Robustness of cheetah asymptotic growth rate and implications to population models*

Joan Lubben[1]†, Amy Keighley[2] A.J. Tyre[3], B. Tenhumberg[4], R. Rebarber[1], S. Townley[5], D. Boeckner[1], J. Boyle[6], A. Deines[7], J. Kogut[8], E. Peterson[9], R. Ryan[10]

[1] *Department of Mathematics, University of Nebraska-Lincoln, Lincoln, NE, U.S.A.*
Email: `jlubben@math.unl.edu`

[2] *Department of Mathematical Sciences, Rensselaer Polytechnic Institute, Troy, NY 12180 U.S.A.*
Email: `amykeeg@gmail.com`

[3] *School of Natural Resource Sciences, University of Nebraska-Lincoln, Lincoln, NE, U.S.A.*

[4] *?? , University of Nebraska-Lincoln, Lincoln, NE, U.S.A.*

[5] *Department of Mathematical Sciences, University of Exeter, Exeter, EX4 4QE, U.K.*

[6] *Department of Mathematics, University of Notre Dame, Notre Dame, IN 46556 U.S.A.*

[7] *Department of Mathematics, Kansas State University, Manhatten, KS 66506 U.S.A.*

[8] *Department of Mathematics, Simmons College, Boston, MA 02115 U.S.A.*

[9] *Department of Mathematics, Wittenberg University, Springfield, OH 45501 U.S.A.*

[10] *Department of Mathematics, University of Rhode Island, Kingston, RI 02881 U.S.A.*

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Abstract: The endangered cheetah *(Acinonyx jubatus)* is in decline due to hunting, poaching, loss of habitat, lack of genetic diversity and death of cubs due to natural predators such as lions and hyenas. Previous cheetah population models contend that increasing the survivorship of adult cheetahs is the best conservation method to ensure long term viability of this endangered species. The age-structured matrix model of the Serengeti Plain cheetahs by Crooks, et al.[5] suggests the asymptotic population growth rate is most sensitive to adult survivorship. Using linear algebra and robustness techniques, we analyze this previously published model and the robustness of its conclusion. Our results reveal a 5% increase in the adult survivorship is necessary in order to achieve a positive growth. Since the mortality of Serengeti cheetahs occur predominately during the first six months of life, we also explore how large an increase in this survivorship is necessary in order to achieve a positive growth rate. Our results show only an 7.7% increase in cub survivorship is necessary in order to achieve positive growth rate; a figure certainly within reach of concerted conservation efforts. In this paper we present a new population model for the Serengeti cheetahs. Our model examines the effect of capturing pregnant cheetahs, then releasing them back into the wild with their cubs six months after birth. This strategy dramatically increases the survivorship of the cubs in the initial six months of their lives. Using this model in combination with the current conservation strategy of increasing the adult survivorship yields a positive robust population growth rate.

Keywords: population projection matrix, cheetah, captive breeding, endangered species

1. Introduction

In 1900, the cheetah *(Acinonyx jubatus)* roamed over much of Africa, Asia and the Middle East with a total population estimated at 100,000 [22, 25]. Now barely 100 years later, the world cheetah population, estimated to be dramatically smaller at somewhere between 12,000 and 15,000 remaining animals, resides mostly in southern Africa [23]. Namibia is home to the largest concentration of cheetahs, with an estimated population of 2500 felines [22, 23, 24]. Kenya's population is estimated to be between 1200 and 2800 animals [8, **?**], while Tanzania accounts for less than 1000 [8]. The majority of the cheetahs in Namibia live outside protected areas and as a result, their demise is linked to the loss of habitat by encroaching farms, poaching, and the reduced number of prey. As the number of farms increase, cheetahs, considered a hazard to domesticated animals, are trapped and killed as a precaution by farmers. [20, 21, 23, 24]. In the Serengeti Plains of Tanzania, approximately 300 cheetahs reside [8]. Much of this area is a protected national park [3], yet the population fails to thrive due to the high cub mortality caused by predation by lions and hyenas [3, **?**, 5, 7, 21, 11].

Demographic data is available for the cheetahs of the Serengeti Plains and the cheetahs living in Namibia [5, 13, 14, 21, 11] (more here). Crooks et al. estimates the 0-6 month old Serengeti cub survivorship to be 8.1% [5]. By six months of age, these young cheetahs are

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† Corresponding author

capable of outrunning predators, hence the 6-12 month cub survivorship increases to 77.1% [5]. In Namibia, where the number of predators is also controlled by humans, Marker et al. [21] calculates the $0-1$ year cub survivorship to be around 75%, close to the survivorship of the Serengeti 6-13 month old cub. This agrees with Caro's estimation that 73.2% of cub mortality is due to this predation [3]; hence without predation the survivorship of the $0-6$ month old Serengeti cub will theoretically jump to 0.754. Once females reach adulthood (> 18 months), 50% of Serengeti cheetahs live to age 6.2 years [11], yet only 14% of the Namibian female cheetahs survive past 6 years of age [21]. Marker et al. classifies old adults as those between 8 to 12 years with those beyond 12 years as very old adults. The oldest Serengeti female cheetah in Kelly et al.'s study lived to 13.5 years [11]. In Namibia, adult females rarely lived past 10 years of age [21].

These figures highlight the difference between the two populations: the Serengeti population with a very low $0-6$ month old cub and higher adult survivorship verses the Namibian population with a (comparably) high $0-6$ month old cub survivorship and a low adult survivorship. Therefore different conservation efforts should be considered for the different populations. In Namibia, cheetah conservation efforts have focused on the education of the local farmers in order to reduce unnecessary killings of the adult. This strategy has been met with some success (references?). This paper will further investigate the Serengeti cheetah population through the use of population projection matrices [4]. We'll model the cheetah population using different conservation strategies to determine if such strategies will guarantee an increasing, or at least, a stable population.

