

Using Stage-Based System Dynamics Modeling for Demographic Management of Captive Populations

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Management of captive populations relies on a complex synthesis of genetic and demographic analyses to guide populations toward sustainability. Demographic analyses of captive populations currently utilize age-based matrix projections to predict a population's trajectory. An alternate approach is to use a stage-based, system dynamics model for captive systems. Such models can more easily incorporate complex captive systems in which population dynamics are dependent on a combination of management and a species' biology. By linking these two areas, population managers can gain a more accurate understanding of how management decisions impact captive populations and which aspects of a species' demography should be of special concern in the future. We present a general stage-based system dynamics model that has been developed for use with captive populations. The utility of the model is then illustrated by applying it to three captive bear populations: spectacled bears (*Tremarctos ornatus*), sloth bears (*Melursus ursinus*), and sun bears (*Helarctos malayanus*). Zoo Biol 22:45–64, 2003. © 2003 Wiley-Liss, Inc.

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INTRODUCTION

The primary goal of cooperative animal management programs like the American Zoo and Aquarium Association's (AZA) Species Survival Plans[®]

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(SSPs) and Population Management Plans (PMPs) is to maintain genetic diversity and demographic stability to ensure the long-term persistence of populations. Traditionally, population biologists have analyzed the demographic aspects of a captive population's viability using age-based projection matrices from software specifically created for zoos, such as Population Management 2000 (PM2000, Brookfield, IL) [Pollack et al., 2001]. These analyses use age-specific rates of fecundity and mortality to estimate population growth rate and determine the annual number of births needed to reach or maintain the target population size [Ballou and Foose, 1996]. Age-based matrix models are also commonly used in human demography and in long-term or detailed studies of wildlife populations [Shryock et al., 1976; Ebert, 1999; for review see Caswell, 2001]. Although the age-based approach is a useful demographic tool, it also has some drawbacks in terms of data requirements, flexibility in representing some life histories, and difficulty of incorporating management considerations associated with captive populations. In this work we present stage-based system dynamics modeling as an alternative to traditional age-based matrix modeling for captive populations.

Models based on life stages offer an attractive alternative to age-structured analysis. Stage models can be based upon differences in size, developmental stage, reproductive status, management category, location, or any other aspect that plays a defining role in the demography of a population. A stage approach is ideal if such factors provide more information about the demographic behavior of the population than do age-specific factors [Caswell, 2001]. Stage-based models have become common in animal demography because of their flexibility in modeling factors of management interest [Crouse et al., 1987; Sauer and Slade, 1987; Doak et al., 1994; Heppel et al., 1994; Crooks et al., 1998].

Stage-based models are useful because they may circumvent some of the issues and problems encountered with age-based models. For example, age-based estimates of mortality and fecundity rates are sometimes unreliable due to small sample sizes, either because of the number of deaths or births in a given age class or because few animals have passed through a particular age class. Age-based models, such as PM2000, cope with this issue by smoothing fecundity and/or mortality data using running averages over the age classes. Because stage models frequently group multiple age classes into a single stage and apply a single mortality or fecundity rate to that stage, sample sizes may be increased, and estimates of mortality and fecundity used in stage models may produce better results. In addition, stage models can provide more flexibility in analyzing management issues that are of importance to captive populations. For managed populations, stage-based models are appealing because of their ability to capture stages that are naturally formed, regardless of the analytical methods being used: demographic management is not implemented for 3-year-olds or 17-year-olds, but for the juvenile stage or the reproductive adult stage. Utilizing management stages rather than multiple independent ages allows for easier modeling of factors essential to the management of captive species, such as social structure and reproductive status.

Many demographic analyses use matrix projection models to predict future demographic trends [van Groenendael et al., 1988; Caswell, 2001; Fieberg and Ellner, 2001]. While these models are theoretically elegant and useful, they often become unwieldy when modified to incorporate complex dynamics. An alternative method, system dynamics, enables modelers to study and understand the dynamics

of how complex systems involving feedback loops will change over time. The development of sophisticated system dynamics modeling software such as Vensim (version 4.0b; Ventana Systems, Inc., Harvard, MA) and STELLA (research version 7.0.1; High Performance Systems, Inc., Hanover, NH) has facilitated the use of this approach in ecological modeling [Marin, 1997; Patten, 1997; Carter et al., 1999; Ford, 1999]. In these programs the user can 1) build a conceptual model of the focal system in an iconographic interface, 2) clarify the mathematical relationships between variables (a process that is facilitated by the software), 3) parameterize the model with data from the focal system, and 4) use simulations to better understand the complex dynamics of the system.

Demography of captive systems is a prime example of a complex feedback system that may be well suited to system dynamics modeling. In captivity, two areas interact to affect a species' long-term persistence: 1) the species' biology (life history, behavioral and social considerations, and current demographic and genetic population structure), and 2) management considerations (institutional exhibit requirements, total available space, husbandry, health, and the spatial structure of the population). System dynamics modeling incorporates the interactions between these elements more easily than a matrix approach, and may yield a clearer understanding of how they can influence a population's long-term trajectory.

In this work we present a stage-based system dynamics model designed to evaluate the interactions between management and biology that affect captive populations. We describe how the model is structured, how data are extracted to parameterize the model, and how the model can be validated. We then illustrate the model's use and flexibility as a tool for evaluating management questions using three SSP species with different management goals and population structures: spectacled bears (*Tremarctos ornatus*), sun bears (*Helarctos malayanus*), and sloth bears (*Melursus ursinus*).

METHODS

Basic Model Description

Using STELLA 7.0.1 (High Performance Systems, Inc.), we created a two-sex, four-stage model. Births, deaths, and management drive the model dynamics. Because most captive populations have few imports and exports, the current model does not include them; it could be adjusted for populations in which these factors appear to significantly affect population dynamics. The results of all model simulations are reported on an annual cycle. This reporting cycle mimics the reality of captive management, in which managers and population biologists meet annually to plan the next year's reproduction. The model allows for the movement of fractional individuals rather than integerizing all stages and flows.

