.788
Pr(class P   Age 2 unpaired)	$\psi_{UP}^{(2)}$	0.243	0.008	0.805
Pr(class P   Age 3 unpaired)	$\psi_{UP}^{(3)}$	0.393	0.034	0.966
Pr(class P   Age 4 + unpaired)	$\psi_{UP}^{(4+)}$	0.297	0.024	0.962
Bird random effect	$\sigma_{PB}$	0.869	0.029	4.332
Time random effect	$\sigma_{PT}$	0.705	0.036	2.218
To nestling class from paired				
Pr(class N   class P)	$\psi_{PN}$	0.153	0.001	0.743
Bird random effect	$\sigma_{PNB}$	1.191	0.047	4.833
To fledgling class from paired				
Pr(class F   class P)	$\psi_{PF}$	0.052	0.0	0.232
Bird random effect	$\sigma_{PFB}$	1.274	0.044	7.022
To fledgling class from classes N or F				
Pr(class F   class N)	$\psi_{NF}$	0.002	0.0	0.028
Pr(class F   class F)	$\psi_{FF}$	0.363	0.121	0.651

<sup>a</sup> Posterior probability of true parameter value lying within indicated bounds = 0.95

<sup>b</sup> P, Paired or historically paired, no history of nestling production; N, nestling producer, no history of fledgling production; F, fledgling producer

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