

Wild-captive metapopulation viability analysis

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Abstract

We developed an interactive management model for wild and captive populations of the ploughshare tortoise or angonoka, *Geochelone yniphora*. Interactive management is based on the translocation of individuals between wild and captive populations to simulate a metapopulation. Demographic parameters of one captive and two wild populations of this rare tortoise were used to conduct a metapopulation viability analysis (MVA). The effectiveness of the conservation strategy proposed for this species was then evaluated by modifying the probability of extinction and growth of the metapopulation over a fixed period of time. Several alternative scenarios of interactive management were then tested and ranked in terms of their effect on the viability of the metapopulation. The model predicted that catastrophic events such as bush fires would likely have a negative effect on the future of remaining wild populations. However, the model also predicted that the use of captive-born offspring to establish additional wild populations would decrease the risk of extinction of the metapopulation as a whole. We believe that, when supported by sound knowledge of the demographic parameters of a species, the use of MVA as part of an interactive management program can be an effective conservation tool that allows assessment of the probable response of both captive and wild populations to different management alternatives. One of the most interesting aspects of this interactive management approach is the link between in situ and ex situ conservation.

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1. Introduction

Natural areas throughout the world are becoming isolated and are often subject to disturbance, which in turn has led to the loss of biodiversity. Small populations that remain in these areas are highly vulnerable to extinction as a result of environmental, demographic and genetic stochasticity (Gilpin and Soulé, 1986). Hence, the development and implementation of innovative, yet practical, conservation methods has become increasingly important. In recent years, the zoo community has shown

a growing commitment to the expansion of its role in wildlife conservation through an interactive wild-captive metapopulation approach. The concept of zoological parks simply maintaining captive stocks of threatened species for future reintroduction (i.e. the Noah's Ark Paradigm) has not proven practical nor biologically sensible for a number of reasons. Ex situ methods are typically prohibitively expensive and single species oriented, and historically, few reintroduction projects have had long term goals beyond the production of as many offspring as possible (Ginsberg, 1993; Balmford et al., 1995; Conway, 1995; Hutchins and Conway, 1995; Snyder et al., 1996). In contrast, interactive management approaches focus on habitat preservation and management of both wild and captive populations (Foose, 1991; Conway, 1995). The goal of interactive management is to create an artificial metapopulation structure, which can,

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in theory, reduce the risk to wild populations from stochastic events (Hanski and Simberloff, 1996).

A true interactive management program seeks to address the cause(s) of the decline of a species, such as habitat loss, and in cases where remaining populations are fragmented and isolated, to use captive populations to augment wild populations. The use of captive-bred animals to supplement wild populations is controversial because of the difficulty and expense of captive breeding, the risk of spreading pathogens and the difficulty of evaluating the success of such programs (Wilson et al., 1994). However, in certain situations reinforcements can result in demographic and genetic enhancement of a wild population. Such programs typically give priority to flagship and/or umbrella species that are threatened in the wild. While the focus on flagship or umbrella species is not a panacea (Simberloff, 1998), targeting management programs at such species is often the most cost-effective mechanism to conserve biodiversity of the entire community (Conway, 1995). Furthermore, focusing conservation efforts on flagship species can generate funds to support habitat preservation.

In order to evaluate how interactive management can be used as a conservation tool, we performed a metapopulation viability analysis (MVA) using both wild and captive populations (defined as “subpopulations”) of a rare Malagasy tortoise, *Geochelone yniphora*. Historically, only a few models have used both wild and captive populations in this manner, and none have truly followed an interactive management scheme as defined above. Until now, MVA has most often been used to manage genetic diversity of captive populations (Earnhardt, 1999), or to estimate the number of individuals that can be withdrawn from a captive population to support a reintroduction program (Bustamante, 1996, 1998; Saltz, 1998).

The ploughshare tortoise or angonoka, *G. yniphora*, provides an excellent example for illustrating the approach outlined above. *G. yniphora* is one of the rarest chelonians in the world with only about 600 individuals remaining in the wild. The world population consists of only five small, isolated populations, all of which are restricted to a patchily distributed scrub habitat within a 30-km radius of Baly Bay in northwestern Madagascar (Smith et al., 1999). The endangered status of the ploughshare tortoise is the result of many centuries of commercial exploitation and of the loss of tortoises and their habitat by bush fires (Pedrono and Smith, 2003). Life history characteristics of chelonians typically include a slow growth rate, delayed maturity and low fecundity, factors which limit the ability of populations to recover from human exploitation (Congdon et al., 1993). The effects of historic exploitation on the demographic characteristics of ploughshare tortoise populations are still evident, despite the fact that few wild tortoises have been collected in recent years.

