

## Quel futur pour la population française d'ours brun ?

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Le laboratoire d'écologie de l'Ecole Normale Supérieure à Paris (CNRS UMR 7625) et l'ONCFS ont développé un modèle mathématique afin d'évaluer la viabilité de la population d'ours bruns dans les Pyrénées. Ce modèle décrit le cycle de vie de l'ours et permet d'étudier la probabilité qu'a cette population de s'éteindre et comment éviter cette extinction. Il est considéré par les scientifiques qu'une population est viable si sa probabilité d'extinction est inférieure à la valeur communément admise de 5% sur 50 ans.

Les résultats résumés brièvement ci-après doivent être plus interprétés en terme qualitatif (i.e. échelle de risque) qu'en valeurs numériques absolues, en particulier parce que les données disponibles ne permettent pas une estimation fine des paramètres démographiques des animaux. Il a été retenu pour ces paramètres des valeurs vraisemblablement égales ou supérieures à celles concernant les ours vivant dans les Pyrénées, correspondant donc à un scénario démographique plutôt optimiste.

Ce travail montre que la mortalité annuelle d'une population d'ours doit rester faible pour que cette population ne décline pas. En d'autres termes, il est important d'éviter toute mortalité induite par l'homme, notamment sur les femelles reproductrices dont la survie a le plus d'effet sur la dynamique de la population.

Il conclut que **la sous-population des Pyrénées Occidentales est confrontée à un risque élevé d'extinction** de l'ordre de 50% sur 50 ans et qu'il serait nécessaire de **lâcher au moins 5 femelles dans un délai court** pour ramener ce risque à la valeur communément admise de 5%. Lâcher un nombre inférieur de femelles ou reporter ces lâchers au-delà de 10 ans reviendrait à prendre un risque accru de voir cette population s'éteindre rapidement. **La sous-population des Pyrénées centrales est dans une situation moins critique à brève échéance**, néanmoins le choix d'un faible risque d'extinction <5% requiert le **lâcher d'au moins 6 individus (2 males et 4 femelles) dans cette décennie**.

Les nombres d'individus à lâcher doivent être considérés comme des valeurs seuils minimales car l'approche de modélisation démographique retenue ignore des facteurs existants mais mal documentés (aspects génétiques par exemple) qui augmentent les probabilités d'extinction.

**La population pyrénéenne d'ours bruns ne peut être considérée comme viable à long terme. Sa conservation requiert le lâcher de plusieurs ours dans un proche avenir.**

# **Evaluating conservation strategies for the French Pyrenean brown bear (*Ursus arctos*) population by using stage-structured population models**

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Running title: *Modeling Pyrenean brown bear conservation strategies*

## **Abstract**

The Pyrenean brown bear (*Ursus arctos*) population is considered as seriously threatened with extinction. We develop deterministic and stochastic stage-structured demographic models to study the viability and need of reinforcements of this population. We show that a small bear population can persist provided its demographic parameters remain high, however the Pyrenean population cannot be considered as viable. Population persistence is more sensitive to breeder survival than to any other parameters. Unless more bears are released, the Pyrenean population will likely reach high extinction risks and a reinforcement program should be carried out in both sub-populations in a short future.

Keywords: Brown bear, *Ursus arctos*, Viability analysis, Reinforcement, Pyrénées

## **Résumé: Modélisation démographique de stratégies de conservation de la population Pyrénéenne d'ours bruns (*Ursus arctos*).**

La population Pyrénéenne d'ours bruns (*Ursus arctos*) est considérée comme gravement menacée d'extinction. Afin d'étudier sa viabilité et son besoin en renforcements, nous avons développé des modèles démographiques déterministes et stochastiques. Nous montrons qu'une petite population d'ours peut survivre mais que la population Pyrénéenne ne peut être considérée comme viable. Le maintien d'une population est plus sensible à la survie des individus reproducteurs qu'à tout autre paramètre. A moins que plusieurs ours soient relâchés, la population Pyrénéenne sera confrontée à un risque d'extinction élevé. Un programme de renforcement est nécessaire pour les 2 sous-populations dans un proche avenir.

Mots-clés: Ours bruns, *Ursus arctos*, Analyse de viabilité, Renforcement, Pyrénées

## 1. Introduction

Human induced mortality remains one of the main factor driving large carnivore populations to extinction [1-3]. Large carnivores can kill domestic and game animals, and for some species can threaten humans. They can be viewed as competitors for resources or can be targeted as trophies and, as a consequence, many species have been facing widespread persecution.

For instance, the French Pyrenean brown bear population underwent a dramatic decline during the past century through overhunting or direct persecution. In 1900 there were 150 bears in the Pyrenean range [4], whereas in 1990, the population had collapsed to less than 10 individuals in the Western Pyrénées [5]. In 1996 and 1997 the French government managed the experimental reintroduction of 3 bears (2 females and 1 male) originating from Slovenia [6] to create a new sub-population in the Central Pyrénées. One of the females was later accidentally killed [7] but the reintroduced sub-population has since grown, and a dispersing male has reached the endemic Western Pyrenean sub-population [7]. However, the future of the bear in the Pyrénées is far from secured. The fact the bear is a charismatic species makes that the question of further reinforcement or how large a viable bear population should be remains controversial and needs to be addressed based on a rigorous approach. This requires the development of a bear specific demographic model that we propose to address here. Demographic models or population viability analyses (PVA) are mathematical descriptions of species life cycles over time [8]. They are now a widely used tool in endangered species conservation and their usefulness lies in comparing management strategies and exploring consequences of different assumptions on population dynamics [9]. Conservation biology owes much of its credibility to demographic modeling [10] and insights gained from modeling should never be dissociated from the model assumptions [11]. Indeed, results are better qualitatively interpreted rather than quantitatively and should not be used to determine a numerical value of a minimum viable population size or of a probability of reaching extinction [12].