The model incorporates demographic stochasticity into the population dynamics by generating normally distributed variation around reproduction. We believe it is appropriate to create demographic stochasticity through variable reproductive rates rather than through mortality rates. In captivity, annual per capita deaths, although dependent upon the current age pyramid, are fairly consistent from year to year because, barring catastrophes, captivity is fairly consistent in high standards of medical care, food quality, etc. Reproductive rates,

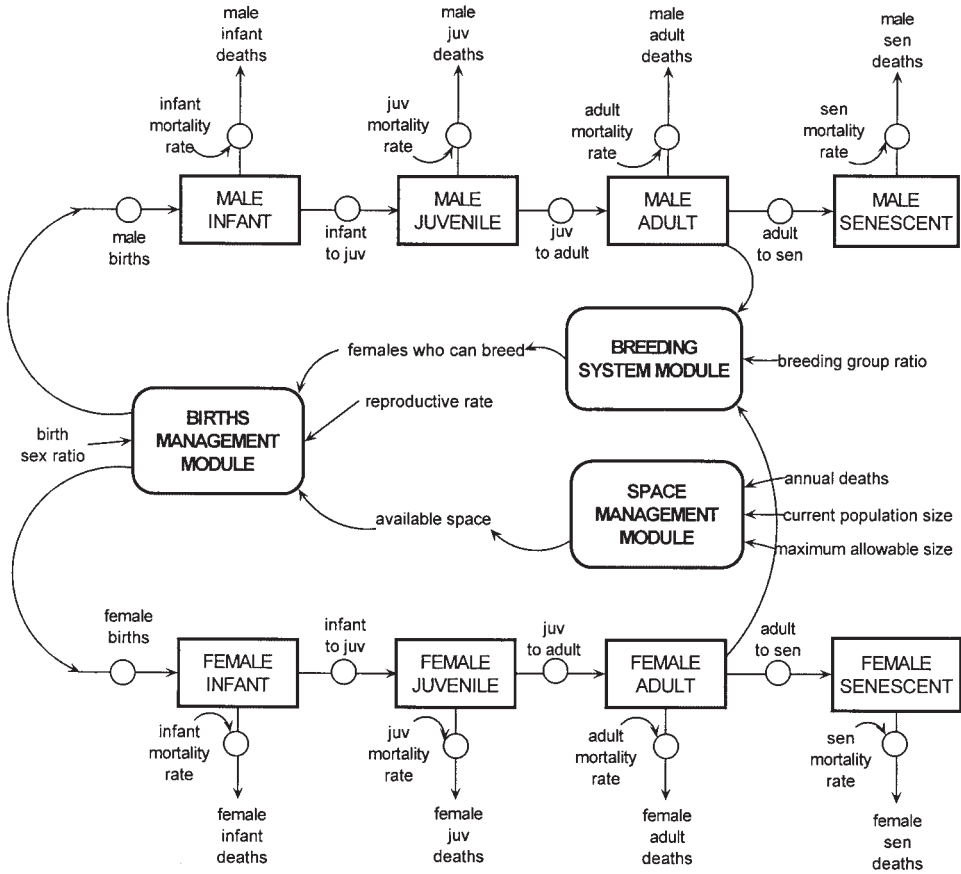


Fig. 1. Diagram of the stage-based demographic model built in STELLA.

on the other hand, can vary greatly because of logistical difficulties with moving animals at the appropriate time for breeding, behavioral difficulties with forming a pair that exhibits breeding behavior, and other potential difficulties that complicate breeding, such as issues of mate choice, nutrition, hormones, etc.

The model integrates four different modules that affect captive demography (Fig. 1): a biological population dynamics module, a breeding system module, a space management module, and a births management module.

Biological population dynamics module

This module includes the basic stage structure of the model and allows the tracking of both sexes through their respective life stages. The module calculates the number of males and females of each stage (infants, juveniles, adults, and senescents), the annual number of deaths for each stage, and the number of individuals transitioning between stages. Each stage is a conveyer, which is a specialized stock variable in STELLA. Stock variables accumulate the individuals that flow into them; a conveyer accumulates individuals in a similar way, but can retain its individuals for a specified amount of time. By treating each stage as a

conveyer, we retain some of the realities of age-specific models while still working within a stage approach. Our stages are initialized with starting densities for males and females; the stage retains these initial individuals for a specific stage duration and simultaneously accumulates individuals transitioning in from the previous stage. The stage tracks how long individuals have been in the stage and transitions them to the next stage after the stage duration has passed. While in a stage, individuals are susceptible to death via a stage-specific mortality rate.

Breeding system module

The breeding system module tracks the number of adult males and females in the population (based on the values of the adult stage in the biological population dynamics module). Based on a user-provided breeding group ratio of the number of males and females in the average captive breeding group, the module calculates how many total breeding groups can be formed. This module allows the basic model to be easily customized for monogamous or polygynous species. The module can also track how many nonbreeding adults there would be in the population, which is valuable to managers of polygynous or herd species for space planning.

Space management module

Because financial resources, physical exhibit space, and the demographic and genetic goals of other species limit the size of individual captive populations, population management is closely tied to the number of spaces available for a given species. The space management module introduces density dependence into the population dynamics by calculating the available spaces that can be filled by new births. The model determines how many spaces need to be filled based on 1) how far the current total population size (calculated by the model based upon the size of each stage) is from the maximum allowable size (a value provided by the user), and 2) forecasting how many deaths are likely to occur in the upcoming year, which is estimated based upon the number of deaths that occurred in the previous year (calculated by the model based upon deaths for each stage and sex). Thus, the number of available spaces = maximum allowable size + total annual deaths – total population size.

Births management module

The births management module calculates the annual number of births. This module uses the number of females that can breed (calculated by the breeding system module) and their reproductive rate (a value provided by the user) to calculate the number of births that are biologically possible each year. This is weighed against the management constraint of available space for the population (calculated by the space management module), and the minimum of the two values is selected as the annual number of births. With this approach, if the population is close to its target population size, there will be few available spaces and breeding will be constrained to the number of available spaces; if the population is far from its target population size but has few adult females, the number of births will be constrained because of the low number of biologically possible births. The calculated annual number of births is then divided into males and females by the birth sex ratio (BSR), defined as the proportion of male births to total births ($BSR > 0.5$ = male-biased, $BSR < 0.5$ = female-biased).

Species-Specific Models

In choosing species to demonstrate the potential uses of our model, we focused on species that are similar in basic biology and life history, but entail slightly different management issues that would illustrate the flexibility of our model. In addition to these basic requirements, we also needed to use species that had been breeding in captivity long enough to provide sufficient data to parameterize the model. We chose three monogamous bear species: spectacled bears (*Tremarctos ornatus*), sun bears (*Helarctos malayanus*), and sloth bears (*Melursus ursinus*).

Spectacled bears

In the year 2000, the spectacled bear SSP population had a population size of 81 and a target population size of 100 [Weinhardt et al., 2000]. There is concern that this population size is too small to permit demographic sustainability; as the population ages and more bears become post-reproductive, the population may not have enough breeding pairs to maintain itself. Coupled with this concern is the increasing sex ratio bias of the adult population. Spectacled bears breed as pairs, and the increasing proportion of males (as of 1 January 2000, the adult (breeding) population sex ratio was 0.65) may exacerbate the effects of an increasing post-reproductive population. Modeling the population will help address management concerns about an aging population close to its target population size, as well as questions about the long-term demographic effects of male-biased BSRs.