Both Crooks et al. [5] and Kelly and Durant [12] calculated the asymptotic growth rate of the Serengeti cheetah. Crooks et al. used a post-breeding, age-structured, population projection matrix with 6-month age classes and calculated a declining growth rate, λ, of 0.9553. Using the elasticities of the stage-specific survivorships, Crooks et al. determined the growth rate was most sensitive to adult survivorship [4, 5]. Through the use of regression analysis they determined that even if the threat of cub predation is eliminated, the survivorship of the adult cheetah still influences the growth rate the most. In Kelly and Durant's [12] population viability analysis, they divided cheetahs into three age classes from which they calculated the growth rate, λ, to be 0.997. From this, they next used their stochastic program, Popgen, and analyzed extinction risks to changes in their original demographic values. Their analysis showed that increasing the 0-1 year cub survivorship from 0.10 to 0.12, i.e. requiring 2 more cubs out of 100 cubs born per year, zero extinction risk occurs. Kelly and Durant commented that this result could be due to their stochastic model, rather than reflecting a true result. In contrast, their model estimates increasing the adult survivorship from 0.85 to 0.91, i.e. if 6 more adult cheetahs survived each year per 100 adults, then zero extinction risk will occur. So while less of a percentage change in the adult survivorships is necessary in order to reduce the extinction risk to zero, a larger number of adults is required [12].

In this paper, we investigate further the age-structured, population projection matrix model presented by Crooks et al. [5] by using robust analysis techniques similar to those outlined

Table 1. **Population projection matrix for wild cheetahs** [5].

Age Classes (months)

$0-6$	$6-12$	$12-18$	$18-24$	$24-30$	$30-36$	$36-42$	$42+$
0	0	0	0	$s_2 f_1$	$s_2 f_1$	$s_2 f_1$	$s_3 f_2$
s_0	0	0	0	0	0	0	0
0	s_1	0	0	0	0	0	0
0	0	s_1	0	0	0	0	0
0	0	0	s_2	0	0	0	0
0	0	0	0	s_2	0	0	0
0	0	0	0	0	s_2	0	0
0	0	0	0	0	0	s_2	s_3

Values Used in PPM

$s_0 = .081$, survival of 0-6 month age class;
$s_1 = .771$, survival of 6-12 and 12-18 month age classes;
$s_2 = .920$, survival of 18-24, 24-30, 30-36 and 36-42 month age classes;
$s_3 = .879$, survival of 42+ month age class;
$f_1 = 1.2476$, fecundity of 24-30, 30-36, and 36-42 month age classes;
$f_2 = 1.4994$, fecundity of 42+ month age class.

This population projection matrix was originally published by Crooks, et al. [5].

by Hodgson and colleagues [9, 10]. Crooks' et al. matrix is given in Table 1 with its corresponding parameter values. Their model consists of eight age classes: 0-6 months, 6-12 months, 12-18 months, 18-24 months, 24-30 months, 30-36 months, 36-42 months, and 42+ months. Our reason for choosing the age-structured model is that it separates the 0-6 month cub age group from the others, thus allowing our model to predict results dependent upon this parameter. Our reason for choosing a different analysis technique is as follows: sensitivity and elasticity analyses determine the effect of small changes in the demographic parameters on the asymptotic growth rate [4]. Extending these results to large changes in the parameters can be misleading, especially if changes in the different parameter values are not proportional [16]. Because of the difference in the $0-6$ month old survivorships of those cubs with little predation, (survivorship = 0.75) [21] verses those in the Serengeti Plains with a survivorship of 0.081, sensitivity analysis is not suitable to make predictions if the threat of predation is dramatically reduced. Our paper will exploit this difference and see if reducing $0-6$ month old cub mortality will be effective in increasing the cheetah asymptotic growth rate.

Rather than begin with the demographic parameter values, we instead begin with the desired growth rate, say $\lambda = 1.0$ and then determine a range of values for those parameters that achieve this goal. Hodgson and colleagues [9, 10] proposed using the transfer function, a technique from the field of robust control theory as one method to view how changes in demographic parameters affect the growth rate. We will also use the transfer function as the path between a beginning growth rate, λ and the corresponding range of demographic parameters necessary to achieve the desired growth rate. Given the goal of increasing the asymptotic growth rate of the cheetah up to a specific value, conservation managers can make better decisions on which demographic parameters they might try to influence. For example, if the 0-6 cub survivorship can be increased enough to achieve a positive growth rate, how much of a decline in the adult survivorship can be tolerated in order to maintain this growth rate? Similarly, if the adult survivorship can be increased enough to achieve positive growth, how much of a decline can be tolerated in the 0-6 cub survivorship? Knowing the range of values for the demographic parameter necessary to achieve a goal tells how robust a parameter is. The greater the tolerance, the more robust a parameter is. Thus the uncertainties of the model inherited from the original data or those from yearly stochastic environmental changes can be accounted for by setting a conservation management goal high enough in the one parameter being influenced by human intervention.

Additionally, since the models published by Crooks et al. [5] and Kelly and Durant [12] show λ is most sensitive to the adult survivorship, it is reasonable to question just how much this survivorship can be increased. Crooks et al. calculates the survivorship of the 24-42 month adult to be 0.92 and that of the older, 42+ month old adult to be 0.879. See Table 1. Using the *International Cheetah Studbook* [17, 18, 19], we determined a 6-month survivorship of adult captured cheetahs to be 0.976, and used this as an approximation for the upper bound of allowed survivorships of wild cheetahs. We examine whether this higher survivorship is enough to achieve a positive growth rate.

