

SOME INSIGHTS INTO SNOW LEOPARD (*UNCIA UNCIA*) DEMOGRAPHY BY USING STAGE-STRUCTURED POPULATION MODELS

By
Guillaume Chapron^{1*} & Stéphane Legendre¹

¹ Laboratoire d'Ecologie, CNRS UMR 7625, Ecole Normale Supérieure, 46 rue d'Ulm, 75230 Paris Cedex 05, France

*Corresponding author: gchapron@carnivoreconservation.org

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Abstract

Based on the limited data available on snow leopard demography, we developed deterministic and stochastic stage-structured demographic models to study the population dynamics of this large cat. Our results reveal that even small leopard populations can persist provided their demographic parameters remain high, but less favorable scenarios would require larger population sizes. Population growth rate is more sensitive to breeder survivals than to any other parameters. A snow leopard population would start declining if yearly mortality claims more than 1/5 of the population. This study identifies poaching as a major threat to snow leopard survival and stresses the importance of long-term studies to better understand snow leopard population dynamics.

Keywords: Snow leopard, *Uncia uncia*, Viability analysis

1. Introduction

Carnivores are particular species and their conservation is different from biodiversity conservation (Ginsberg 2001). Large carnivores can kill domestic and game animals, and 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 faced widespread persecution. These particularities make controversial the questions of conservation policy-making or how large a viable population should be. Such a context mandates that scientists enter the scene and use a rigorous approach to solve the difficult question of carnivore viability versus human needs. This requires the development of a specific demographic model that we propose to address here for the snow leopard (*Uncia uncia*). Demographic models or population viability analyses (PVA) are mathematical descriptions of species life cycles over time (Peck 2000). 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 (Coulson et al. 2001). Conservation biology owes much of its credibility to demographic modeling (Beissinger & Westphal 1998); however insights gained from modeling should never be dissociated from the model assumptions (Man & Plummer 1999). Indeed, results are better qualitatively interpreted rather than quantitatively and should not be used to determine an accurate numerical value of a minimum viable population size or a probability of reaching extinction (Reed et al. 2002).

In this paper, we build and analyse deterministic and stochastic stage-structured models to study the dynamics and viability of a snow leopard population. Given the limited amount of available data for the snow leopard demography, we use a simple and robust modelling approach, intended to provide basic insights into snow leopard population dynamics and we show how our results may be used in terms of conservation strategies.

2. Methods

2.1 Snow leopard biology

The snow leopard is a long-lived solitary large cat. Mating usually occurs between late January and mid-March (Jackson 1988). Young are born in April-July and litter size is most commonly 2-3 cubs (rarely 1-5 cubs) (Heptner & Sludskii 1972, Blomqvist & Sten 1982, Wharton & Freeman 1989). Young disperse around 18-22 months and siblings may remain together briefly upon independence (Jackson 1988). Sexual maturity is reached when 2-3 years old (Petzch 1968, Koivisto et al 1977, Rieger 1980). No data is available on interbirth interval and we hypothesize that this should not be radically different from the other mountain dwelling large cat, the mountain lion (*Felis concolor*), where females usually reproduce once every 18-24 months (Lindzey 1987).

2.2 Model structure and simulations

The population is divided into several stages defined as follows. Leopards can be cubs (0-12 months), juveniles (12-24 months), floaters (> 24 months) or breeders (> 36 months). Age at first reproduction is therefore 3 years, but entering the breeding category requires also settling on a vacant territory. The model is female based with

breeding females always reproducing. Transitions between classes are explained hereafter and shown on the life cycle graph (Figure 1).

1. Surviving female juveniles become floaters
2. Surviving female floaters that found a territory become breeding females
3. Surviving female floaters that did not find a territory stay floaters
4. Surviving breeding females keep the same status
5. Surviving breeding females give birth to female cubs that become juveniles

From this life cycle, we build a stage-structured model (Caswell 2001). Population vector at time $(t+1)$ is calculated by multiplying population vector at time t with the population projection matrix, which incorporates transition probabilities from one class to another (Figure 2). No spatial structure is included in the deterministic model: there is therefore no limiting carrying capacity and all floaters older than 36 months become breeding females.