In this paper, we build and analyse deterministic and stochastic stage-structured models to study the dynamics and viability of the Pyrenean brown bear population. We evaluate the need for further reinforcements and try to define how many females or males -if any- should be released in order to secure the long term future of this population.

## 2. Methods

### 2.1 Bear biology

In Europe, female and male brown bears reach sexual maturity between 3.5 to 5 years old. Mating occurs in June-July and a male may accompany a female for up to two weeks. In Autumn, the development of inseminated ovi stops until nutrition level of the mother is adequate to feed the embryo. The young are born from January to March. The litter size ranges from 1 to 4, but 2 is most common and interbirth interval is most frequently 3 years. Under most circumstances, brown bears live as lone individuals, except for females accompanied by their cubs. Brown bears are distributed in overlapping home ranges and male home ranges are larger than those occupied by females. The Pyrenean brown bear population presently hosts 11 individuals dispatched into 2 sub-populations (Figure 1). The Western sub-population consists of 1 female and 5 males [5, 13] whereas the Central population consists of 2 females and 1 males [7]. Furthermore, 2 males have dispersed from the Central to Eastern Pyrénées in an area where no female is available (Quenette, unpubl. data).

### 2.2 Model structure and simulations

The population is divided into several stages defined by sex and age. Bears can be cubs (0-12 months), juveniles (12-24 months), floaters (24-36 and 36-48 months) or breeders (> 48 months) for both sexes. Age at first reproduction is therefore 4 years. Transitions between classes are explained hereafter and shown on the life cycle graph (Figure 2).

1. Surviving female juveniles become floaters 1
2. Surviving male juveniles become floaters 1
3. Surviving female floaters 1 become floaters 2
4. Surviving male floaters 1 become floaters 2
5. Surviving female floaters 2 become breeding females
6. Surviving male floaters 2 become breeding males
7. Surviving breeding females keep the same status
8. Surviving breeding males keep the same status
9. Surviving breeding females give birth to female cubs that become juveniles
10. Surviving breeding females give birth to male cubs that become juveniles

We build a 2-sex model where females can reproduce as soon as at least one male is present in the population. We define a carrying capacity as the number of adult-sized bears an area can host. Survival and fecundity are treated as binomial and Poisson variates, respectively. Our Monte Carlo simulations involve 1000 runs each [10]. A population qualifies as extinct once all

classes are empty. We use this definition for extinction to consider cases of reinforcement where only individuals of the same sex would remain. We use a deterministic matrix model to compute asymptotic population growth rate  $\lambda$  [14]. We also calculate elasticities of  $\lambda$  [14] to assess to which parameter  $\lambda$  is most sensible and calculate left eigenvector [14] to show the impact of removing individuals on  $\lambda$ . We use a stochastic model to seek what would be the minimum size  $N$  of a viable bear population assuming an initial settlement at carrying capacity  $K=N$ .

We assess the effects of releasing bears on population persistence with emphasis on number and sex of released bears. We try to identify a strategy that would maximize population persistence with the lowest number of released bears. We selected the smallest number of released bears that would lead to an extinction probability lower than 5% and investigate the best sex-ratio for this number. We study the impact of delaying in time the implementation of this optimal strategy. We model the Pyrenean bear population spatial structure and a possible indirect Allee effect [15] by considering reinforcement strategies for the 2 existing sub-populations rather than for the whole metapopulation. We hypothesize that connections were null between the 2 sub-populations. A male has shown to be able to disperse from the Central to the Western sub-population [7] but since we cannot estimate the probability a young male reaches the other sub-population or a part of the range where no female is available, we ignore this possibility. Moreover, since females are the limiting sex in the population and are most often philopatric in unsaturated populations [16, 17], we believe our assumptions are conservative.

All analyses and simulations are performed with the computer program ULM (Unified Life Models) [18, 19] that allows one to handle any time-discrete stage-structured population model. ULM has already been used to model the population dynamics of several carnivore species such as grizzly bears *Ursus arctos horribilis* [20], arctic foxes *Alopex lagopus* [21], Iberian lynxes *Lynx pardinus* [22] and wolves *Canis lupus* [23].

### 2.3 Demographic parameters

Since no accurate estimation of Pyrenean brown bear survival parameters was available, we define 4 scenarios, denoted by S0 to S3 from pessimistic to optimistic, that involve different combinations of parameter values (Table I). Cubs have the lowest survival probabilities to account for the effect of predators, starvation and accidental deaths. An analysis of mortality for 150 cubs in the Cordillera Cantabrica between 1982 and 1991 yields a mean cub mortality rate of 0.4 [24]. Survival probabilities of floaters, especially males, appear to be slightly lower than those of breeding bears: floaters travel through unknown areas, are not familiar with prey distribution, can be killed by resident bears and support a higher human induced mortality because of conflicts with humans. Reproducing bears have the highest survival. We estimate these survivals from several European and North American studies [24, 25]. Data on litter size give a mean value of 1.6 in the Western Spanish population [26] and 1.9 in Italy [27]. In the

Eastern Spanish population (Cordillera Cantabrica), mean litter size was 2.3 cubs whereas for reintroduced bears in Austria [28] and France (Quenette, unpubl. data) it was 2.6. Interbirth interval is usually comprised between 3 and 5 years [24], despite cycles of 2 years have been observed [29]. We fix mean litter size at 2.1 and interbirth interval at 3 years. We keep the primary sex-ratio fixed at 0.5.