In 1986, at the request of The World Conservation Union, the Durrell Wildlife Conservation Trust initiated a recovery program for the ploughshare tortoise (Durrell et al., 1994). The recovery plan included an in-country captive-breeding program and research on the status and ecology of wild populations. Over the course of 10 years, more than 250 offspring were produced from a founder stock of 20 tortoises at the multi-species breeding facility at Ampijoroa in Madagascar. The goal of the captive breeding program was to produce offspring that could be used to supplement wild populations, if deemed necessary. An experimental release of five juvenile ploughshare tortoises in part of their former range demonstrated that captive-born tortoises could survive in the wild (Pedrono and Sarovy, 2000). In addition, efforts are underway to protect wild tortoise populations with the support of the local people (Durbin et al., 1996). If these efforts are successful, the ploughshare tortoise will have the potential to function as a flagship species for the protection of the biological community around Baly Bay.

In this paper we used projection models to address the potential effectiveness of an interactive management approach to managing captive and wild populations of *G. yniphora*. We examined the likelihood of the persistence of this metapopulation (both wild and captive subpopulations) under various management options. We considered a purely demographic framework of extinction probability because as yet there is no genetic information available for this species. However, given the relatively long generation time exhibited by *G. yniphora* (about 30 years), general goals for the maintenance of genetic variability within a fixed time period are easier to achieve than with species with a shorter generation time.

2. Methods

2.1. Population modeling

We developed a size and age matrix for wild and captive subpopulations, based on the life cycle of *G. yniphora* (Fig. 1). In adult chelonians, maturity and fecundity are more size- than age-related (Shine and Iverson, 1995), whereas in juveniles growth annuli counts are highly correlated with carapace length ($r^2 = 0.96$, $N = 115$). Because information on the variability of growth rates in wild ploughshare tortoises was lacking, we developed an age-structured approach to model the juvenile phase (Crouse et al., 1987; Crowder et al., 1994; Doak et al., 1994). This approach is based on a Lefkovich matrix where all individuals in a given stage exhibit identical survival, fecundity and individual growth rates. We felt safe in assuming that there was no emigration or immigration in the populations considered, since the current spatial distribution of wild

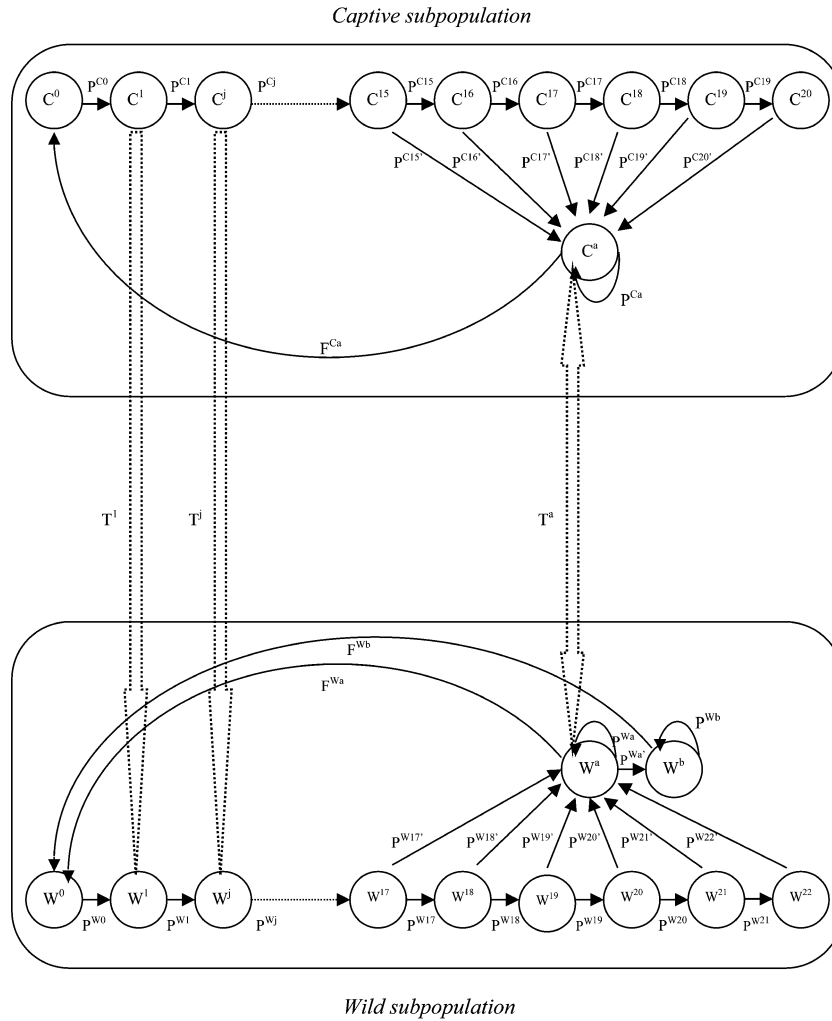


Fig. 1. Age and class-structured life-cycle graph of the ploughshare tortoise metapopulation. W^j : number of wild individuals; W^a : number of wild adults 300–345 mm carapace length (CL); W^b : number of wild adults 345–420 mm CL; C^j : number of captive individuals; F^* : size-specific fecundity; P^* : age-specific transition probability; j : juveniles; a, b : adults; T^j : number of individuals translocated; P^j : transition rate to a superior reproductive class. Transition rates are age-specific survival rates until maturity and size-dependent fecundity for adults. Transition to adulthood occurs between ages of 17 and 22 for wild individuals, and between ages of 15 and 20 for captive individuals.