Sloth bears

The North American sloth bear population is smaller (n=44 individuals in 2000), and it has been recommended that the target population should increase to 60 to improve demographic stability, which is at risk due to its small size, low fecundity, high infant mortality rate, and the population decline (average annual population growth rate=0.9872) since the mid-1980s [Wachsberg et al., 2000]. Sloth bears, a monogamous species, are facing a female bias in adult sex ratio (as of 1 January 2000, the breeding population sex ratio was 0.40). Modeling the population will help address questions about the general population decline and the effects of female-biased BSRs.

Sun bears

The sun bear population is a particularly appropriate species for a flexible, complex demographic model. This species has a target population size of 60 specimens. Within the existing population of 61 bears, 19 are of the Bornean subspecies (*Helarctos malayanus euryspilus*) and 42 are of mainland or unknown origin. The SSP plans to gradually phase out the mainland/unknown portion of the population and focus on breeding the Bornean subspecies to ultimately fill the 60 spaces; to do this, population managers have recommended breeding the Bornean subpopulation at the highest rate possible [Frederick et al., 2000]. Thus the subpopulation eligible to breed (19 bears) is well below the target population size, while the 42 mainland or unknown-origin bears take up much of the current holding space.

To accommodate the need to track the two groups separately, we subdivided all relevant model structures and parameters (stages, initial abundances, reproduc-

tive parameters, etc.) into two categories: Bornean and unknown. The model was modified to allow only the initial 19 Bornean animals (or their descendants) to be eligible for breeding, while the 42 unknown individuals simply hold spaces until they have lived out their natural lifespan. Modeling the population in this way may help ascertain whether creating a sustainable population based on the Bornean subspecies is a feasible goal.

Model Parameters

All variables that are constants entered into the model are indicated in italics. We designed the model to be parameterized with demographic data from the Single Population Analysis and Record Keeping System (SPARKS) 1.42 studbook database format (International Species Information System (ISIS), Apple Valley, MN). SPARKS studbooks are a complete record of the historic and current data of a population, including births, deaths, pedigrees, and locations, from all institutions across North America (for regional studbooks) or the world (for international studbooks). We extracted all data for model parameters from the North American SSP management versions of the spectacled bear [Rosenthal, 2000], sloth bear [Wachsberg, 2000], and sun bear [Frederick, 2000] studbooks.

The first step in data extraction is selecting an appropriate date range or window in which mortality and fecundity data are considered to be reasonably accurate and representative of the biology and contemporary management practices for each species. For example, a date window that is too broad could include the beginning stages of a captive population in which population growth is fueled mainly by imports of wild specimens rather than by reproduction. Including such data within the date window would not provide accurate estimates of mortality and fecundity that are representative of contemporary management. To avoid such problems, our date window for each species started at the beginning of the first 3 consecutive years in which captive births exceeded imports (1971, 1975, and 1979 for spectacled, sloth, and sun bears, respectively); the end of the date window was always the beginning of 2000. This date window was used for all subsequent data extraction unless otherwise noted.

We simplified the basic mammalian life history into four distinct stages: infant, juvenile, adult, and senescent. These stages divide the lifespan into a pre-reproductive phase (with an infant stage of high mortality and a juvenile stage of low mortality), a reproductive phase (with the adult stage), and a post-reproductive phase (with the senescent stage of increasing mortality). Using age-specific life tables from SPARKS for each species, we utilized patterns of mortality (Q_x) and fecundity (M_x) to divide the lifespan into the four stages; the ages that correspond to these divisions are the model's *stage durations*. *Initial stage abundances* for each stage were calculated from the SPARKS age pyramid by tallying the number of individuals in each stage on a particular date (either the first date in the date window or 2 January 2000).

Deaths in the model are generated by stage-specific *mortality rates*, defined as the proportion of individuals entering stage _{x} that will die before reaching stage _{$x+1$} . For example, with 100 animals entering a 5-year adult stage, an adult stage mortality rate of 0.20 would result in 20 individuals dying over the 5 years; these deaths would be evenly spread throughout the time period. Mortality rates for each gender were calculated by extracting age-based Q_x tables using LIFESAVER- Q_x [Thompson, 2001], a software program that extracts mortality data without prorating [Odum and

Smith, 2001]. A stage's mortality rate is the number of deaths occurring during a given stage divided by the total number of individuals entering that stage, which is calculated as the number of individuals in the first age class of the stage plus the number of individuals imported into the population at any point during the stage class.

The species' *breeding group ratio* is based on the species' biology and management in captivity; monogamous species, such as the three bear species modeled here, have a breeding group ratio of one male: one female. The *birth sex ratio (BSR)* is the proportion of male births (number of male births/number of total births). Three BSRs were used: 1) a historic rate, calculated by averaging the annual BSRs for each year during the date window (excluding years with 2 or fewer births); 2) a baseline rate, set at even BSR (0.5); and 3) a biased rate, which was set at two hypothetical levels (0.7 and 0.3). The *maximum allowable size (MAS)* is the ceiling placed on population growth in the model. Two MASs were used for each population: a target population size used for simulations, and a carrying capacity used for validations. Simulation sizes are the current target population sizes set by the Bear Taxon Advisory Group (TAG), an AZA group that makes decisions on space allocation for all bear populations in North American institutions. These sizes are based on genetic and demographic goals for each population. However, target population sizes are a relatively new development in the history of captive populations; before cooperative management programs existed, population growth was governed by supply and demand between institutions, and in this case the MAS can be thought of as a carrying capacity that governed growth (i.e., overshoots of the carrying capacity resulted in offspring that could not be placed, and undershoots resulted in institutions soliciting offspring). We used the largest annual population size observed during a date window as each species' carrying capacity for historic validation.

Calculation of fecundity measures for captive population projections are often problematic because it is difficult to establish from the available data which females in a reproductive age class had the opportunity to reproduce; SPARKS considers all females passing through a reproductive age class as eligible to conceive, even if they are housed alone or in a single-sex group, are contracepted, are currently lactating/gestating, or are sterile. In addition, because we explicitly model management constraints on fecundity, we require an estimate of fecundity based upon a date window without management restrictions on reproduction (in effect, the biologically possible fecundity). We used a novel approach to calculate a *reproductive rate* that circumvents some of these issues. For each species we extracted the number of adult males and females and the number of total births from the studbook for each year in the previously established date window. We calculated the annual potential number of pairs, which for monogamous species is simply the minimum of the number of adult males or females. We then calculated the annual reproductive rate for the population as the number of births divided by the number of potential pairs, and made a visual inspection of these data to determine whether there were any trends that could be attributed to management constraints. The sun and sloth bears did not have any noticeable trends, and thus the previously established date window was appropriate. The spectacled bear had a noticeable declining trend in the last 10 years due to space limitations (there were only about 85 actual available spaces for this species in the 1990s); because of this, data from 1974–1990 were used rather than the

originally established date window. We then used the average of the annual reproductive rates within each species' date window as the model's reproductive rate. To generate stochasticity we added normally distributed variation around the mean reproductive rate for each bear using a random normal function and the standard deviation (SD) of the annual reproductive rates; this distribution was justified because the distribution of each bear's annual reproductive rate fit the normal distribution (spectacled bear Kolmogorov-Smirnov (K-S) $d=0.084$, $P=n.s.$ different from normal; sloth bear K-S $d=0.063$, $P=n.s.$; sun bear K-S $d=0.057$, $P=n.s.$).