We next developed a new age-structured post-breeding model consisting of wild, captured and released cheetahs using data from Crooks et al. [5] and available *International Cheetah Studbook*s [17, 18, 19]. This model explores one way to increase the 0-6 month cub survivorship since due to political reasons, culling lions and hyenas from the habitat is not possible [12]. Furthermore breeding cheetahs in current facilities and releasing the offspring back into the wild is also infeasible due to the low fecundity of captured cheetahs and the lack of hunting skills of the released animals. [3, 23]. Our model is to capture pregnant females; place them in a large secure enclosure within their current habitat but devoid of predators. Mother cheetahs can raise their cubs free from predators, hence increasing cub survivorship. A ready supply of appropriate live prey will stimulate natural hunting skills and enable the mother to teach her young how to hunt. Such a large, enclosed habitat can provide enough stimuli for the cheetah cubs in order for them to learn how to adapt and respond to environmental changes. The mothers with their 4-6 month old cubs are then released once the cubs are fast enough to outrun predators. With a gestation period of 3 months [3], the mother is held in captivity fewer than 9 months. Since the survivorship of adult cheetahs is not affected by captivity, such a plan is not detrimental to the mother's later survival skills

[21]. A similar conservation approach has also been suggested to augment the endangered Iberian lynx (*lynx pardinus*) population in Europe [6]. Using the same techniques which we used to analyze Crooks et al. matrix [5] we determine the robustness of a positive growth rate when facing uncertainties in the survivorships of the young cubs, the released cubs and the adults. Our calculations show that if such a model can be implemented, the model will be successful in obtaining a robust growth rate.

2. Methods

2.1 Modification of Crooks et al. Model

2.1.1 Survivorship

As mentioned previously, Crooks et al. [5] indicate λ is most sensitive to the adult survivorship, hence the question must be asked: what adult survivorships yield a positive growth rate and are these survivorships obtainable? Using the original model proposed by Crooks et. al [5], (see Table 1), we begin with $\lambda = 1$, and then determined the range of values for the adult survivorships, s_2 and s_3, necessary to achieve this figure.

From data available in the *International Cheetah Studbook* for the years 1999-2002 [17, 18, 19], the number of adult captive cheetahs alive on January 1 of each year was calculated and then compared to how many were still alive on December 31 to obtain a simple average of the one year survivorship of the adult cheetah. Taking the square root of this number establishes a six month survivorship of 0.976 captive adults, though this number is high due to unreported deaths [17, 18, 19]. Using this survivorship figure, of the cheetahs who achieve adulthood, 50% of them will die by age 16 years.

Next we compared this survivorship to that of wild cheetahs. According to Kelly et al. [11], Serengeti females who survived into adulthood lived an average of 6.2 years, much less than those living in captivity. Using the survivorships provided by Crooks et al. [5], we calculate that 50% of cheetahs who survive into adulthood will die by age 5.5 years. Given the difference between the 6-month adult survivorship in captivity verses that of a wild cheetah, it is reasonable to assume a survivorship of 0.976 is an upper bound for the survivorship of wild cheetahs, if in fact it is even reachable. Since there exists a difference in the survivorship of the young adults ($s_2 = 0.92$) verses that of the older adult ($s_3 = 0.879$), we assume we can increase the younger wild adult's survivorship by 0.056 to 0.976, but that we can only increase the older adults by the same amount, i.e. we set 0.935 as the upper bound for the survivorship of the older adult cheetah. This entails 5.6 per 100 more females surviving each year. Since our original figure of 0.976 is conservative, we feel this assumption is valid. Therefore we considered 0.976 and 0.935 to be the upper bounds for s_2 and s_3 respectively. Using these upper bounds, 50% of females who survive into adulthood live to just under 8 years of age, almost two years longer than values given by Kelly et al.'s study and 2.5 years longer than predicted by Crooks et al.'s model [5, 11].

Given this range of values for the two adult survivorships, we examine how much of this range yields a growth rate greater than 1. Additionally, we combine a range of values for the adult survivorships with a range of values for the $0-6$ month cub survivorship to determine what combinations result in a positive growth rate.

(Brigitte, should we use a more reasonable upper range for our adult survivorships?)

2.2 Capture/Release Model

One possible conservation method which increases the 0-6 month cub survivorship is to headstart the young cheetah cubs, i.e. provide a safe environment for the cubs until they can outrun predators. We suggest placing pregnant adults in a large secure enclosure in order to completely eliminate the threat of lions and other native predators, hence increasing the survivorship of the cubs.

To model this method, we created an all female, age-structured, post-breeding model comprised of wild, captured, and released females as shown in Table 2, where c is the percentage of adult females captured. Since we use the same survivorships for wild cheetahs as in Crooks et al.[5], this model also uses the same 6-month age classes for the wild cheetah population along with the corresponding survivorships. Since cheetahs begin to reproduce at 24 months, the captured adult age classes consist of 30-36 months, 36-42 months, and 42+ months. The cubs born in captivity are in their own captured 0-6 month age class. Since little is known concerning the resulting effect captivity has on the survivorship of the cubs, the model also incorporates a released 6-12 month age class. If the released cubs survive past one year of age, we assumed their survivorship reverts back to that of their wild counterpart.

2.2.1 Survivorship

During the age classes when the female is captured and when the female is in captivity, we assume the survivorship of a wild cheetah. This figure is conservative since before capture, the cheetah has survived into the age class long enough in order to be captured and while in captivity, an adequate food source is supplied. Additionally, some preventive health care may occur while in captivity. Since the capturing process does not increase the female's mortality [21], we assume once the mother was released back into the wild, her survivorship reverts back to the survivorship of the corresponding wild age class. We do consider a range of values for the wild adult survivorships, but these figures provide an initial conservative estimation around which we can choose an acceptable range.