### 3. Results

#### 3.1 Bear future in the Pyrenean range

Asymptotic growth rate  $\lambda$  computation shows that a brown bear population increases under our S1, S2 and S3 scenarios but decreases under the more pessimistic one S0 (Table I). Pessimistic scenario gives a 2.5 % decline per year whereas more optimistic one gives a 7.1 % increase per year. Elasticities are larger for breeder survival (Table II). Elasticities to all other class survival rates and litter size are far lower. We check through  $\lambda$  level curve computations [14] that the great importance of elasticity to breeder survival extends to parameter space and is not restricted to the local parameter value. Impact of removing a single bear on  $\lambda$  is the largest if this bear is a breeding female (Table III).

#### 3.2 Minimum viable population size

We compute probabilities of extinction on 100 years for several carrying capacities and under our 4 demographic scenarios (Figure 3). A population under scenario S0 reaches extinction with high probabilities irrespectively of carrying capacity, whereas a population under scenario S3 goes nearly never extinct for carrying capacity as small as 12 bears. For intermediate scenarios S1 and S2, probabilities of extinction is lower than 5% for carrying capacities respectively greater than 40 and 20.

#### 3.3 Reinforcement strategies

Our computations reveal that not releasing any bear in these sub-populations would likely lead them to very high extinction risks. For the Western sub-population, keeping the extinction probability at low levels would mean releasing at least 5 bears (5 females / 0 male, Figure 4) under scenario S2, whereas the Central sub-population would require at least 6 bears (but 4 females / 2 males, Figure 5). These reinforcements would be more efficient if they were carried out in a short future, i.e. releasing the same number of bears in 10 or 15 years would not prevent both these sub-populations to reach higher level of extinction probabilities (Figures 6 and 7). Considering the best scenario S3 changes only the numerical value of the smallest number of bear required, but does not change the fact that reinforcements are needed in a near future.

#### 4. Discussion

Our results show that even small bear populations can persist provided their demographic parameters remain high, but less favorable scenarios would require larger population sizes. Population persistence is more sensitive to breeder survivals than to any other parameters. When focusing specifically on the present Pyrenean brown bear population, our results reveal that this population is unlikely to persist unless more bears are released. These bears should be mainly females and be released in both sub-populations and in a near future.

Our analysis relies on several important assumptions.

- (1) Individuals in a given class have all the same demographic parameters and could not be differentiated, which is an inherent assumption of stage-structured population models.
- (2) Cub survival is independent of mother age and senescence is not explicitly considered. Taking a breeding bear survival rate of 0.925 under scenario S2 (0.95 under scenario S3) yields an expected breeding expectancy of 13.3 years (20 years under scenario S3).
- (3) We ignore environmental and genetic stochasticity because data are too scarce to incorporate these factors into our model. Our stage-structured approach did not allow us to incorporate genetic factors such as inbreeding because all individuals in a class were considered identical. As a consequence, all our probabilities of extinction were probably underestimated.
- (4) We do not model interbirth interval reduction when a litter dies. However, the reduced elasticity of  $\lambda$  to litter size suggests this is unlikely to change our conclusions.
- (5) We do not model possible infanticide by floater males which has recently been shown to be potentially detrimental to population survival [30,31,20]. However, this phenomenon is most likely to occur in highly hunted populations which is not the case in the Pyrénées.
- (6) Model parameters are kept constant during simulation (implying no habitat change).

There has been few population viability analyses for European brown bear as compared to the North American grizzly bears and because the ecology of grizzly bears is different from the ecology of the European brown bear, it is preferable to develop specific population models [24]. In Scandinavia, Swenson et al. [25] found higher population growth rate (13%) than other studies did mainly because their radio-tracking data reveal high survival rates. In the Cordillera Cantabrica, where the ecosystem is more similar to the Pyrenean one, the brown bear population suffered high poaching rates and this population did not qualify as being viable. In Romania, average growth rate calculated on several decades was 7% [32-33] which corresponds to a population under our optimistic scenario. Our consideration of several scenarios, from

pessimistic to optimistic values in survival rates, allow us to provide insights in possible Pyrenean population fates despite the lack of exact survival rate estimation. Given the current uncertainty in parameter estimation, it would be hazardous to retain only very high survival rates and a conservative approach should interpret our results in a qualitative rather than a quantitative way.

Our study has major implications in terms of conservation recommendations. It shows that unless a reinforcement program is launched, the Pyrenean brown bear population is expected to go extinct. Moreover, delaying further such a program would be risky in term of probability of extinction. It is fortunate that the expertise to reintroduce bears has been developed several years ago during the experimental program and this should make actions we recommend easier to perform in a near future. The brown bear is protected by the 92/43/EEC directive known as “Habitat Directive” as a strictly protected species (Annex IV) requiring special protected areas (Annex II). The Pyrenean population is considered in a very critical status by the “Action Plan for Conservation of the Brown bear in Europe” [34] which includes among the required actions the reinforcement of the Pyrenean population. Releasing bears into previously extirpated or quasi-extinct populations is now a strategy that has been successfully implemented in Austria [28] and is being carried out in Italy [36]. A range wide bear conservation program on the Pyrénées should not be detrimental to other ongoing wildlife or ecosystem conservation programs [35]: bear predation on ungulates is low [37-38] and bears have no negative impact on forest or alpine ecosystem dynamics [38,39,40].