Model Validation

We used three different approaches to evaluate and gain confidence in our model. The first approach focused on evaluating the basic model's internal consistency by determining whether the logical and mathematical relationships within the model are consistent with our expectations. We conducted extensive logic testing during the building phases, in which the model results were compared to independent calculations to determine whether the model was matching expectations, and to help clarify the relationships between variables. After finalizing the basic model, we also conducted extreme behavior tests, in which we varied parameters over a wide range of values and examined whether model behavior was plausible [Ford, 1999]. Both of these levels of testing were used to detect any additional flaws in the mechanics of the model.

The second approach focused on evaluating the model's consistency with the observed behavior of populations, to determine whether the model accurately predicted the dynamics of the focal system on which it was based. We conducted historical validations for each bear species in which the model performance was compared to the observed population dynamics from the previously chosen date window [Rykiel, 1996]. We initialized each bears' model with parameter values existing either at the beginning of the chosen date window (for stage abundances) or average values observed over the course of the date window (for mortalities, reproductive rates, BSRs). We projected each species' model forward for the appropriate number of years to reach 2 January 2000 (29, 25, and 21 years for the spectacled bear, sloth bear, and sun bear, respectively); each bear's model was run 500 times, and the reported results are an average of these runs. We compared the model results to historic observed studbook data for annual population size.

Our final approach for gaining confidence in our model was to compare the model results to an alternative model approach, the age-based matrix model in PM2000. We did not necessarily expect that the two methodologies would produce identical results; rather, the comparison helps us to determine whether our stage model produces feasible results (as, presumably, PM2000 does). To generate comparable PM2000 results, we extracted mortality and fecundity data from SPARKS from the chosen date window for each species and imported it into PM2000. Mortality and fecundity data were smoothed once. We initialized the age pyramid in PM2000 with abundances from the beginning of the date window and projected each model forward the appropriate number of years. The age-based matrix in PM2000 is a deterministic model, and thus the results reported are from a single run.

Model Simulation

Model simulation can be a useful tool to evaluate the potential impacts of different management strategies on captive populations. We used each species' model to simulate future population dynamics under a variety of management scenarios. All simulation results are reported as mean annual values averaged over 500 runs. Where appropriate, we calculated the average annual population growth rate (λ) as the geometric mean of each year's λ over the date window; for simulations in which the population reached its maximum allowable size, λ was calculated as the geometric mean of each year's λ before reaching the maximum size.

For each species we ran baseline simulations and then varied specific model parameters to address management concerns and questions for each population, including modeling the effects of varying BSR bias and altered breeding scenarios (Table 1). All simulations were projected forward 30 years from January 2000.

Many programs have experienced significant runs of multiple years of biased BSRs in a single direction (male or female), with an average run length of 9.5 years (based on data from 53 captive mammal species) [Faust and Thompson, 2000]. We modeled the effects of such a run by comparing simulations that had an even BSR (0.5) with simulations with a 9-year run of male- (0.7) or female- (0.3) biased BSR from years 1–9, followed by a return to a 0.5 sex ratio (male-biased BSR and female-biased BSR simulations of Table 1).

Managers of the sun bear population are attempting to utilize the Bornean subpopulation as the breeding stock for the SSP, and based on this management goal we also simulated a variety of altered breeding scenarios to address whether this decision will allow the population to reach its target population size (ALLBOR and

TABLE 1. Conditions for model simulations

Species	Simulation name	Description
Spectacled bear	Baseline	“Simulation” conditions of Tables 2 and 3
	Male-biased BSR	9 year run of 0.7 BSR from years 1–9, followed by a return to 0.5 bsr
	Female-biased BSR	9 year run of 0.3 BSR from years 1–9, followed by a return to 0.5 bsr
Sloth bear	Baseline	“Simulation” conditions of Tables 2 and 3
	Male-biased BSR	9 year run of 0.7 BSR from years 1–9, followed by a return to 0.5 bsr
	Female-biased BSR	9 year run of 0.3 BSR from years 1–9, followed by a return to 0.5 bsr
Sun bear	Baseline	“Simulation” conditions of Tables 2 and 3
	Male-biased BSR	9 year run of 0.7 BSR from years 1–9, followed by a return to 0.5 bsr; breeding as in baseline
	Female-biased BSR	9 year run of 0.3 BSR from years 1–9, followed by a return to 0.5 bsr; breeding as in baseline
	ALLBOR	All Bornean (paired and unpaired) females allowed to breed
	ALLPOP	All paired females (Bornean and unknown) allowed to breed

BSR, birth sex ratio.

ALLPOP from Table 1). The baseline model allows only paired females of Bornean descent to breed (Bornean females paired with Bornean males); the ALLBOR simulation allows all Bornean females to breed, regardless of whether a male is available to be paired; the ALLPOP simulation allows all paired females to breed, regardless of origins (e.g., allows Bornean and unknown/mainland origin bears to breed).

RESULTS

Parameter Estimation

Baseline and historic parameter values were estimated from the spectacled, sun, and sloth bear studbooks for input into the model (Tables 2 and 3). We were able to define clear stages based on patterns in mortality; when comparing the stage durations and mortality rates for each species from Table 2, obvious breakpoints exist in mortality patterns. For instance, for sun bears the high mortality infant stage (e.g., male mortality=0.38, female=0.2) was followed by a juvenile stage of very low mortality, an adult stage of moderate mortality, and a terminal senescent stage (see sun bear stage mortality rates, Table 2). We were also able to gather information on the MAS for each population for use in validation and simulation models (Table 3). Simulation values are the current target population sizes set by the bear TAG, and are taken directly from population management plans for each species [Frederick et al., 2000; Wachsberg et al., 2000; Weinhardt et al., 2000]. Validation MAS values are