Since the enclosure is devoid of predators, the survivorship of the captured 0-6 month age class is calculated by removing the mortality due to predation from the wild cheetah 0-6 month age class. According to Caro, predation causes 73.2% of the cubs' mortality [3]. Removing this threat increases the survivorship of the cubs from 0.081 to 0.754. In Namibia, where the pressure from lions and hyenas is not as great as in Serengeti, Marker et al. estimated the yearly Namibian cub mortality to be between 20% and 28% [21], thus 0.754 is a conservative estimate for this parameter. (check)

For the released 6-12 age class, it is unknown what effect captivity has on the cubs when they are released under the care of their wild mother. By four months of age, the cubs are large enough to outrun predators [3], thus increasing their survivorship. The model considers a survivorship range of 0.60 to 0.771, where 0.771 is the survivorship of the wild cheetah in the same age class.

2.2.2 Fecundity

The model first assumes the capture of the pregnant female does not reduce her fecundity in any way. The average litter size per female cheetah is 3.5 cubs with the ratio of male to female cheetahs being one to one [3]. Because we only consider females in this model, this translates to a fecundity of $f_c = 1.75$ female cubs per pregnant female. Since this is a post-breeding model, we multiplied the fecundity by the survivorship of the appropriate wild age-class.

When calculating the fecundity of the cheetahs remaining in the wild, the removal of pregnant cheetahs decreases the average fecundity of the remaining wild females. Since the overall fecundity of all female cheetahs remains the same, the fecundity per remaining wild young adult female cheetahs, f_{w1} is calculated by subtracting the contribution of the captive cheetahs' fecundity from the original value and dividing by $1 - c$ to obtain a fecundity per wild female cheetah, i.e

$$f_{w1} = (f_1 - cf_c)/(1 - c).$$

The fecundity of older cheetah age classes in the wild, f_{w2}, is calculated similarly.

Next, we assumed the fecundity of the female is reduced by 20% due to the capturing process and again determine a range of parameters which yield $\lambda = 1$.

Table 2. **Population projection matrix for wild, captured, and released female cheetahs.**

Wild								Captured				Released
$0-6$	$6-12$	$12-18$	$18-24$	$24-30$	$30-36$	$36-42$	$42+$	$0-6$	$30-36$	$36-42$	$42+$	$6-12$
0	0	0	0	$(1-c)s_2f_{w1}$	$(1-c)s_2f_{w1}$	$(1-c)s_2f_{w1}$	$(1-c)s_3f_{w2}$	0	0	0	0	0
s_0	0	0	0	0	0	0	0	0	0	0	0	0
0	s_1	0	0	0	0	0	0	0	0	0	0	s_r
0	0	s_1	0	0	0	0	0	0	0	0	0	0
0	0	0	s_2	0	0	0	0	0	0	0	0	0
0	0	0	0	$(1-c)s_2$	0	0	0	0	0	0	0	0
0	0	0	0	0	$(1-c)s_2$	0	0	0	s_2	0	0	0
0	0	0	0	0	0	$(1-c)s_2$	$(1-c)s_3$	0	0	s_2	s_3	0
0	0	0	0	cs_2f_c	cs_2f_c	cs_2f_c	cs_3f_c	0	0	0	0	0
0	0	0	0	cs_2	0	0	0	0	0	0	0	0
0	0	0	0	0	cs_2	0	0	0	0	0	0	0
0	0	0	0	0	0	cs_2	cs_3	0	0	0	0	0
0	0	0	0	0	0	0	0	s_{c06}	0	0	0	0

s_0	=	.081,	survival of 0-6 month age class;
s_1	=	.771,	survival of 6-12 and 12-18 month age classes;
s_2	=	.920,	survival of 18-24, 24-30, 30-36 and 36-42 month age classes;
s_3	=	.879,	survival of 42+ month age class;
s_{c06}	=	.754,	survival of 0-6 month old captured cubs;
s_r			survival of released 6-12 month olds; this value is unknown and is perturbed in the model;
f_{w1}	=	1.1725,	fecundity of wild 24-30, 30-36, and 36-42 month age classes;
f_{w2}	=	1.4620,	fecundity of wild 42+ month age class;
f_c	=	1.75,	fecundity of captured female, all age classes;

3 Results

3.1 Modification to Crooks et al. Model

Figure 3.1 shows the threshold when the asymptotic growth rate, λ, equals 1. Since a positive change in survivorship increases λ while a negative change decreases λ [2], it is easily seen what survivorships yield a positive growth rate. Even if the adult survivorships can be increased to 0.976, i.e. the upper bounds calculated for adult survivorship, the growth rate, λ, is increased to only 1.005. These values do not lead to a robust positive growth rate as $\lambda = 1.005$ is not high enough to guarantee a positive growth rate when considering uncertainties in the data.

In Figure 3.2, it is easily seen how increasing in the 0-6 month old cub survivorship, s_0 provides a robust λ. Note that the y-axis is the perturbation on the adult survivorship rather than the actual survivorship since the beginning values of s_2 and s_3 differ. Both s_2 and s_3 are always perturbed at the same rate, mainly due to the difficulty in viewing a three dimensional graph over that of a two dimenasional graph. The curve represents $\lambda = 1$. The three points shown are for original $s_0(= .081)$, $s_0 = .158$, and $s_0 = .281$. These yield $\lambda = .9553, 1.0006$, and 1.0521 respectively. If the $0-6$ month cub survivorships can be increased by 0.20, i.e. increasing the number of surviving cubs by 20 out of every 100, a very robust growth rate is possible without increasing the adult survivorships. The graph also shows if the adult survivorships, s_2 and s_3 can both be increased by 0.056, then a smaller increase in cub survivorship will yield to robust population growth. Therefore it makes sense to consider other conservation policies which boost the survivorship of the 0-6 month age class.