While our research has provided information regarding the demographic aspects of a reinforcement program, it is now widely recognized that carnivore conservation, especially planned return of larger ones, is a multidisciplinary task [41] requiring a collaborative approach between biologists, economists and sociologists. For the Pyrenean brown bear, some of the core issues are conflict with sheep farming, forestry and road use, and human dimension. The latter has shown to be particularly critical in large carnivore conservation and refers to the concept of social carrying capacity [42]. Indeed, projects of restoration of large carnivores have often to deal with the level of acceptance by local populations which can be highly variable both among the different social groups (hunters, farmers, hikers, local elected representatives, workers of tourist industry, craftsmen) and within a social group (Quenette unpubl. data). In fact, bear reinforcement strategies that our modeling approach has contributed to precise would turn out to be a success only if people who live with and near bears every day become convinced that cohabiting with bears is possible.

## 5. Acknowledgements

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## FIGURES

Figure 1: Present distribution of the Brown bear in the Pyrénées.

Figure 2: Life cycle graph for a bear stage-structured population. J: juveniles, F1: floaters, F2: floaters, R: Reproducing individuals. See text for arrow details.

Figure 3: Extinction probabilities on 100 years as a function of population size assuming an initial settlement at carrying capacity.

Figure 4: Extinction probabilities on 50 years for the Western Pyrenean bear sub-population as a function of number of released bears and number of released females under scenario S2.

Figure 5: Extinction probabilities on 50 years for the Central Pyrenean bear sub-population as a function of number of released bears and number of released females under scenario S2.

Figure 6: Extinction probabilities on 50 years for the Western Pyrenean bear sub-population under an optimal reinforcement strategy (5 females / 0 male) and scenario S2 as a function of time for various delays in releasing individuals.

Figure 7: Extinction probabilities on 50 years for the Central Pyrenean bear sub-population under an optimal reinforcement strategy (4 females / 2 males) and scenario S2 as a function of time for various delays in releasing individuals.