TABLE 2. Stage parameter values for historic validation and simulation models

	Infant		Juvenile		Adult		Senescent	
	Male	Female	Male	Female	Male	Female	Male	Female
Spectacled bear								
Stage duration	0	0	1	1–2	2–26	3–22	27–31	23–31
Stage mortality ^a	0.39	0.39	0.00	0.04	0.21	0.20	1.00	1.00
Validation IA	0	0	2	4	15	10	0	2
Simulation IA	0	1	1	1	50	27	1	6
Sloth bear								
Stage duration	0	0	1–2	1	3–20	2–27	21–30	28–33
Stage mortality ^a	0.51	0.36	0.02	0.08	0.51	0.48	1.00	1.00
Validation IA	3	2	1	1	20	28	1	0
Simulation IA	1	1	4	1	14	21	1	1
Sun bear								
Stage duration	0	0	1–2	1–2	3–26	3–19	27–31	20–34
Stage mortality ^a	0.38	0.2	0.05	0.05	0.44	0.25	1.00	1.00
Validation IA	0	1	2	1	29	47	0	1
Simulation IA	0b, 0u	0b, 0u	1b, 1u	2b, 0u	4b, 11u	12b, 17u	0b, 2u	0b, 11u

^aStage durations (in age classes) and stage mortalities are used for both validation and simulation models for all bears.

^bFor sun bear simulation initial abundances, b, Bornean subspecies and u, unknown/mainland subspecies; see text for more detail.
IA, initial stage abundances.

TABLE 3. Model parameter values for historic validation and simulation models

	Maximum allowable size		Birth sex ratio bias		Reproductive rate ^a	
	Validation	Simulation	Validation	Simulation	Mean	SD
Spectacled bear	81	100	0.52	0.5	0.34	0.13
Sloth bear	56, 45	60	0.58	0.5	0.34	0.13
Sun bear	89	60	0.37	0.5	0.13	0.085

^aReproductive rates are used for both validation and simulation models for all bears.

the carrying capacity, estimated as the maximum population size for the time window used for validation. The sloth bear population had a maximum population size over the time window of 56; we also simulated the sloth bear validation model at 45 (the largest population size over the past 10 years) based on observations that the overall population decline of the population in the past 10 years may be due to a lack of interest in maintaining the population before active management began.

Model Validation

Internal consistency and extreme behavior tests did not reveal any unexpected model behavior that indicated logical or mechanical flaws in the model equations of the final version of the basic model. For historical validations, model projections were compared with studbook data for total population size, deaths, and births for each species. When comparing each model's projections to historic population data, spectacled bears and sun bears had similar trajectories to the observed (studbook) population size (Table 4, Fig. 2). The sloth bear model was sensitive to the maximum allowable size, and we validated the model with two different sizes; the model did not match the historic population well with a MAS of 56, but matched fairly well with a size of 45 (Fig. 2). We also compared each bear's stage model projections to the PM2000 results (Table 4, Fig. 2).

TABLE 4. Comparison of average annual population growth rates from historic validations

Species	Source	Lambda ^a
Spectacled bear	Studbook	1.0364
	Stage model	1.0366
	PM2000	1.0597
Sloth bear	Studbook	0.99
	Stage model (MAS=56)	0.9996
	Stage model (MAS=45)	0.9887
	PM2000	0.9961
Sun bear	Studbook	0.9973
	Stage model	0.9814
	PM2000	0.9789

^aFor spectacled bears, lambda is calculated as the geometric mean of annual growth rates until MAS is reached; for other populations, lambda is the mean over all annual growth rates from the date window.

MAS, maximum allowable size.

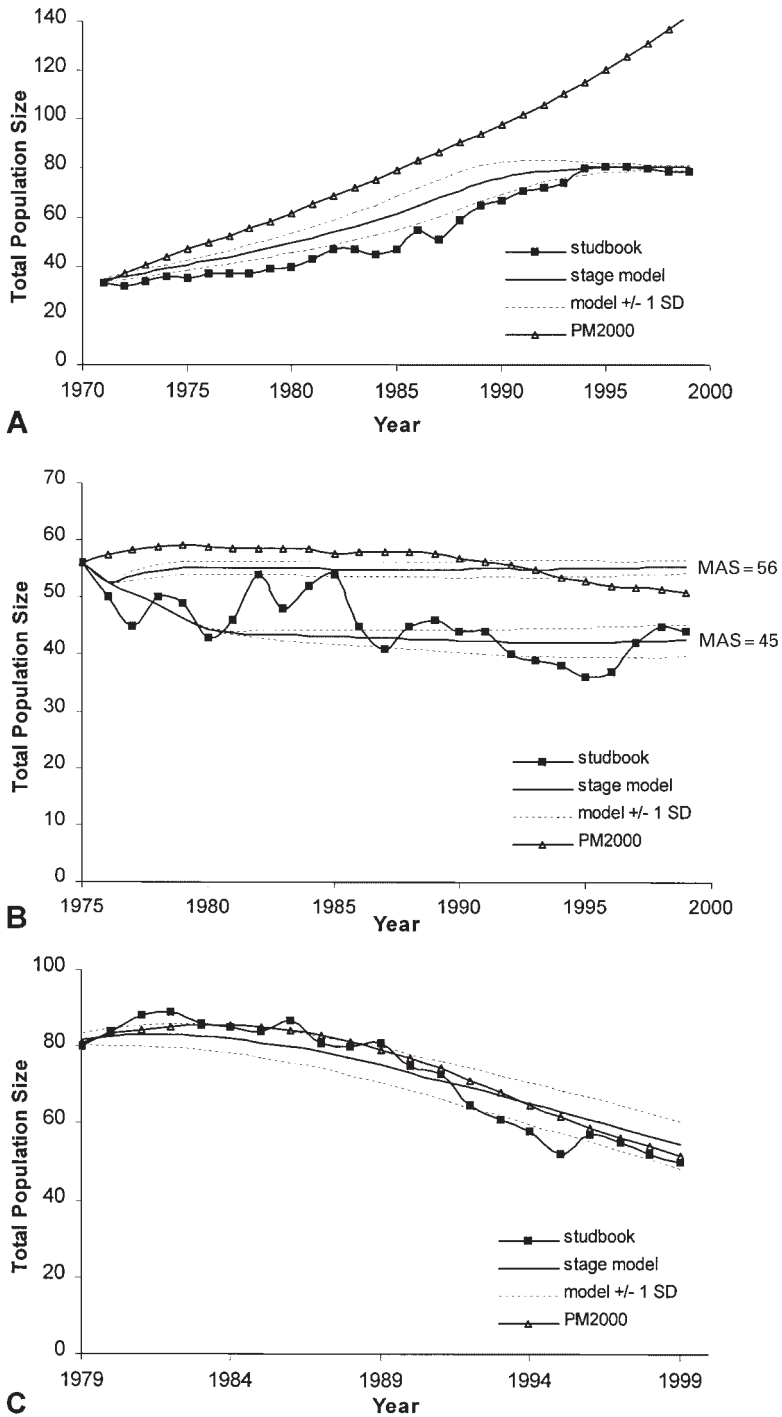


Fig. 2. Historic validation results comparing population sizes for stage model projections (± 1 SD), PM2000 projections, and observed studbook sizes for (A) spectacled bears, (B) sloth bears, and (C) sun bears. Sloth bear validations were run at two maximum allowable population sizes: 56 and 45.