ploughshare tortoise populations does not allow a natural metapopulation dynamic (Smith et al., 1999).

Our model had a discrete annual time step, which began immediately prior to the reproductive season. The survival rate was calculated for 22 age classes (j) of wild juveniles. The age at sexual maturity for females was ≈ 300 mm straight-line carapace length (CL), a size which corresponded to an age of 17–22 years, depending on the relative growth rate of individuals (Pedrono et al., 2001). All individuals with < 300 mm CL were considered to be juveniles. The probability of a juvenile attaining maturity was considered to increase with age. The relative growth rate is faster in captivity than in the wild, and as such, the sexual maturity of captive individuals was estimated to correspond to an age of 15–20 years. Results of demographic research indicated that in the wild females of this species reproduce annually. Reproductive success increased with female size in the

wild subpopulations (Pedrono et al., 2001), and therefore, wild adult females were placed in one of two size classes. The first size class (W^a) consisted of individuals with 300–345 mm CL and the second size class (W^b) contained those with 345–420 mm CL. In captive adult females, fecundity varied greatly among individuals and apparently was not related to body size (Reid, 1995). Thus, only a single class of adult females (C^a) was used for the captive subpopulation. Juveniles in the wild population were denoted W^j , whereas those in the captive population were denoted C^j . The corresponding transition probabilities for the two subpopulations were P^{W^j} and P^{C^j} , respectively. The coefficients P^{W^j} and P^{C^j} represented the probability of an individual reaching the highest reproductive category. The probability that an individual would remain in the same adult size category was P^{W^a} , P^{W^b} and P^{C^a} . This was in accordance with the survival and the relative growth rate at this size class.

Because of the extreme longevity of chelonians (Gibbons, 1987), and of *G. yniphora* in particular, the probability of an individual attaining reproductive senescence was not considered.

The current population densities of ploughshare tortoises are much lower than those reported for other Malagasy testudinids (Pedrono and Smith, 2003) and therefore, we did not include density dependence in the model. However, for the same reason, we anticipated that variations in sex ratio could potentially have a significant effect on population viability. Therefore, a two-sex model was used to express the influence of a sex ratio imbalance. In such a model, the asymptotic growth rate of all or part of the population (females or males) depends only on the female growth rates. The loss of males (by death or other reasons) affects the sex-ratio in the population and the age structure in the male set. The demographic costs of translocation were not incorporated in our model since none were observed in a previous study (Pedrono and Sarovy, 2000).

We selected the values for model parameters using data obtained from five years of demographic study on two wild populations and one captive population. Details of these studies are published elsewhere (Smith et al., 1999; Pedrono et al., 2001). Demographic parameters used in the model are presented in Table 1, and it is noted that these parameters were not sex-dependent. Initial conditions used in the model corresponded to the 1998 subpopulation structure (Table 1) with the 'sub-

population size' corresponding to all individuals in the subpopulation.

2.2. Simulating stochasticity of demographic parameters

Simulations of the MVA were performed with ULM software (Legendre and Clobert, 1995). In the first iteration, the dynamics of each subpopulation were analyzed separately. The probability of subpopulation survival during a given time was estimated by the proportion of trajectories remaining at the end of this interval. Extinction corresponded to a decline of one sex to zero rather than a specified threshold of pseudo-extinction. Demographic stochasticity was incorporated through a binomial distribution for the survival rates and a Poisson distribution for fecundities. Additional variations due to catastrophes were included through a Bernoulli distribution. The actual subpopulation sizes of ploughshare tortoises are so low that no significant variation of demographic parameters was detected over time (Pedrono et al., 2001). Therefore, we were unable to include variability due to environmental stochasticity in the models.