Figure 1

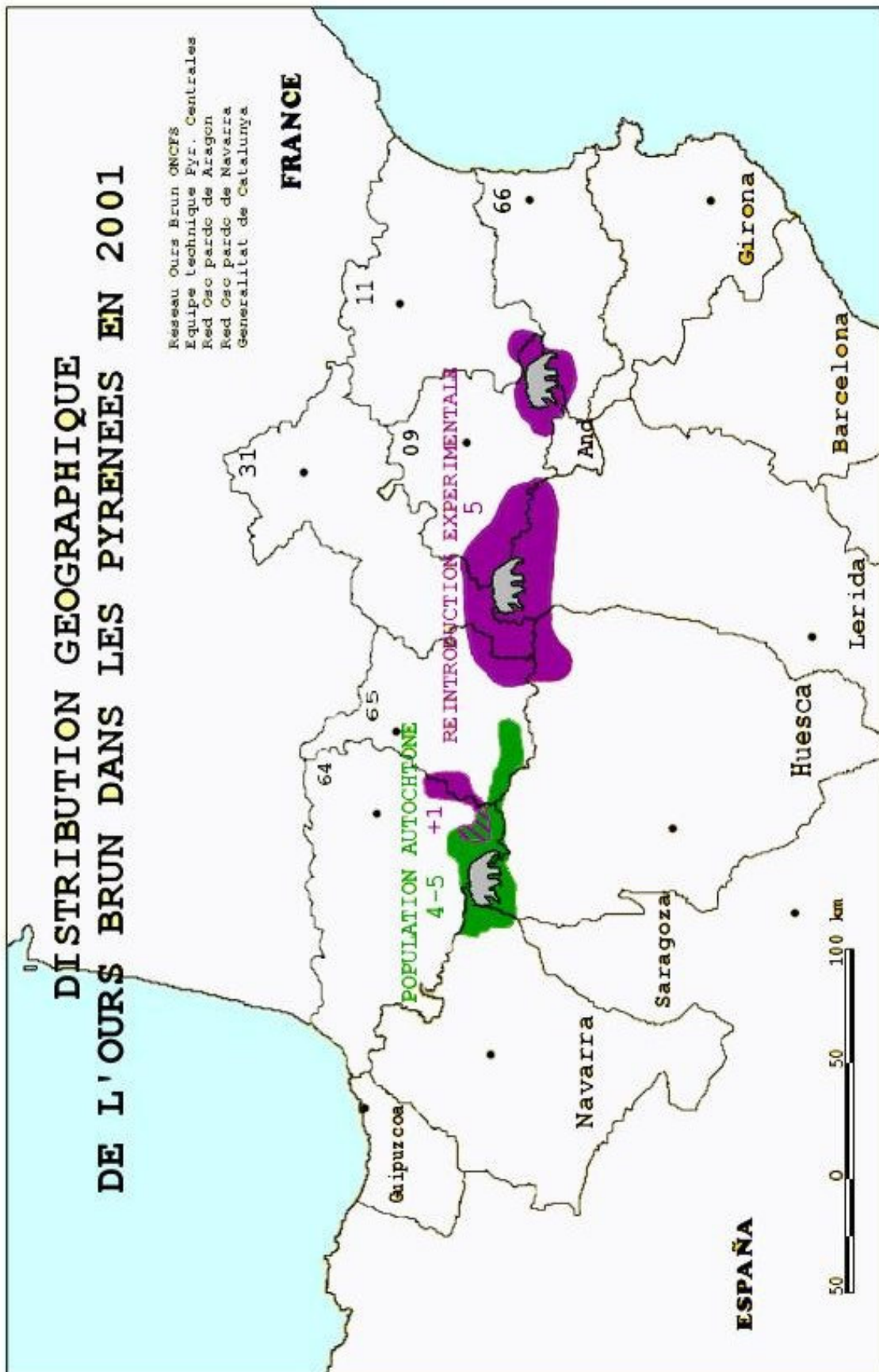


Figure 2

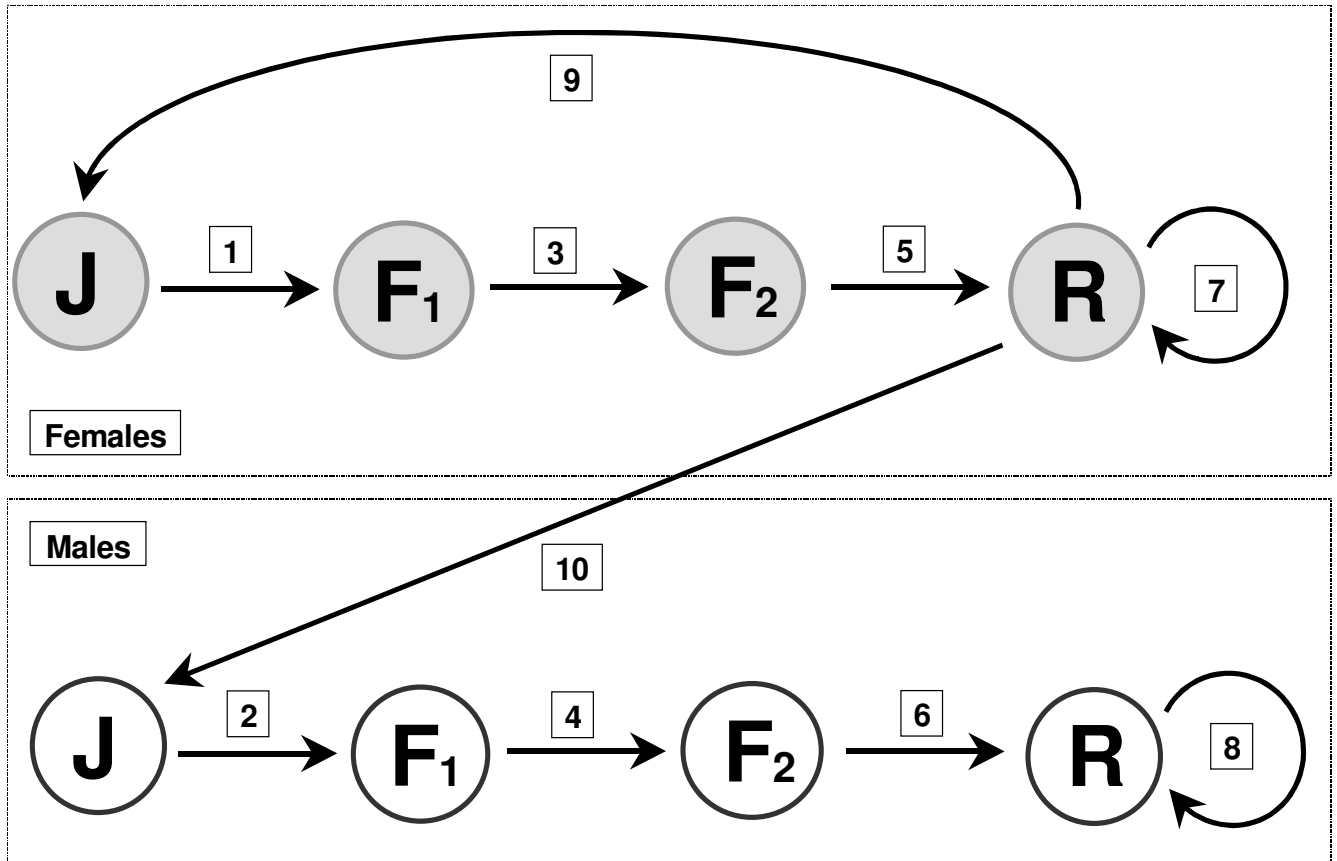


Figure 3