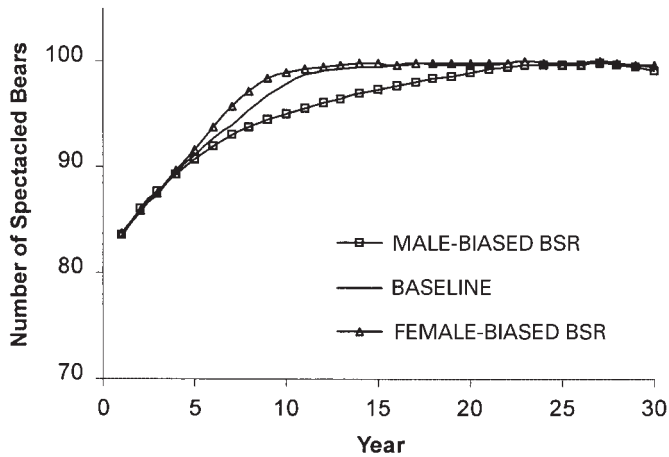


Fig. 3. Simulation results for spectacled bear model projections under three simulation scenarios; for details see Table 1.

Model Simulation

Spectacled bear

Under baseline simulation conditions, the spectacled bear population increased from 81 to its target population size of 100 individuals in 100% of 500 runs. On average over those 500 runs, the population reached the target size in approximately 10.7 years. The female- and male-biased BSR simulations did not differ greatly from the baseline run (which remained at 0.5 BSR for the entire simulation); all three simulations reached the target population size, although the male-biased simulation did so more slowly ($\lambda=1.008$) and the female-biased simulation slightly more quickly ($\lambda=1.017$) than the baseline ($\lambda=1.013$) (Fig. 3). The biased runs produced slightly different population sex structures at the end of 30 years: at the beginning of all simulations, the sex ratio in the entire population was 0.6 (49 males/81 total bears); after 30 years, the baseline simulation sex ratio was 0.52, the male-biased BSR simulation sex ratio was 0.58, and the female-biased BSR simulation sex ratio was 0.46.

Sloth bear

Under baseline simulation conditions, the sloth bear population increased from its starting population size of 44 individuals up to the target population size of 60 individuals in 94% of 500 runs. The average time to the target population size over those 500 runs was approximately 16.2 years. The female- and male-biased BSR simulations did not differ greatly from the baseline run; all three simulations reached the target population size, although the male-biased simulation did so more quickly ($\lambda=1.0153$) and the female-biased simulation slightly more slowly ($\lambda=1.0082$) than the baseline ($\lambda=1.0097$) (Fig. 4). The biased runs resulted in slightly different final population sex structures: at the beginning of all simulations, the sex ratio in the entire population was 0.45 (20 males/44 total bears); after 30 years, the baseline simulation sex ratio was 0.4, the male-biased BSR simulation sex ratio was 0.44, and the female-biased BSR simulation sex ratio was 0.37.

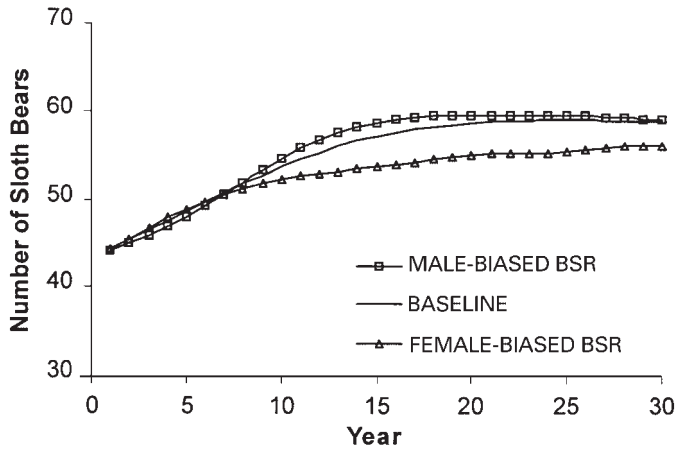


Fig. 4. Simulation results for sloth bear model projections under three simulation scenarios; for details see Table 1.

Sun bear

Under baseline simulation conditions, the sun bear population steadily decreased from its starting population size of 61 individuals (19 of Bornean origin, 42 of mainland/unknown origin). In an extended (60-year) baseline simulation, the unknown portion of the population was not phased out until year 33 (Fig. 5). The strong population decline occurred under all simulation scenarios (baseline, $\lambda=0.929$; ALLBOR, $\lambda=0.958$; ALLPOP, $\lambda=0.971$) (Fig. 6). Introducing biased runs of BSR did not affect the population’s trajectory (baseline simulation $\lambda=0.929$, male-biased BSR simulation $\lambda=0.931$, female-biased BSR simulation $\lambda=0.926$). At the beginning of the simulations, the population sex ratio was 0.31; final population sex ratios under baseline conditions were slightly altered (baseline simulation sex

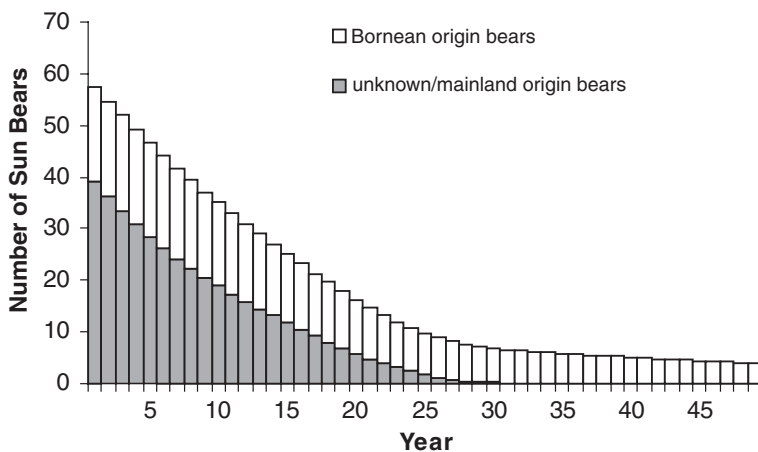


Fig. 5. Simulation results for sun bear model projections under baseline conditions, showing the two subpopulations, Bornean and unknown/mainland.