The matrix model is translated into a stochastic one using recurrent relations. We include demographic stochasticity but neither environmental nor genetic stochasticities nor demographic catastrophes. Survival and fecundity are treated as binomial and Poisson variates, respectively. We include a spatial structure and one breeding female can occupy only one territory. A breeding female population cannot exceed a carrying capacity K defined as the number of available territories. Floaters become breeding females only when some territories are empty. This generates density-dependence with a ceiling at K . We assume that breeders have stable territories. Monte Carlo simulations are run on 1000 repetitions for a duration of 50 years. A population qualifies as extinct once all classes are empty.

We use the deterministic matrix model to compute asymptotic population growth rate λ (Caswell 2001). We calculate elasticities of λ (Caswell 2001) to assess to which parameter λ is most sensible. We calculate left eigenvector (Caswell 2001) to show the impact of removing individuals on λ and right eigenvector (Caswell 2001) to investigate stable stage structure. We also investigate the highest mortality rate a snow leopard population could sustain by fixing the same value of survival rates to all adult-sized classes (juveniles, floaters and breeders).

We use the stochastic model to seek what would be the minimum size N of a viable snow leopard population assuming an initial settlement at carrying capacity $K=N$. We study the effect of various poaching pressure on population persistence. We model poaching by considering that each adult-sized snow leopard has a probability p_o to be poached, where p_o is given by the ratio (number of poached individuals)/(adult-sized population). We therefore multiply survival probability of juveniles, floaters and breeders by $(1-p_o)$.

All analyses and simulations are performed with the computer program ULM (Unified Life Models, Legendre & Clobert 1995, Ferrière et al. 1996) 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* (Wielgus et al., 2001) and European brown bears *Ursus arctos* (Chapron et al. submit.), arctic foxes *Alopex lagopus* (Loison et al., 2001), Iberian

lynxes *Lynx pardinus* (Bessa-Gomes et al., 2001) and wolves *Canis lupus* (Chapron et al. submit.).

2.3 Demographic parameters

Since no accurate estimation of snow leopard survival parameters is available, we define 4 scenarios, denoted by S0 to S3 from pessimistic to optimistic, that involve different combinations of parameter values (Table I). We consider that snow leopard demography should not be radically different than the one of other large cats and choose parameter values based on tiger (*Panthera tigris*), leopard (*Panthera pardus*) and cougar data available from long-term field studies (reviewed in Karanth & Stith 1999). Breeding females have the highest survival rates. Survival rates of floaters (and juveniles to a lesser extent) appear to be lower than rates of resident leopards. Floaters travel through unknown areas, are not familiar with prey distribution and support a higher human-induced mortality. Cub survival has the lowest value to account for starvation, diseases and predators. We fix mean litter size f at $2.5 / 2 = 1.25$ and interbirth interval at 21 months ($ib=21/12$). Litter size at birth does not vary from a scenario to another.

3. Results

3.1 Deterministic population dynamics

Asymptotic growth rate λ computation shows that a snow leopard population increases under our S1, S2 and S3 scenarios but decreases under the more pessimistic one S0 (Table I). Pessimistic scenario gives a 6.3 % decline per year whereas the most optimistic one gives a 16 % 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 λ level curve computations (Caswell 2001) 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 leopard on λ is the largest if this leopard is a breeder (Table III). Stable stage structure shows that a population at λ comprises mainly breeders (Table III). When adult-sized leopards have the same survival rate, we show that population starts declining once mortality is higher than 0.21 % each year (Figure 3).

3.2 Minimum viable population size

We compute probabilities of extinction in 50 years for several carrying capacities and under our 4 demographic scenarios (Figure 4). A population under scenario S0 reaches extinction with high probabilities irrespectively of carrying capacity, whereas a population under scenario S3 nearly never goes extinct for carrying capacities larger than 3 female leopards. For intermediate scenarios S1 and S2, probabilities of extinction are lower than 10% for carrying capacities respectively greater than 15 and 5.