2.3. Simulating catastrophes

We simulated the impact of two possible catastrophic events: bush fires in the wild subpopulation and theft of individuals from the captive subpopulation. In our experience, these two scenarios represent the most likely events to impact the ploughshare tortoise recovery

Table 1
Population parameters used for the basic model simulations

	Wild subpopulation (<i>W</i>)	Captive subpopulation (<i>C</i>)
Density dependence	None	None
Age at sexual maturity (<i>j</i>)	17–22 years	15–20 years
Contribution of breeders	100%	50%
<i>Fecundity (F)</i>		
Adults <345 mm CL	2.73 hatchlings	–
Adults >345 mm CL	6.22 hatchlings	9.9 hatchlings
<i>Transition rate (P)</i>		
P^{W0}/P^{C0}	0.40	0.90
P^{Wj}/P^{Cj}	From 0.44 to 0.96 according to their size	1
$P^{W17} - P^{W17'}/P^{C15} - P^{C15'}$	0.87–0.09	0.9–0.1
$P^{W18} - P^{W18'}/P^{C16} - P^{C16'}$	0.77–0.19	0.8–0.2
$P^{W19} - P^{W19'}/P^{C17} - P^{C17'}$	0.39–0.58	0.4–0.6
$P^{W20} - P^{W20'}/P^{C18} - P^{C18'}$	0.29–0.68	0.3–0.7
$P^{W21} - P^{W21'}/P^{C19} - P^{C19'}$	0.19–0.77	0.2–0.8
$P^{W22'}/P^{C20'}$	0.97	1
$P^{Wa} - P^{Wa'}/P^{Ca}$	0.77–0.19	0.99
P^{Wb}	0.97	–
Catastrophes	Fire/exploitation	Theft/disease
<i>Initial population size</i>		
Hatchlings	17	32
Juveniles	22	150
Adults	41	18

Hatchlings were defined as individuals less than one year old; juveniles as individuals greater than one year old but not sexually mature; and adults were sexually mature individuals (>300 mm CL). P^{W*} : proportion of sexually immature 17-year old wild individuals; $P^{W's}$: proportion of sexually mature 17-year old wild individuals.

program. Anthropogenic bush fires are a frequent phenomenon in the region and are known to cause direct mortality in this species (Pedrono and Sarovy, 2000). Moreover, in 1996, nearly half of the captive-born juveniles and two adult females were stolen from the tortoise breeding center (Webster, 1997). The magnitude of catastrophes was based on 20% and 30% reduction of the wild subpopulation and on 50% and 60% reduction of the captive subpopulation. Because it is impossible to accurately predict the frequency of these events, we used a range of different frequencies of catastrophes in the simulations: 10% and 20% with the subpopulations, and 30% and 60% with the metapopulation.

Because the role of the captive population in interactive management programs is to augment the wild population, we modeled conditions that minimized the probability of extinction (E) for the captive and wild subpopulations combined. The model included augmentation of the wild subpopulation with 10 year old, captive-born juveniles (T^j). These “translocated” individuals would represent two thirds of each cohort produced at the breeding center over a period of 10 years. This level of removal could be supported by the captive population with its current growth rate (see 3.1. *Subpopulation viability*). Alternative management strategies were then evaluated to determine the relative effect on the metapopulation. Except in the circumstances noted later in this paper, basic survival rates were depressed during each simulated catastrophic event to compare the probability of extinction of the wild and captive subpopulations under those minimum survival estimates.

During the selection of alternative scenarios for restocking, the model considered the release of 10 individuals of various ages each year, over five years, for a total of 50 individuals. The sex ratio of the tortoises released was assumed to be 1:1. To achieve a realistic outcome, our restocking scenario integrated the conservative catastrophes defined above. The change in the probability of extinction resulting from the augmentation of the wild subpopulation was compared with the change in the probability of extinction induced by establishing a new wild subpopulation.

The probability of extinction corresponding to each scenario was assessed by Monte-Carlo simulations (500 replicate simulations per scenario). The effectiveness of the proposed strategies was evaluated by comparing the probability of extinction of the metapopulation or by whether metapopulation size increased or decreased. The probability that both

subpopulations would become extinct was calculated by multiplying the probability of extinction of each subpopulation. During simulation of catastrophes, the projection period was fixed at 50 years for both subpopulations. Although ploughshare tortoises are long-lived, we felt that using a more lengthy timeframe for the analyses was unjustified for formulating a management framework and risk estimates for longer timeframes are increasingly imprecise (see Ellner et al., 2002). Extinction probabilities were reported with the corresponding standard errors ($E \pm SE$) and projected population sizes with the related standard deviations ($N \pm SD$).

3. Results

3.1. Subpopulation viability

With demographic stochasticity alone, the asymptotic growth rate (r_m) for the wild and captive subpopulations was 0.01 and 0.14, respectively and both subpopulations were predicted to continue to increase ($E = 0 \pm 0.6\%$). Adult mortality had the greatest effect on the trajectories of the two subpopulations (elasticity: survival rate of small wild-adults $S^{Wa} = 0.08$; survival rate of large wild-adults $S^{Wb} = 0.46$; survival rate of captive-adults $S^{Ca} = 0.22$). The wild subpopulation was particularly sensitive to adult mortality and its probability of extinction was high ($E = 67 \pm 2.3\%$) when wild-adult mortality increased from 3% (actual) to 8% per year. The maximum adult mortality that the wild subpopulation can sustain was 5% per year ($E < 0\%$).