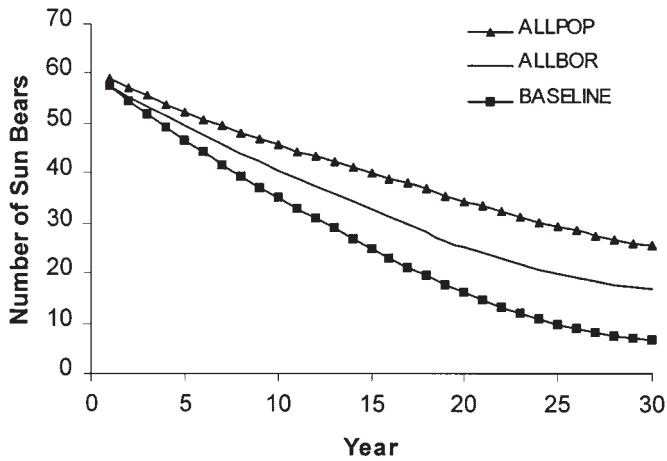


Fig. 6. Simulation results for sun bear model projections under various breeding scenarios.

ratio=0.48, male-biased BSR simulation sex ratio=0.52, female-biased BSR simulation sex ratio=0.44).

DISCUSSION

The process of building a model involves a great deal of iterative working and reworking of both the concepts driving the model and the mechanical relationships of the model itself. In the course of this project, our model of captive demography evolved through multiple iterations and software packages. We began with a simple stage-based matrix model utilizing RAMAS/stage [Ferson, 1993], but after continually struggling with this matrix-based approach we shifted to a system dynamics approach using Vensim and finally STELLA. These packages improved our modeling process because they allowed us to focus on the conceptual structure and relationships of the captive system by facilitating the building of mathematical relationships and the specific syntax of formulas. As our systems dynamics model evolved in STELLA, we focused on the elements of the captive system that are essential to the biological population dynamics (the population sex and stage structure, and the observed vital rates) and what management elements are necessary to project the future trajectory of captive populations (the population's housing requirements as dictated by the breeding system, and its target population size, which constrains future growth). An essential aspect of being able to capture this complexity was using the stage approach: lumping all adult ages into a single stage simplified the modeling process without losing biological information. The result of this model-building process is a stage-based system dynamics model that has been constantly revised and incorporates the essential dynamics of captive populations.

Another phase of the model-building process focuses on testing and evaluation. The purpose of validation for any model is not to prove that the model is truthful, but rather to build confidence in the design and implementation of the model [Mayer and Butler, 1993; Power, 1993; Rykiel, 1996; Ford, 1999]. Our validation approaches addressed the internal and external consistency of the model. The first approach

revealed that the mathematical relationships in our basic model operate in the manner we expected (extreme behaviors tests). Results from the historic validation revealed that for individual species, model projections closely resembled historically observed behavior (e.g., the sun and spectacled bears, Fig. 2). It is also clear that for certain populations (e.g., the sloth bear) the model is sensitive to the maximum allowable size for the population, and that this size may determine how well the population matches observed behavior. It is difficult, of course, to determine what the historic carrying capacity was for these species; closer scrutiny of the sloth bear population trajectory (studbook of Fig. 2b) shows a population that fluctuated at around 50 individuals from 1975–1985, and then declined in the 1990s until an upsurge in 1998. These observed population fluctuations may be due to the species' popularity, which may have imposed different carrying capacities over the date window. The maximum sizes for the future, however, are TAG-designated target population sizes, and thus we believed it was reasonable to simulate future dynamics for the sloth bear population.

In proposing an alternative methodology for demographic modeling of captive populations, it is also important to assess the proposed model against strategies already being used. We attempted to replicate our historic validation using PM2000 to compare those results to our stage model's projections (Table 4, Fig. 2). For one population, the spectacled bear, our model predicted the historic population size better than PM2000. This is partly because no upper limit for population size can be set and then applied to the projections in PM2000; however, even before the point at which the population would reach its maximum population size, the PM2000 projections overpredicted (Table 4). For the sun bear and sloth bear populations, both PM2000 and our stage model predicted the historical population sizes fairly well. Clearly, for certain populations, stage and age models might produce fairly similar results; other studies for certain species (*Drosophila* [Law and Edley, 1990] and spotted owls [Goldwasser, et al., as cited in Groom and Pascual [1998]) have shown similar long-term results between age and stage models. Although an age-based approach produces similar results, our stage-based model still benefits from the simplicity of modeling four stages rather than 30+ ages for each bear species. Our model also captures some important aspects of population demography that are impossible to address with the current version of PM2000. The ability to consider issues of BSR biases, to assess a population's ability to reach a target population size given the population structure, and to subdivide the population (as with the sun bears) is critical in regards to management questions. It is likely that a stage-based approach will prove even more useful as we use it with a variety of species with different life histories and management goals in future studies.

The main goal of building most models is to test model behavior in the future while varying parameters of interest. There is a clear difference between assuming that a model will accurately forecast the future and using the model as a tool: "A forecast is an attempt to predict what *will* happen. A projection is an attempt to describe what *would* happen, given certain hypotheses" [Caswell, 2001, p. 20]. We used our species-specific models to ask what would happen to the bear populations if current management practices are maintained or altered in specific ways. The spectacled bear population, which is reasonably large and stable, is projected to continue its population growth until its target population size is eventually reached. Managers of the spectacled bear population can focus on the challenges of

preserving high genetic diversity while maintaining the target population size for the foreseeable future. Although the sloth bear population has been experiencing a decline over the last decade, our model illustrates that, were space available, the population could meet its target population size. As of the 2000 management meeting, however, only a few additional spaces were available, and population growth will only be achieved with the recruitment of additional institutions [Wachsberg et al., 2000]. The sun bear population, on the other hand, has serious demographic problems that are cause for concern. All population projections produced a declining population (Fig. 6). The SSP goals of producing a population of Bornean bears and phasing out all bears of unknown and/or mainland descent may be difficult to accomplish given the current demographic rates and population structure. Even under more generous breeding scenarios the population declined. In the ALLBOR simulation, all Bornean females were allowed to breed, regardless of whether they were paired (this scenario could be practically accomplished by housing multiple females at an institution and switching a single male between the females, by rapidly moving a male between institutions so that multiple females could be inseminated per year, or by using artificial insemination techniques). Despite this alteration, the population declined. This decline also occurred when the model was altered to allow all animals to breed regardless of background (ALLPOP simulation), indicating that current demographic rates are unsustainable for the sun bear population (Fig. 6). The presence of only five Bornean male bears, as well as the goal of only breeding the Bornean subpopulation, may be demographically unsustainable unless breeding success can be improved and/or further importations can be made. Also, because of the long life span of these bears, phasing out the unknown/mainland background subpopulation may take over 30 years (Fig. 5).