3.3 Impact of poaching

We compute probabilities of extinction in 50 years for several carrying capacities and under our scenario S2 (Figure 5). We show that a snow leopard population is particularly sensitive to poaching and only a population larger than 15 females would be able to sustain a poaching rate of 1 individual every 2 years. Higher poaching rates will lead a population to extinction irrespectively of its carrying capacity.

4. Discussion

Our results show that a snow leopard population can potentially have a high growth rate (up to 16 %) and small leopard populations can persist provided their demographic parameters remain high. However, less favorable scenarios would require larger population sizes. Population growth rate is more sensitive to breeder survivals than to any other parameters. A snow leopard population would start declining if yearly mortality claims more than about 1/5 of the population and as a consequence even low intensity poaching can drive a population to extinction.

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 survival rate of 0.9 under scenario S2 (0.95 under scenario S3) yields an expected breeding expectancy of 10 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 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 λ to litter size suggests this is unlikely to change our conclusions.
- (5) Model parameters are kept constant during simulation (implying no habitat change).

Despite the fact that we use a very simple model, our study has some implications in terms of conservation recommendations. It reveals that a leopard population has a good potential growth rate under favorable ecological conditions but shows dramatic decline if mortality rate reaches a threshold. The snow leopard is a large cat sensitive to high killing rates as exemplified by its eradication from several regions. This PVA illustrates poaching as being a major threat to snow leopard survival and this result should help conservationists in the decision making process. Our consideration of several scenarios, from pessimistic to optimistic values in survival rates, allows us to provide insights in possible 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 (Beissinger & Westphal 1998).

This paper illustrates the advantage of specially constructed but simple stage-structured models (Ferrière et al. 1996). Their underlying mathematical framework allows careful analysis of model assumptions and a complete sensitivity analysis (Wiegand et al. 1998). Spatially-explicit, individual-based models have been advocated since they allow scientists to model at the behavioral level and can be connected to a Geographical Information System (Wiegand et al. 1998); however such models require a large amount of data to be correctly parameterized (Beissinger & Westphal 1998). This data is

presently not available for most wild cat species and this should argue for models being kept simple. Developing PVA has been identified as a priority by the IUCN Cat Specialist Group (Breitenmoser 2001) as well as further research on snow leopard population dynamics (ISLT 2002). As long-term field studies are carried out and deliver their results (see Caro 1993, Bailey 1993, Logan & Sweanor 2001), it will be possible to build more complex models in order to provide further insights into snow leopard population dynamics and optimize conservation strategies.

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TABLES

Table I: Model parameters for various scenarios and associated asymptotic growth rate λ .

Parameter	Scenario			
	S0	S1	S2	S3
Cub survival s_c	0.5	0.55	0.6	0.65
Juvenile survival s_j	0.7	0.75	0.8	0.85
Floater survival s_f	0.6	0.65	0.7	0.75
Breeder survival s_r	0.8	0.85	0.9	0.95
λ	0.937	1.010	1.084	1.16

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

Parameter	Elasticity
Cub survival	0.126
Juvenile survival	0.126
Floater survival	0.126
Breeder survival	0.747
Litter size	0.126

Table III: Right and left eigenvectors (corresponding to stable stage structure and reproductive values) computed for a population under median scenario S2.

Class	Stable stage structure	Reproductive value
Juveniles	0.2199	0.2246
Floaters	0.1623	0.3043
Breeders	0.6178	0.4711

FIGURES

Figure 1: Life cycle graph for a snow leopard stage-structured population. J: juveniles, F: floaters, R: Reproducing individuals. See text for arrow details.

Figure 2: Snow leopard female matrix population models. n_j : juveniles, n_f : floaters, n_r : reproducing individuals, f : litter size, ib : interbirth interval.

Figure 3: Asymptotic growth rate λ computed when all adult-sized classes have the same survival rate.

Figure 4: Extinction probabilities on 50 years as a function of population size (carrying capacity) assuming an initial settlement at carrying capacity for several scenarios.

Figure 5: Extinction probabilities on 50 years as a function of population size (carrying capacity) assuming an initial settlement at carrying capacity for scenario S2 and several poaching pressures.