A simultaneous increase in the frequency and magnitude (surface area burned) of bush fires resulted in a considerable increase in the risk of extinction (Table 2). A catastrophic event such as a bush fire, occurring once every 10 years resulting in a 20% reduction of the wild subpopulation would drive this population to extinction within 50 years ($E = 1.6 \pm 1.1\%$). In contrast, the captive subpopulation would have to experience a catastrophe every 10 years, resulting in the loss of 60% of the individuals, to exhibit a similar probability of extinction ($E = 2 \pm 1.7\%$).

3.2. Metapopulation management

The models predicted that the likelihood of persistence of the metapopulation increased with

Table 2
Probability of extinction (E) of the wild and captive subpopulations under alternative catastrophic scenarios (results are reported as the mean \pm SE)

Catastrophic event		Wild subpopulation		Captive subpopulation	
Magnitude		20%	30%	50%	60%
Frequency	10%	0.0 \pm 0.0	0.6 \pm 0.5	0.0 \pm 0.0	0.0 \pm 0.0
	20%	1.6 \pm 1.1	2.8 \pm 0.3	0.2 \pm 0.1	2.0 \pm 1.7

metapopulation size. The probability of the metapopulation becoming extinct during the next 50-years was nil if the frequency of catastrophes affecting one of the two subpopulations was <15%, or if the frequency of catastrophes was <25% in both subpopulations (Fig. 2). Under the first catastrophic scenario (fire/exploitation), the transfer of wild adults into captivity and 10 year old juveniles released to the wild, would reduce the probability of extinction of the metapopulation by 50% during this time frame (Table 3). However, reinforcement of the wild population with captive-born juveniles alone did not reduce the probability of extinction in any significant manner. Under conditions of the second catastrophic scenario (theft/disease), the transfer of wild breeding adults to captivity greatly increased the probability of extinction of the metapopulation.

However, it is difficult to assess the real benefits of reinforcing the captive subpopulation with additional wild-founders to the metapopulation as a whole, since the probable frequency and magnitude of the catastrophes occurring in the wild and in captivity are very different. Therefore, the potential benefits of transferring wild individuals into captivity in the absence of catastrophic events was also calculated. If reproductively mature wild individuals (5 males and 5 females) were transferred to the captive population, in 10 years, there would be a net gain of 45 ± 4 individuals in the captive population, 89 ± 11 individuals after 15 years and 195 ± 16 individuals after 20 years.

Table 3
Extinction risks (E) of the metapopulation after 50 years under different management scenarios

Frequency of catastrophes (wild vs. captive subpopulations)	Management strategy	E (%) ($x \pm SE$)
60% vs. 30%	A	20.2 ± 1.8
	B	15.6 ± 2.3
	C	6.0 ± 1.5
	D	8.8 ± 1.3
30% vs. 60%	A	10.0 ± 1.6
	B	6.1 ± 2.0
	C	49.6 ± 0.8
	D	24.7 ± 1.4

A: no intervention; B: augmentation of the wild subpopulation with 2/3 of the 10 year old captive individuals over a 10-year period; C: augmentation of the captive subpopulation with 1/4 of the wild adults over 10 years; D: scenarios B and C combined.

3.3. Restocking strategies

If 50 four-year old juveniles were released to an unoccupied site, the resulting “new” population was projected to contain 57 ± 9 tortoises after 50 years, as compared to 155 ± 26 tortoises if the founding individuals were released at 10 years of age and 223 ± 39 if they were released at 20 years of age. Therefore, release of 10 years old individuals appears to be a good compromise between the length of the rearing phase and minimum size at release. At 10 years of age, the tortoises have no natural predators and the population dynamic will be similar in the wild or captive population. A comparison