3.2 Capture/Release Model

Figure 3.3 shows the proportion of females captured verses λ for the survival of the released 6-12 month old cubs at $0.60, 0.65, 0.70,$ and 0.771 respectively where 0.771 is average survival of wild 6-12 month old cubs. Using a 0.65 survivorship of the released 6-12 month cubs, a positive growth rate requires only 14% of the female cheetahs to be captured. With a one-to-one ratio of males to females, this corresponds to approximately 21 Serengeti female cheetahs if the proposed model is implemented. If the survivorship of the released cubs is 0.771, approximately 11.5% of the female cheetahs need to be captured in order to obtain a positive growth rate. If the survivorship of the released 6-12 month age class, falls below 65%, then a greater percentage of females would need to be captured in order to obtain a positive growth rate.

Next, we consider if the fecundity of the captured females was reduced by 20% due to the capturing process. (No, Brigitte, I do not have a reason why I chose this percentage.....)

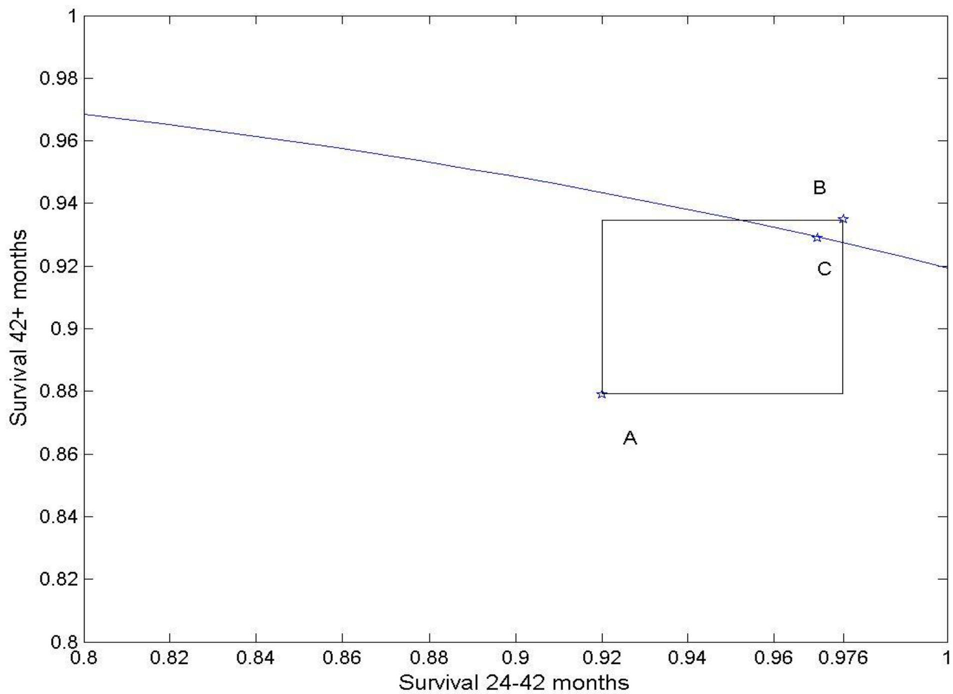

Figure 3.1: *Perturbed survivorships of younger and older adults. The line denotes* $\lambda = 1$*. Points above the line produce positive growth; points below the line produce negative growth. Point A marks the unperturbed survivorships (*$s_2 = .92, s_1 = .879$*,* $\lambda = .9553$*) reported by Crooks et al. [5]. Point B marks these survivorships perturbed by* 0.056*, yielding* $\lambda = 1.005$*. Point C marks a* 0.05 *increase increase in survivorships, yielding* $\lambda = 1.000$*. Values within the box are within the upper bounds of the feasible positive perturbations of* s_2 *and* s_3*.*