Figure 1

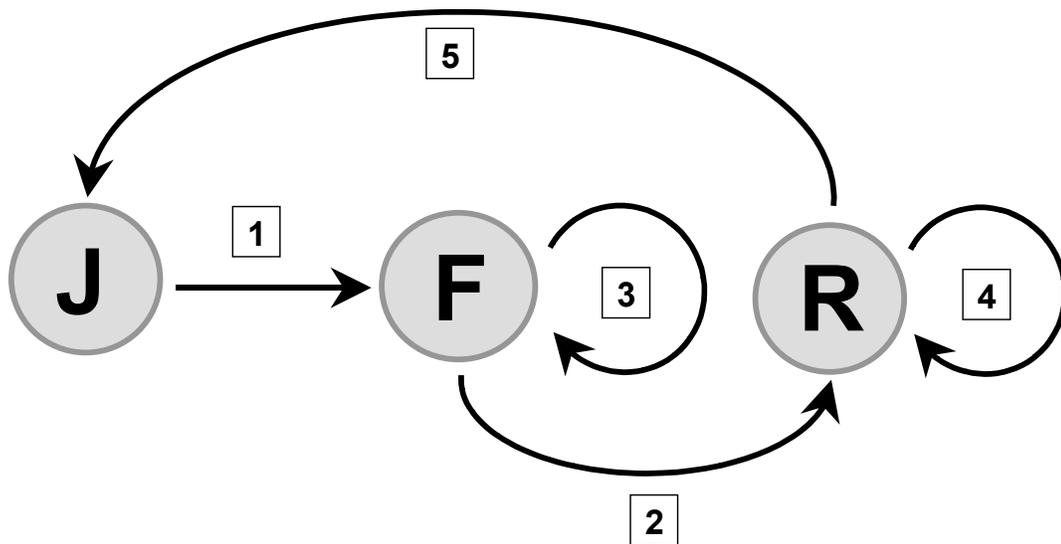


Figure 2

$$\begin{pmatrix} 0 & 0 & \frac{f}{ib} \cdot s_r \cdot s_c \\ s_j & 0 & 0 \\ 0 & s_f & s_r \end{pmatrix} \cdot \begin{pmatrix} n_j \\ n_f \\ n_r \end{pmatrix}_t = \begin{pmatrix} n_j \\ n_f \\ n_r \end{pmatrix}_{t+1}$$