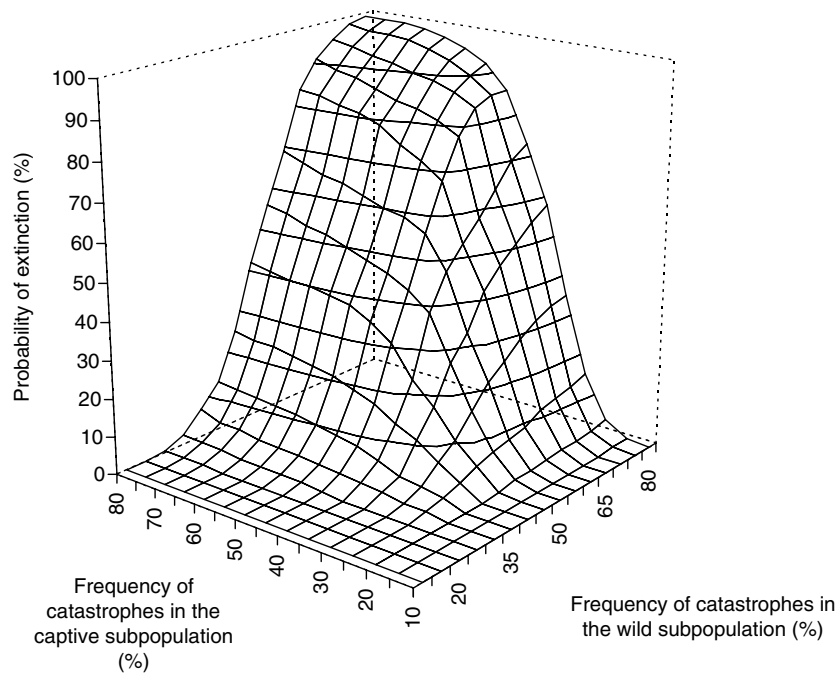


Fig. 2. Extinction risks (E) for the metapopulation over a time-frame of 50 years when 2/3 of 10 year old captive born individuals are translocated to the wild subpopulation.

of the outcome of releasing 50 individuals in year one to that of releasing 10 individuals per year over a five years period revealed essentially no difference in population size ($N = 155 \pm 26$ when all individuals were released in the same year vs. $N = 154 \pm 24$ when individuals were released over five years).

The analysis of the influence of the size of a founder population (T^j , Fig. 1) indicated that it would be necessary to release at least 50 10-year old individuals for

the population to persist for 50 years ($E < 1$ for this reintroduced population) (Fig. 3). If only 10 individuals were released, the probability of extinction was $27 \pm 0.9\%$ over this time span. With the stochastic conditions defined above and assuming a 1:1 sex ratio, the reintroduced population would contain 155 ± 26 individuals after 50 years. If the sex ratio was female biased (1 male:3 females), the reintroduced population would contain 197 ± 28 individuals over the same time

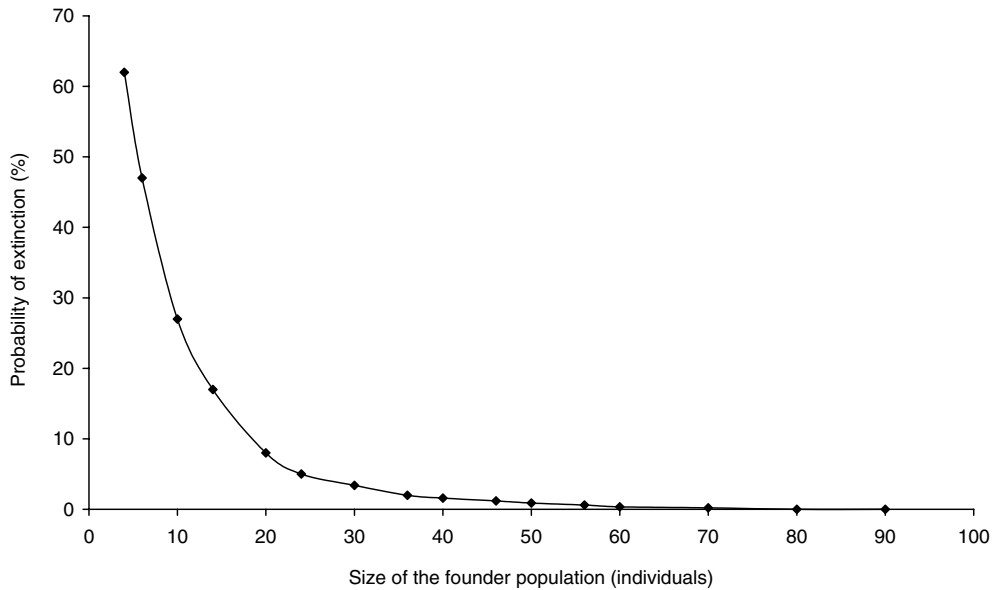


Fig. 3. The effect of founder population size on probability of extinction (E) for reintroduced populations of ploughshare tortoises over a time-frame of 50 years.