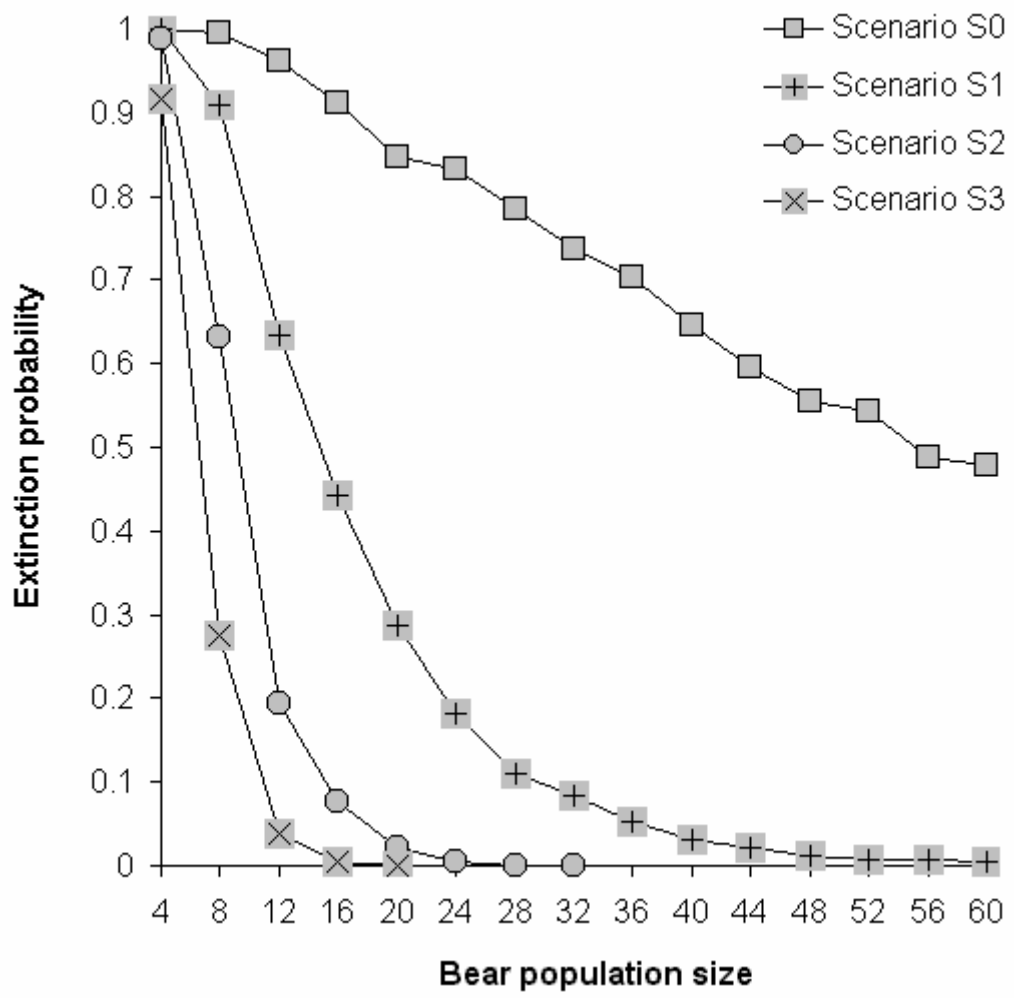


Figure 4

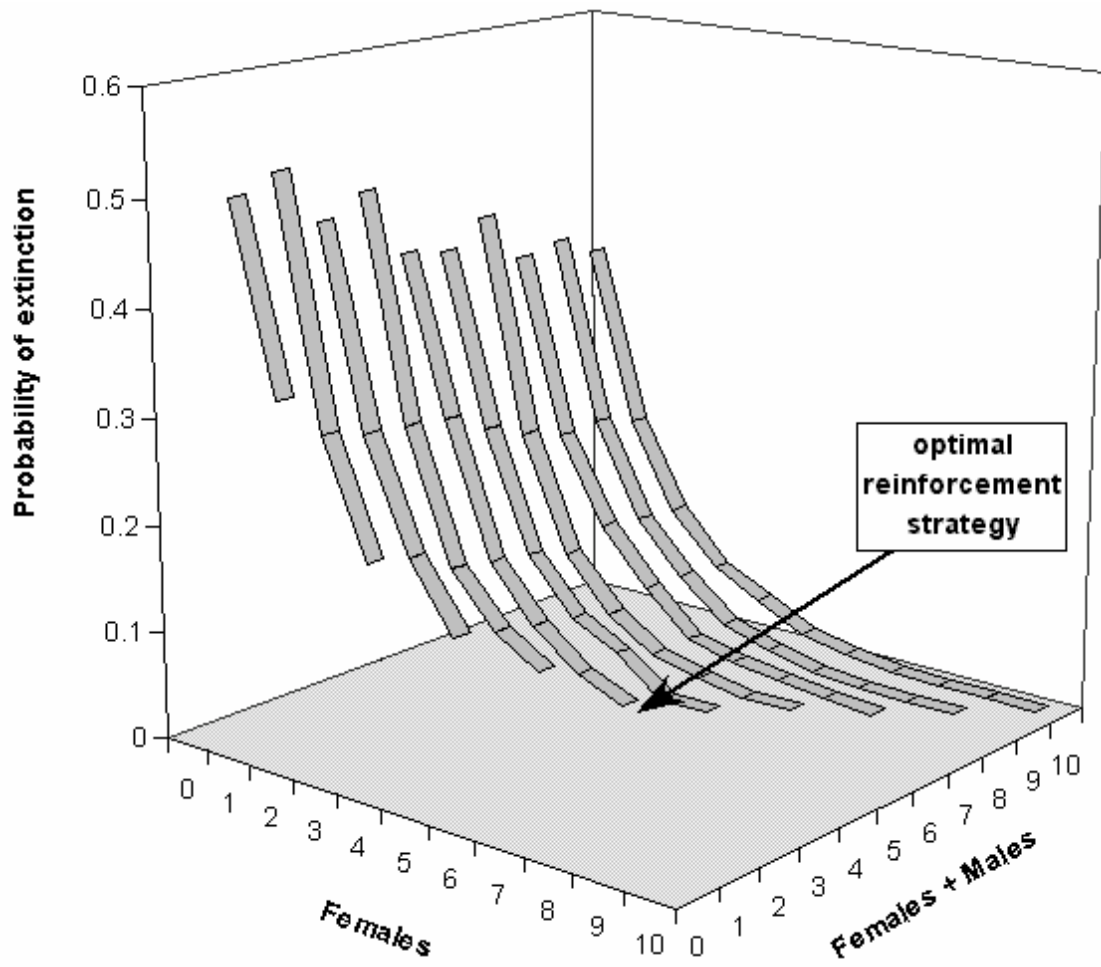


Figure 5:

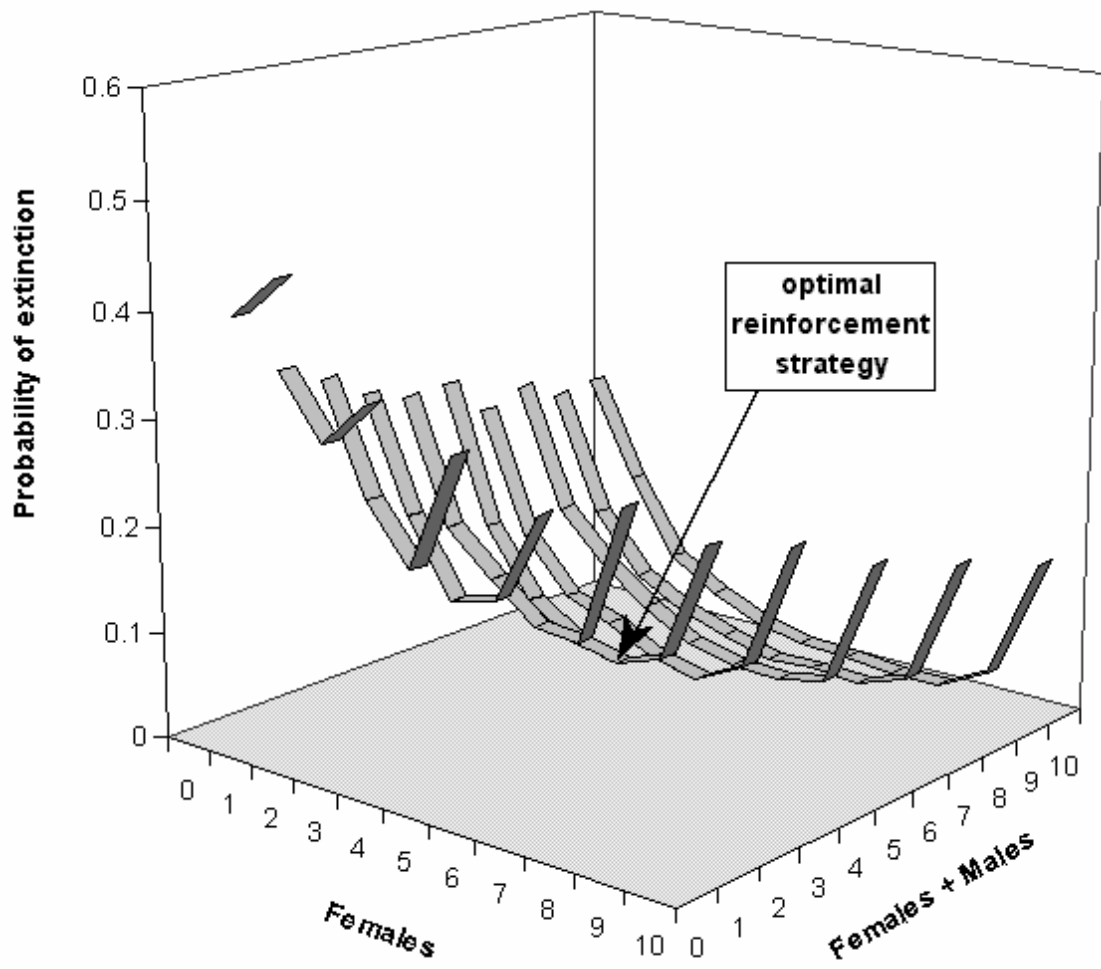


Figure 6

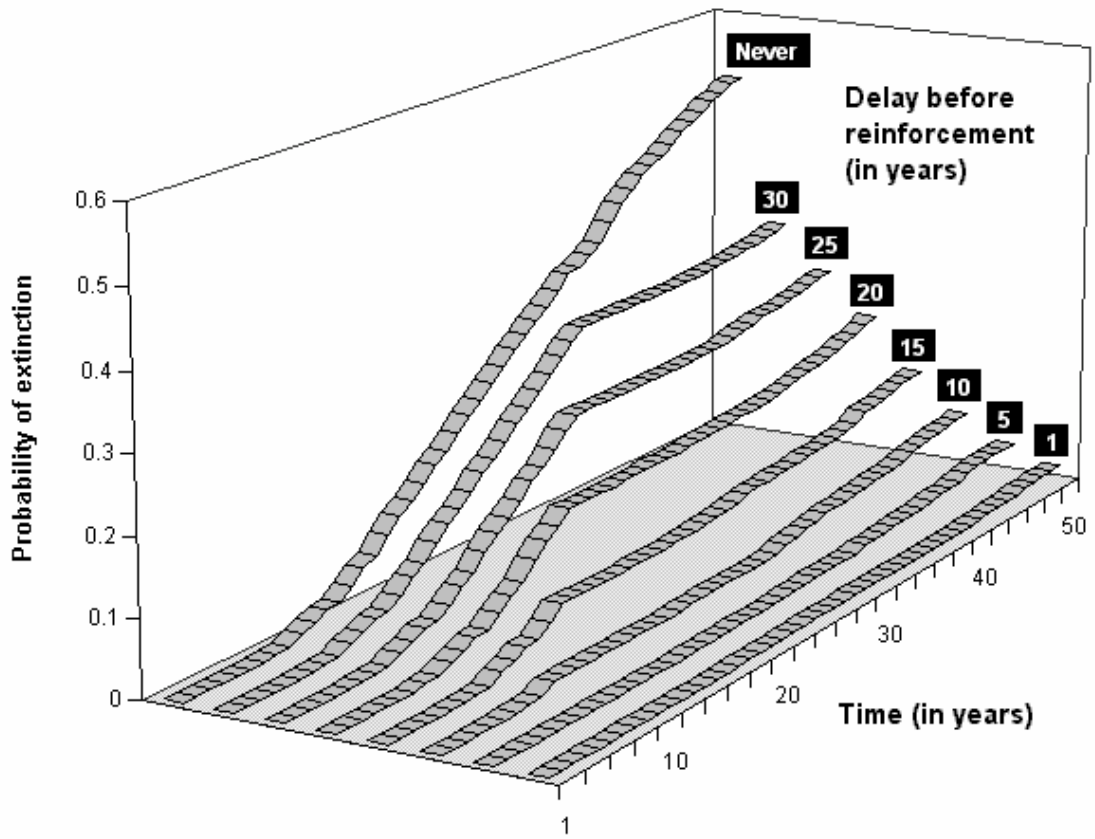
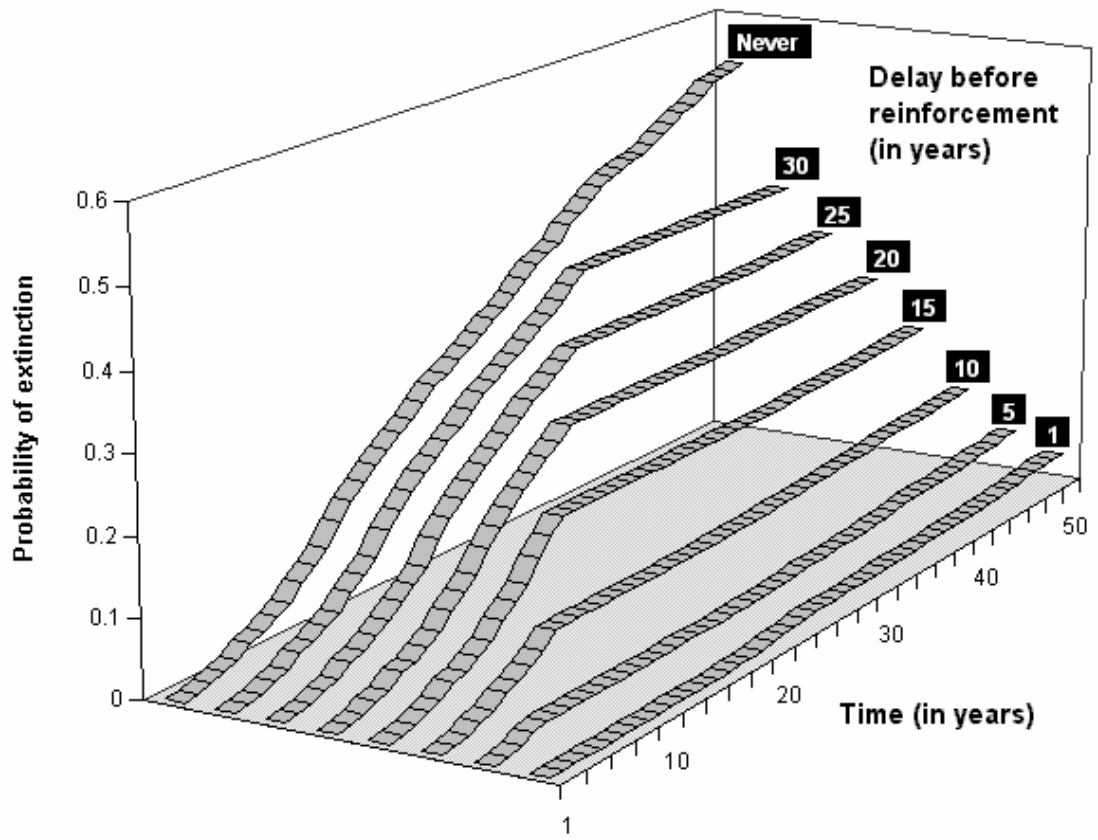


Figure 7



## □A□LES

Table I: Model parameters for various scenarios and associated asymptotic growth rate  $\lambda$ .

Parameter	Scenario			
	S0	S1	S2	S3
Female & Male Cub survival	0.575	0.6	0.625	0.65
Female & Male Juvenile survival	0.775	0.8	0.825	0.85
Male Floater survival	0.775	0.8	0.825	0.85
Female Floater survival	0.825	0.85	0.875	0.9
Female & Male Breeder survival	0.875	0.9	0.925	0.95
Litter size	2.1	2.1	2.1	2.1
$\lambda$	0.975	1.006	1.039	1.071

Table II: Elasticities computed for a population under median scenario S2.

Parameter	Elasticity
Male Cub survival	0.137
Male Juvenile survival	0
Male Floater 1 survival	0
Male Floater 2 survival	0
Male Breeder survival	0
Female Cub survival	0.137
Female Juvenile survival	0.104
Female Floater 1 survival	0.098
Female Floater 2 survival	0.098
Female Breeder survival	0.845
Litter size	0.122

Table III: Left eigenvector (corresponding to reproductive values) computed for a population under median scenario S2.

Class	Reproductive value
Male Juveniles	0
Male Floaters 1	0
Male Floaters 2	0
Male Breeders	0
Female Juveniles	0.1808
Female Floaters 1	0.2277
Female Floaters 2	0.2704
Female Breeder	0.3211