Figure 3

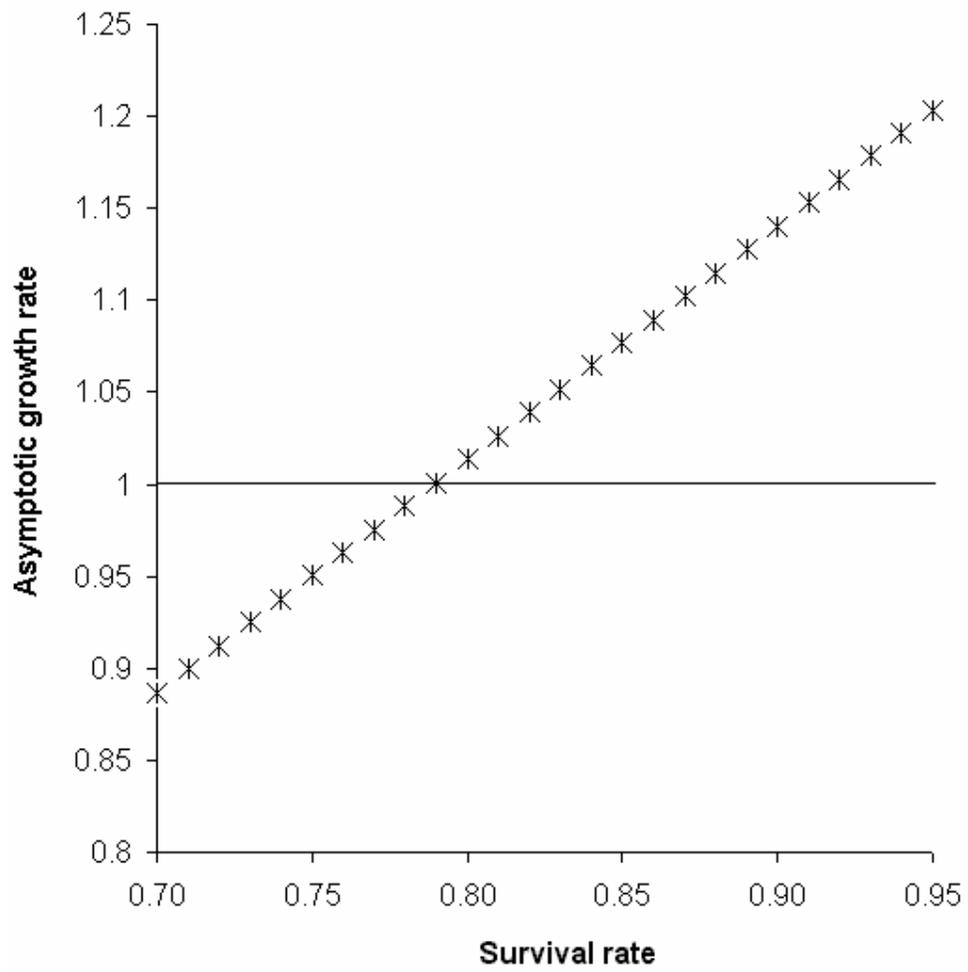


Figure 4

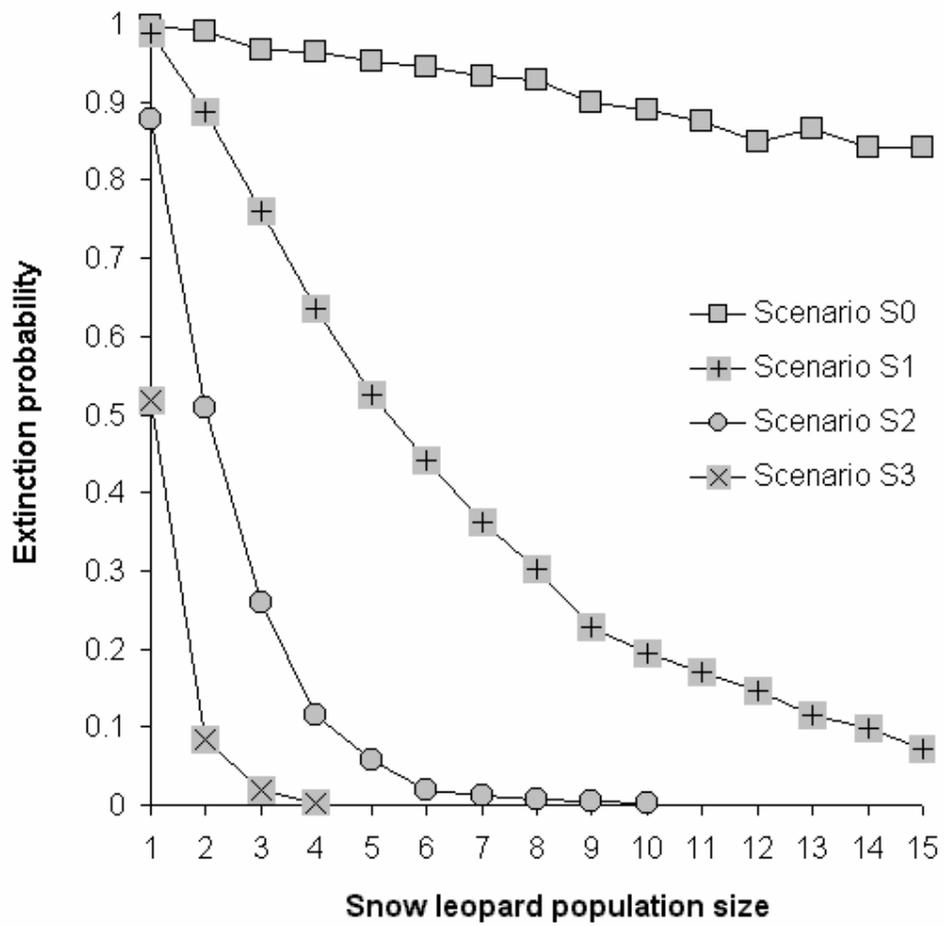


Figure 5