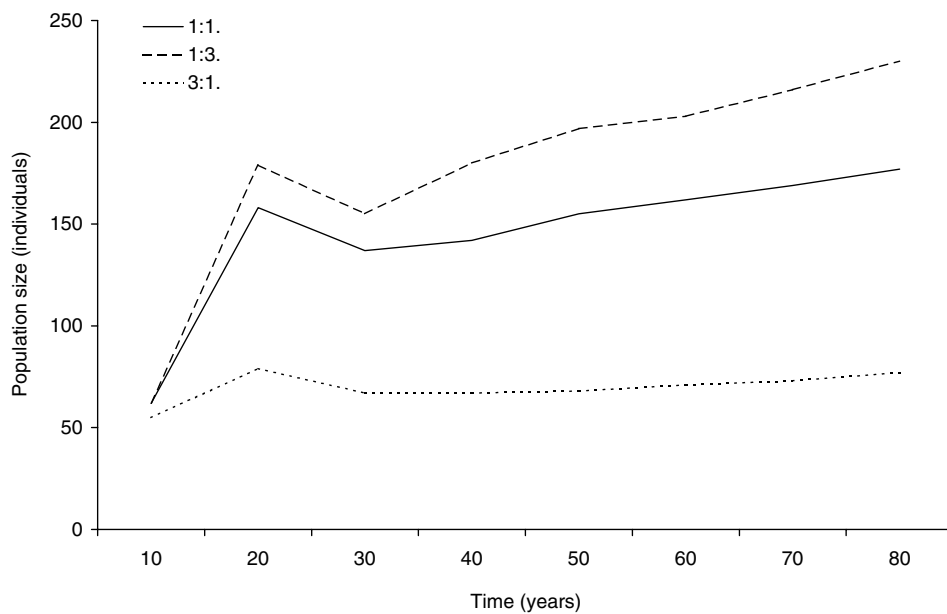


Fig. 4. Population trajectories over a time-frame of 50 years for a reintroduced subpopulation of ploughshare tortoises under different sex ratio scenarios. Male:female.

frame. However, if the sex ratio was male biased (3 males: 1 female), the population would contain only 68 ± 12 individuals after 50 years (Fig. 4).

Under the conditions of defined stochasticity, it would be preferable to reintroduce a single population of 50 individuals rather than two populations of 25 individuals ($E = 0.22 \pm 0.12\%$ vs. $0.37 \pm 0.10\%$). Similarly, two populations of 20 individuals were less likely to become extinct than four populations of 10 individuals ($E = 0.64 \pm 0.41\%$ vs. $0.72 \pm 0.33\%$).

Finally, we attempted to determine whether it was preferable to use captive born individuals to augment the wild subpopulations or to use them to establish new populations. The decline in probability of extinction under each of these two scenarios was not significantly different ($E = 0.0028 \pm 0.0012\%$ vs. $0.0023 \pm 0.0007\%$ for 50 individuals translocated).

4. Discussion

When supported by sound knowledge of relevant subpopulation parameters, MVA can be a useful analytical tool for conservation (Caswell, 2001). Such models allow managers to assess the probable responses of wild and captive subpopulations to alternative management options and to set quantitative goals, thereby avoiding subjective conservation decisions (Lubow, 1996). Furthermore, MVA models can have utility in managing habitat patches as opposed to less versatile models that deal with single large areas inhabited by a single panmictic population (Drechsler and Wissel, 1998).

Ploughshare tortoise populations are highly sensitive to mortality of the adult life stages. The high sensitivity of this stage is characteristic of chelonian species (Crouse et al., 1987; Doak, 1994) and to long-lived species in general (Boyce, 1992). Therefore bush fires, which are known to kill adult tortoises, present a potentially severe problem for the long-term viability of the species in the wild. Catastrophic events such as this have been implicated in the extinction of other species (Simberloff, 1986; Mangel and Tier, 1994). The ultimate outcome depends on the frequency and magnitude of catastrophes, and on the time scale of the analysis. Our model predicted that if bush fires cannot be controlled (e.g., frequency <10-year intervals and impact <20% of mortality on the tortoise subpopulation), survival of wild ploughshare tortoise subpopulation cannot be assured beyond the year 2050. Bush fires may also affect habitat quality, resulting in increased habitat fragmentation and a net loss of tortoise habitat. Therefore, control of bush fires must become a management priority for this species. Fires are set seasonally by the local Sakalava people to promote growth of grasses for free-ranging cattle. The survival

of ploughshare tortoise populations will depend upon our ability to educate local people in alternative ways of managing rangeland. In addition, although commercial exploitation of wild ploughshare tortoises for food is apparently not a problem at this time, remaining populations may be particularly vulnerable to poaching for the international trade in exotic species, as underscored by the recent theft of captive ploughshare tortoises (Webster, 1997). The impact of poaching on the wild population would be similar to that of bush fires, in that adults removed from the population are effectively “dead”. Therefore, all efforts should be made to protect wild and captive subpopulations from poaching.