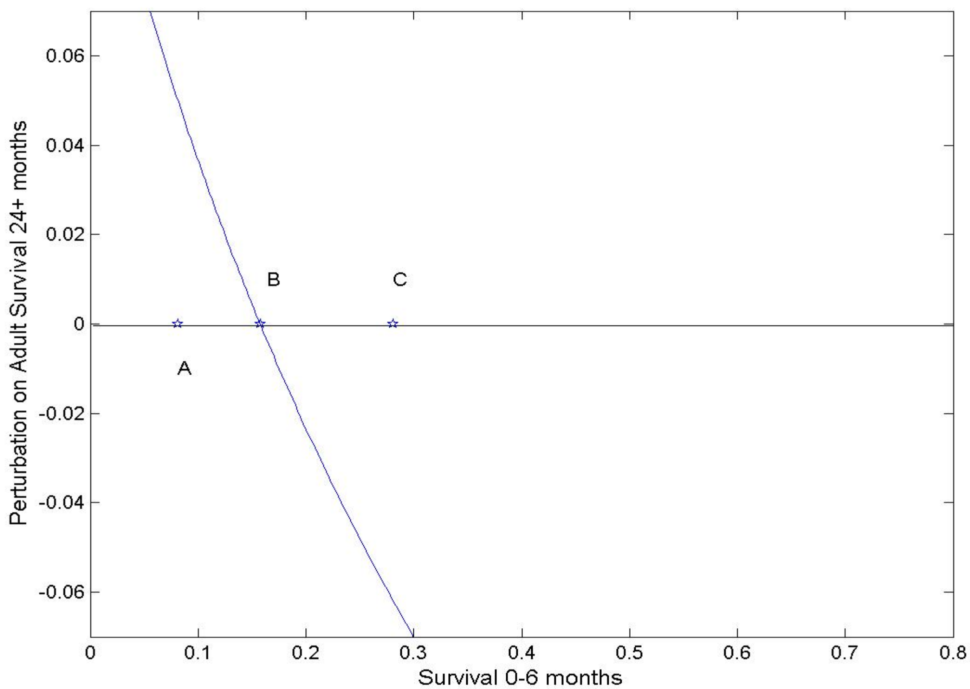

Figure 3.2: *Perturbed survivorships of 0-6 months cubs and all adults. The horizontal line denotes no changes in the adult survivorship. The curve denotes* $\lambda = 1$. *Points to the right of the curve line produce positive growth; points to the left of the curve produce negative growth. Point A marks current values:* $s_0 = .081, s_2 = .92, s_3 = .879, \lambda = .9553$. *Point B marks an increase of* 0.077 *in the 0-6 month cub survivorship:* $s_0 = .158, s_2 = .92, s_3 = .879, \lambda = 1.0006$. *Point C marks a* 0.20 *increase in 0-6 month cub survivorship:* $s_0 = .281, s_2 = .92, s_3 = .879, \lambda = 1.0521$.

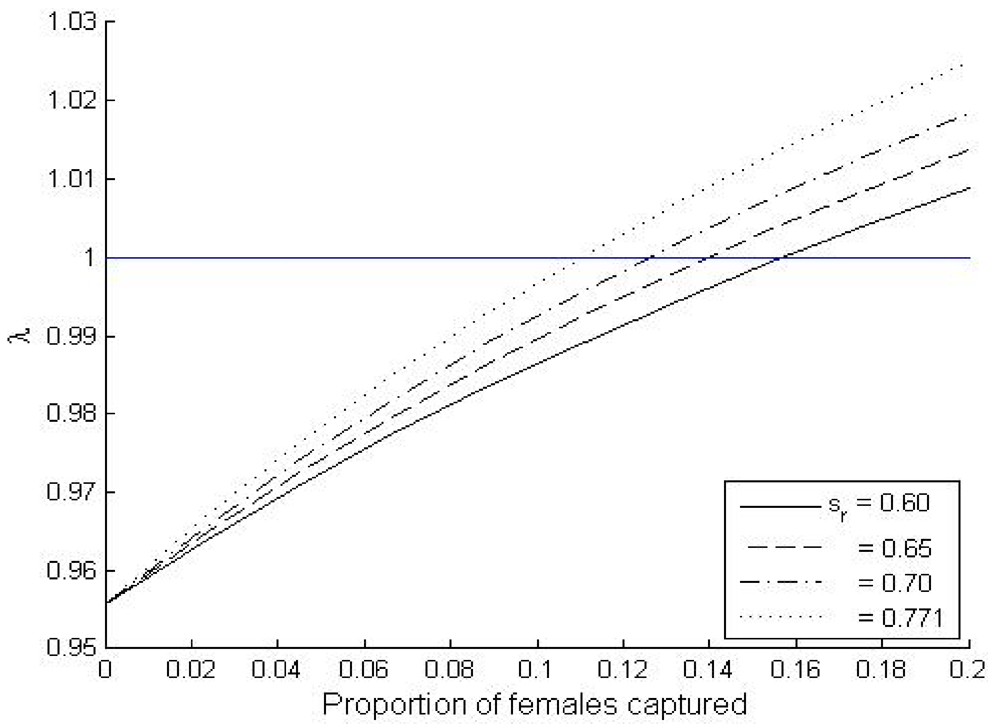

Figure 3.3: *Proportions of female captured verses λ for various survivorships of released 6-12 month old cubs with $s_{c06} = 0.754$.*

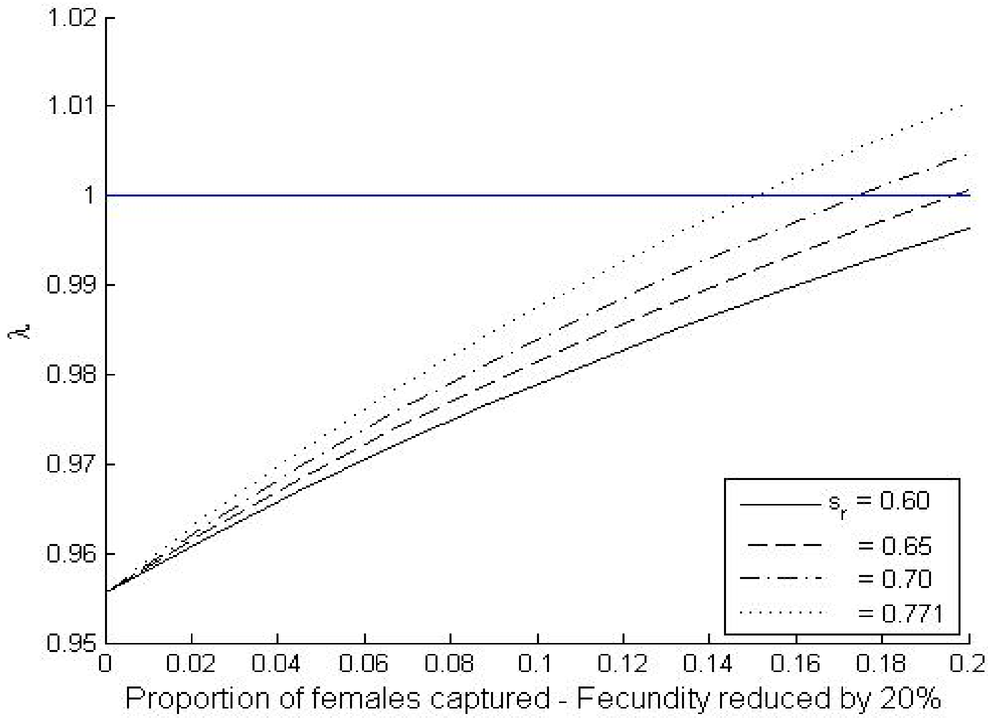

Figure 3.4: *Proportions of female captured verses λ for various survivorships of released 6-12 month old cubs with $s_{c06} = 0.754$ and a 20% reduction in the captured females' fecundity.*

Figure 3.4 shows that if the fecundity of the captured females is reduced by this 20% to 1.4 females born per litter, and if the survivorship of the released cubs is 0.771, just over 15% of the female cheetahs need to be captured in order to obtain a positive growth rate.