This model also enabled investigation of the implications of long runs of BSR bias, such as those experienced in the spectacled bear population [Faust and Thompson, 2000]. Despite concerns on the part of population managers about the effects of such runs, model simulations of all three bear species suggest that even fairly long and severe runs of bias may not perturb population dynamics enough to disrupt the population trajectory. It is interesting to note, however, that male- and female-biased runs had different effects on the spectacled and sloth bear simulations. The existing male bias of the spectacled bear population clearly benefits from a run of female-biased births, which allows faster population growth than either no-bias or male-biased simulations (Fig. 3). In contrast, the sloth bear population's existing female bias creates an initial population structure that cannot benefit from a female-biased BSR; in sloth bear simulations, the male-biased simulation allows faster growth than no-biased or female-bias simulations (Fig. 4). Theoretically, short runs of BSR bias might be more significant for small or declining populations, as small population size magnifies the effects of stochastic processes such as biased BSR. Further experimentation with variable populations (skewed population sex ratios, very small populations, shorter-lived species, etc.) would shed more light on the role played by BSR bias runs in population dynamics. The issue of BSR biases clearly demonstrates one of the most beneficial uses of such a model as a tool to quantitatively assess whether concerns based on anecdotal observations truly impact the population trajectory of a species. This assessment would be impossible without a flexible model designed to formalize the process of evaluating alternative scenarios.

CONCLUSIONS

1. It is feasible to build a demographic model for captive species that replicates the interactions between biological population dynamics and contemporary population management practices. Data exist in studbook databases that can be used to parameterize the model.

2. The model presented here produces credible projections in most cases. Validation procedures can be utilized to build confidence in projection models.

3. This model can be a valuable tool to address questions and concerns of population managers. The flexibility and ease of altering model features such as the BSR and population structure allows population biologists to easily assess management options, and will help to inform future management decisions.

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REFERENCES

- Ballou JD, Foose TJ. 1996. Demographic and genetic management of captive populations. In: Kleiman DG, Allen ME, Thompson KV, Lumpkin S, editors. *Wild mammals in captivity: principles and techniques*. Chicago: University of Chicago Press. p 263–314.
- Caswell H. 2001. *Matrix population models: construction, analysis, and interpretation*. Sunderland, MA: Sinauer Associates, Inc. 722 p.
- Carter J, Ackleh AS, Leonard BP, Wang H. 1999. Giant panda (*Ailuropoda melanoleuca*) population dynamics and bamboo (subfamily Bambusoideae) life history: a structured population approach to examining carrying capacity when the prey are semelparous. *Ecol Model* 123:207–23.
- Crooks KR, Sanjayan MA, Doak D. 1998. New insights on cheetah conservation through demographic modeling. *Conserv Biol* 12:889–95.
- Crouse DT, Crowder LB, Caswell H. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecol* 68:1142–23.
- Doak D, Kareiva P, Klepetka B. 1994. Modeling population viability for the desert tortoise in the Western Mojave Desert. *Ecol Appl* 4:446–60.
- Ebert TA. 1999. *Plant and animal populations: methods in demography*. San Diego: Academic Press. 312 p.
- Faust LJ, Thompson SD. 2000. Birth sex ratios in captive mammals: patterns, biases, and the implications for management and conservation. *Zoo Biol* 19:11–25.
- Ferson S. 1993. *RAMAS/stage: generalized stage-based modeling for population dynamics*. Setauket, NY: Applied Biomathematics.
- Fieberg J, Ellner SP. 2001. Stochastic matrix models for conservation and management: a comparative review of methods. *Ecol Lett* 4:244–66.
- Ford A. 1999. *Modeling the environment: an introduction to system dynamics modeling of environmental systems*. Washington, DC: Island Press. 401p.
- Frederick C. 2000. *North American regional studbook for the sun bear (Helarctos malayanus)*. Seattle: Woodland Park Zoological Gardens.
- Frederick C, Long S, Lynch C. 2000. *Sun bear Species Survival Plan masterplan*. Chicago: Lincoln Park Zoological Gardens.
- Groom MJ, Pascual MA. 1998. The analysis of population persistence: an outlook on the practice of viability analysis. In: Fiedler PL, Kareiva PM, editors. *Conservation biology: for the coming decade*. New York: Chapman and Hall. p 4–28.

- Heppel SS, Walters JR, Crowder LB. 1994. Evaluating management alternatives for red-cockaded woodpeckers: a modeling approach. *J Wildl Manage* 58:479–87.
- Marin VH. 1997. A simple-biology, stage-structured population model of the spring dynamics of *Calanus chilensis* at Mejillones del Sur Bay, Chile. *Ecol Model* 105:65–82.
- Law R, Edley MT. 1990. Transient dynamics of populations with age- and size-dependent vital rates. *Ecology* 71:1863–70.
- Mayer DG, Butler DG. 1993. Statistical validation. *Ecol Model* 68:21–32.
- Odum RA, Smith BR. 2001. The effects of prorating risk in the development of life tables. *Zoo Biol* 20:279–91.
- Patten BC. 1997. Synthesis of chaos and sustainability in a nonstationary linear dynamic model of the American black bear (*Ursus americanus* Pallas) in the Adirondack Mountains of New York. *Ecol Model* 100:11–42.
- Pollack JP, Lacy RC, Ballou JD. 2001. Population management 2000, version 1.12. Brookfield, IL: Chicago Zoological Society.
- Power M. 1993. The predictive validation of ecological and environmental models. *Ecol Model* 68:33–50.
- Rosenthal M. 2000. North American regional studbook for the spectacled bear (*Tremarctos ornatus*). Chicago: Lincoln Park Zoological Gardens.
- Rykiel EJ. 1996. Testing ecological models: the meaning of validation. *Ecol Model* 90:229–44.
- Sauer JR, Slade NA. 1987. Uinta ground squirrel demography: is body mass a better categorical variable than age? *Ecology* 68: 642–50.
- Shryock HS, Siegel JS, Stockwell EG. 1976. The methods and materials of demography. San Diego: Academic Press. 577 p.
- Thompson SD. 2001. Lifesaver-Q_x. Chicago, IL: Lincoln Park Zoological Gardens.
- van Groenendael J, de Kroon H, Caswell H. 1988. Projection matrices in population biology. *Trends Ecol Evol* 3:264–69.
- Wachsberg L. 2000. North American regional studbook for the sloth bear (*Melursus ursinus*). Kansas City, MO: Kansas City Zoological Gardens.
- Wachsberg L, Long S, Lynch C. 2000. Sloth bear Species Survival Plan masterplan. Chicago: Lincoln Park Zoological Gardens.
- Weinhardt D, Long S, Lynch C. 2000. Spectacled bear Species Survival Plan masterplan. Chicago: Lincoln Park Zoological Gardens.