Provided bush fires can be controlled, the release of captive-bred individuals into the wild should be considered as a potential conservation strategy for this species. The high population growth rate and reduced sensitivity to catastrophes exhibited by the captive subpopulation provides a good basis for developing management strategies that will allow the wild subpopulation to be supported by the captive subpopulation. Given the fragmented nature of the wild subpopulation there are several possible options to achieve this support. These options involve the use of captive-born animals either to augment existing populations or to establish new ones. Most conservation biologists recognize that there are many potential problems with reinforcement programs (IUCN, 1987; Cunningham, 1996), and given that the population models in this study predict similar outcomes with either of these two options, we recommend using captive-bred individuals to establish new populations of ploughshare tortoises as part of an interactive management program. This strategy can be designed, monitored and evaluated using MVA (Kleiman et al., 2000). Our results suggest that it would be preferable to reintroduce a single large population rather than two small ones. However, once the first new population is established, it could be beneficial to reintroduce a second population to further reduce the chance of a catastrophic event wiping out the entire metapopulation (Gilpin, 1987; Quinn and Hastings, 1987). To further ensure long term viability, the founder group should have an equal sex ratio, or be slightly biased toward females, and should contain at least 50 individuals. The reduction in the value of demographic parameters of captive-bred individuals after their release to the wild (Griffith et al., 1989) can influence the release strategy, i.e. whether to release young or adult individuals (Sarrazin and Legendre, 2000). It has been demonstrated that reintroduced captive-born juvenile ploughshare tortoises can have survival rates equivalent to those of wild tortoises (Pedrono and Sarovy, 2000); therefore we feel that it is not necessary to rear captive offspring beyond ≈ 10 years of age, an age/size that

protects them from predators. However, before launching a release program, measurable goals should be set with a clear endpoint. For example, it would be important to determine the optimal duration and rate of release, such as the establishment of a minimum number of wild populations consisting of 60 breeding adults by a particular target date. Furthermore, financial costs of the various options should be considered in order to ensure the optimal use of available funds (Lindburg, 1992).

This type of metapopulation model also could be used to determine the ideal size of captive populations (Saltz, 1998). Beyond the selection of species that should be part of captive-breeding programs (Hutchins et al., 1995; Balmford et al., 1996), the number of breeding populations can be planned and controlled by calculating the number of captive individuals and populations necessary to maintain a viable metapopulation. Moreover, if captive populations are properly managed using data obtained from MVA, it would eliminate redundancy in zoological collections, thus freeing space for breeding additional rare species (Conway, 1995). The maintenance of computerized studbooks such as the Single Population Analysis and Record Keeping System (SPARK; ISIS, 1995) used by the majority of the zoos supports the implementation of an interactive management approach. The size of the captive ploughshare tortoise population at Ampijoroa is currently at capacity with about 250 tortoises, which is enough to supply a release program.

We recommend that the captive ploughshare tortoise population be divided into two geographically distinct locations to lessen the risk of a catastrophic event such as disease or theft (Gilpin, 1987; Quinn and Hastings, 1987). The breeding facility currently houses several species of chelonians and therefore, it is possible that disease could be transmitted to captive, and ultimately, wild ploughshare tortoises. All chelonians at Ampijoroa should be screened for diseases and isolation techniques should be implemented at both subpopulations. Moreover, it will also be important to determine the sex of all offspring produced in the captive breeding program and whether the ploughshare tortoise has environmental sex-determination (Ewert and Nelson, 1991). If ploughshare tortoises have environmental sex-determination, offspring already produced at the breeding center may have disparate sex ratios (see Kuchling and López, 2000), which will affect potential reintroduction scenarios. If required, nests could potentially be manipulated to produce more females. However, such manipulations might also have negative impacts on the wild population structure and mating system (Lovich, 1996).

Finally, wild individuals should be used to supplement the captive subpopulation if it is necessary to enhance genetic diversity or if catastrophic events are incompatible with the maintenance of a viable natural

subpopulation. For example, in the case of the California condor (*Gymnogyps californianus*), the alarming demise of most of the wild population led to the decision to capture the last wild individuals for captive breeding (Meretsky et al., 2000). We also recommend research on the genetic diversity of both subpopulations to clarify the importance of tortoise exchange between them. Since the remaining genetic diversity of the ploughshare tortoise is probably contained in the wild subpopulation, we feel that a higher value must be placed on conservation of intact wild populations.

From a broader perspective, one of the most interesting aspects of the interactive management approach is the link between in situ and ex situ conservation. Instead of conserving a few species in zoos, we could potentially save many species under the umbrella of a few flagship species. Beyond their simple role as demographic and genetic reservoirs, specimens of flagship species in zoological collections can thus become veritable ambassadors for their original biological communities. Although any high profile species can be used as a flagship, selection of species candidate for interactive management from amongst the more species-rich communities, has the potential to increase the role of zoos in the conservation of biodiversity. Conservation programs and financial efforts would thus best be centered on flagship vertebrates inhabiting megadiverse countries or hot-spots, whose conservation requires predominantly habitat protection. The interactive management program for the ploughshare tortoise is an effective way to stop the extinction spasm in northwestern forests of Madagascar, a region harboring a wealth of biodiversity. However, while it is a useful support to multi-species conservation strategies, attention must be given to the selection of the species subject to interactive management approaches, as good flagship and umbrella species may not necessarily be good candidates for captive propagation.

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