Using the same methods outlined previously, we next perturbed the survivorship of the released 6-12 month cubs and used the same perturbation for the survivorship of all adult age classes in the wild. Figure 3.5 shows the values of perturbation necessary to achieve $\lambda \geq 1$. Note that the y-axis is the perturbation on the adult survivorship rather than the actual survivorship since the beginning values of s_2 and s_3 are different. Again, points above each line produce a positive growth rate ($\lambda > 1$); points below the line produce a negative growth rate ($\lambda < 1$). If conservation efforts increase the adult survivorship by 3%, as shown by the horizontal line on the graph, then a much lower value for the survivorship of the released 6-12 month cheetahs can be tolerated and/or a lower percentage of females captured. For example, if the survivorships of the adults is increased by 0.03 and the released cubs' survivorship is 0.771, then only 4% of the females need to be captured. This correlates to only 6 female Serengeti cheetahs per year.

Figure 3.6 shows the robustness in the uncertainty of the survivorship of the released 6-12

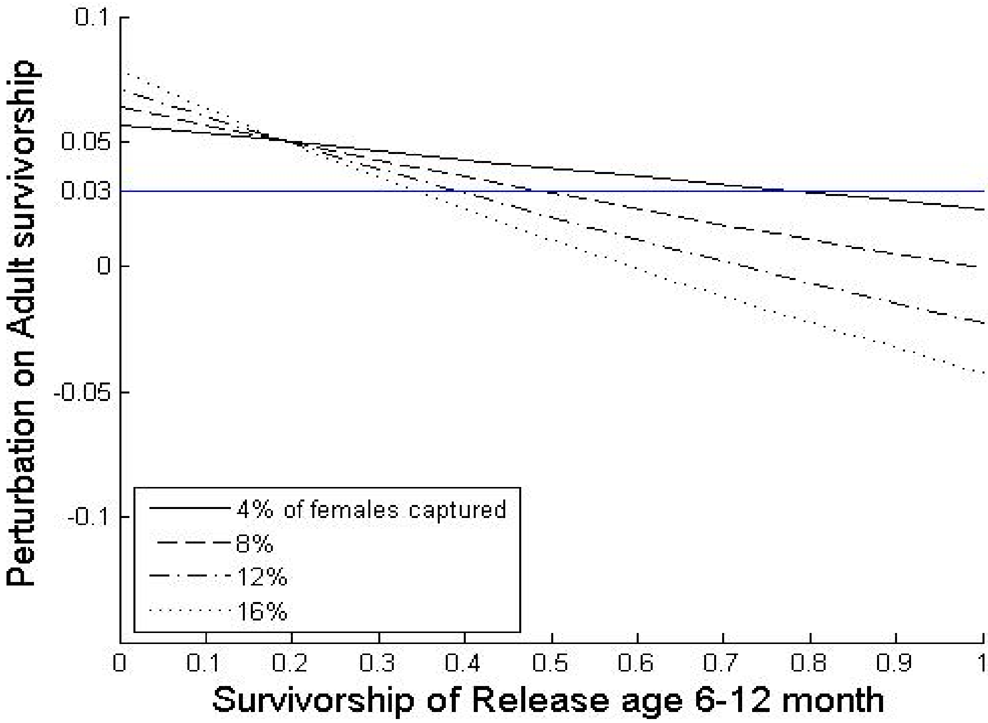

Figure 3.5: *Perturbations in necessary to achieve* $\lambda = 1$. *The negatively sloped lines correspond to* $\lambda = 1$ *for* 4%, 8%, 12% *and* 16% *of females captured. Points above the line produce* $\lambda > 1$*; points below the line produce* $\lambda < 1$. *The horizontal line indicates an increase of* 0.03 *in the survivorships of* s_2 *and* s_3.

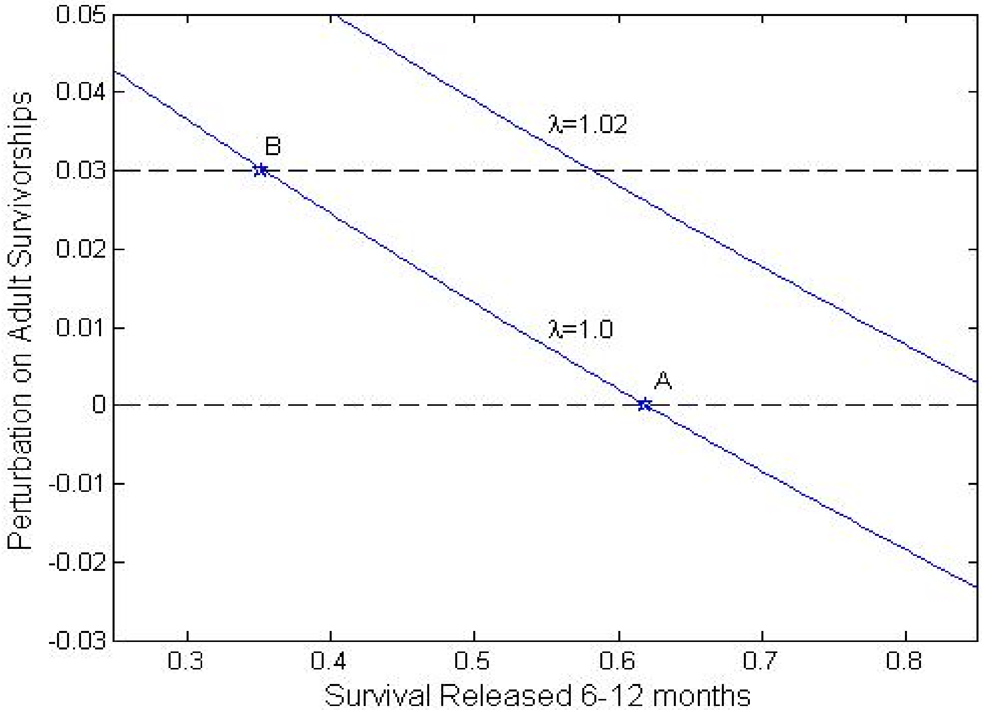

Figure 3.6: *Survivorships of released 6-12 month old cubs verses the perturbation in adult survivorships (24+ months) when* 15% *of the females are captured. The slanting lines indicate* $\lambda = 1$ *and* $\lambda = 1.02$*. The two horizontal lines show when* s_2 *and* s_3 *are increased by* 0.03 *(top line) or not at all (bottom line). Point A is* $s_r = .531, s_2 = 0.92, s_3 = 0.879$*. Point B is* $s_r = .27, s_2 = 0.95, s_3 = 0.919$.

month old cubs when 15% of the females are captured. As in the previous robustness graphs, the y-axis is the perturbation on the adult survivorships since s_2 and s_3 are not equal. Point A on the graph shows that if the survivorship of the released 6-12 month old cubs is greater than or equal to 0.62, with no changes in adult survival, then λ is greater than or equal to 1. Allowing the adult survivorships to both increase by .03 requires s_r to be above 0.35 in order to achieve a positive growth rate; see point B. If s_r is 0.60, then a very robust $\lambda = 1.02$ is achieved. Note also that if the survivorship of the released $6 - 12$ month old cub is at 0.771, then a positive growth rate is always achieved even if the adult survivorship decreases by 0.015.

□

4. Discussion

Previous sensitivity and elasticity analyses of the Serengeti cheetah population show the asymptotic growth rate, λ, is most sensitive to adult survivorship [?, 12]. As our results show, using the population projection matrix in Crooks et al. [5], if the the adult survivorship of wild cheetahs is increased to that of captive cheetahs, the corresponding growth rate is $\lambda = 1.005$. We do not consider this result robust since uncertainties in the data could easily push λ to be less than 1. Therefore, if the goal is to maintain or increase the cheetah population in the Serengeti Plains, other conservation strategies should be considered.

We next looked at increasing the survivorship of the 0-6 month old cubs, s_0. While λ is less sensitive to changes in s_0 [5, 12], there is much more latitude in increasing this value of 0.081 to obtain a positive growth rate over that of increasing the adult survivorships. Our results showed that increasing the 0-6 month cub survivorship to 0.20 will dramatically increase the growth rate to a very robust $\lambda = 1.0521$. Possible ways to increase this survivorship include decreasing the number of predators, which is not a politically popular idea [12], or directly trying to increase the survivorship of the 0-6 month old cubs by providing a safe, "semi-captive" environment until the cubs are old enough to outrun predators.

The above results suggest that perhaps the best management strategy to increase the cheetah population growth rate is a program which increases both the adult and 0-6 month cub survivorship. We presented a capture/release model which achieves this goal. Beck et al. [1] states successful reintroductions transpire if they occur alongside community education programs and contribute to the local economy by providing local employment. Indeed, the instigation of such a "semi-captive" program may increase the awareness of the plight of the cheetah by educating the local population, and perhaps as a by-product, cause a decrease in the adult mortality due to hunters and poachers [15].

For such a "semi-captive" environment, we have little information on the survivorship and fecundity of the captured female, the survivorship of the 0-6 month captured cubs and the survivorship of the released 6-12 month cubs. Acknowledging the uncertainties in these parameters, we allowed these variables to vary in our model. Additionally, the survivorship of released 6-12 month cubs is completely unknown, thus we varied this parameter more so than the survivorships mentioned above.

For example, in our proposed model, if the survivorship of the wild adult cheetah can be increased by 0.03 and the survivorship of the released 6-12 month cubs is greater than 0.60, only 15% (or 23) of the Serengeti females need to be captured in order to obtain a robust growth rate of $\lambda = 1.02$, i.e. given a small range of uncertainties in the original data, the model still predicts a positive growth rate.

Before such a model is implemented, further study is needed on the survivorship of the released 6-12 month old cubs. In our model, even though the cubs are released as soon as they can outrun predators, the cubs do not seem to reliably detect predators until 10 months of age [3]. It is uncertain whether a secure environment will delay their predator recognition skills and result in a lower survivorship, as compared to wild born cubs, when the released cubs move from one age class into the next. It also remains to be seen whether cubs raised in this manner are fully wild, i.e. capable of hunting and surviving on their own and passing this skill onto the next generation.

Learning how to effectively raise these "semi-captive" cheetahs is worth the effort not only for cheetahs, but also for other mammals with poor captive breeding results. Considering the rapid decline of the wild cheetah population, regard must be given to all conservation options available to maintain the population. Our model does show us that if we can overcome these problems, the asymptotic growth rate of the cheetah population can be increased to a robust positive value.

□

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