

# The impact on tigers of poaching versus prey depletion

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## Summary

1. There exists a continuing dilemma in prioritizing conservation actions for large carnivores. Habitat loss, poaching, and prey depletion have often been cited as the three primary threats, but there is debate over the relative importance of each.
2. We assess the relative importance of poaching and prey depletion rates, and use existing information in the literature and multi-type branching process and deterministic felid population models to address four lines of evidence used to infer that tiger populations are inherently resilient to high mortality rates.
3. Our results suggest that tigers, more so than leopards or cougars, require large populations to persist, are quite susceptible to modest increases in mortality, and less likely to recover quickly after population declines. Demographic responses that would ensure population persistence with mortality rates that are sustainable for cougars or leopards are biologically unrealistic for tigers.
4. We propose alternative interpretations of evidence used to suggest that tigers are inherently resilient to high mortality rates. In contrast to other solitary felids, tigers breed later and their inter-birth interval is larger, making them less resilient to poaching. A model used to support the contention that prey depletion has greater impact on population persistence than poaching appears to be based on false premises. Camera-trapping data that suggest positive population growth despite low survival rate cannot differentiate mortality from emigration, and does not differentiate the impact of varying survival rate on different sex-age classes; for example, low survival rate of dispersers is tolerable if survival rate of adult breeding females is high.
5. *Synthesis and applications.* While high prey numbers are essential to sustain tiger populations, our results suggest prey recovery efforts will not be sufficient if mortality rates reach 15%. Extrapolating demographic responses from other, even closely related species to develop conservation strategies can be misleading. Reduction of human-caused mortality, especially of resident breeding females, appears to be the most essential short-term conservation effort that must be made. Since mortality rates are usually unknown and generally stochastic in nature, any management policy that might reduce survival rates should be firmly avoided.

**Key-words:** branching process model, deterministic model, *Panthera tigris*, poaching, prey depletion, population viability, tiger

## Introduction

There exists a continuing dilemma in prioritizing conservation actions for large carnivores. For tigers *Panthera tigris* (Linnaeus 1758), as well as many other large carnivores, it is recognized

that ultimately, loss and degradation of habitat is the primary long-term threat (Wikramanayake *et al.* 1998; Miquelle *et al.* 1999a; Dinerstein *et al.* 2007). Poaching, driven largely by the demand for tiger parts in traditional Asian medicines, has frequently been cited as the most pressing short-term threat to tigers (Nowell 2000; Newman 2004; Shepherd & Nolan 2004; Check 2006). Yet recently, there has been a focus on the importance of prey depletion in maintaining healthy tiger

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populations (Karanth & Stith 1999; Miquelle *et al.* 1999b; Karanth *et al.* 2004) because in many areas across Asia, there still exist large tracts of suitable habitat, but tigers are absent or at exceedingly low numbers, presumably due to lack of prey (Rabinowitz 1993; Check 2006).

The impact of poaching on tigers was first quantitatively investigated by Kenney *et al.* (1995) who provided an analysis of tiger poaching as a basis for policy action. Using an individual-based, stochastic spatial model based on extensive field data, they demonstrated that a critical zone exists in which a small, incremental increase in poaching greatly increases the probability of extinction. Karanth & Stith (1999) challenged the results of this analysis, developing a stage-based population model and concluding that the impact of prey depletion on population size is significantly higher than the impact of tiger poaching. Their results suggest that even small, insular populations of tigers have a low probability of extinction due to the high reproductive potential, and consequently, tiger populations were characterized as highly resilient (Sunquist, Karanth & Sunquist 1999), a pattern considered typical for most large felids (O'Brien, Kinnaird & Wibisono 2003). The clear relationship between prey density and tiger numbers (Ramakrishnan, Coss & Pelkey 1999; Karanth *et al.* 2004; Miquelle *et al.* 2005a) generally supports the contention that prey density ultimately dictates potential tiger density.

Nonetheless, the hypothesis that prey depletion is a more critical factor than human-caused mortality in conserving tiger populations appears contradictory to historical records of the dynamics of the Amur tiger *P. t. altaica* population in Russia where, despite large tracts of adequate habitat and reasonable densities of prey, the population was nearly exterminated by 1940 due to intensive hunting (Miquelle *et al.* 2005b). Recovery of this population from an estimated low of 20–30 individuals (Kaplanov 1948), to an estimated 415–476 adults in 1996 (Miquelle *et al.* 2007), was dependent largely on outlawing of hunting and strict controls on poaching, but required about 40 years.

Intensive tiger poaching following the collapse of the Soviet Union (Galster & Vaud Elliot 1999) and the recent loss of tigers from Sariska National Park, India (Check 2006), due to poaching have raised new alarms about the impact of poaching across Asia and new concerns about the validity of the prevailing conservation paradigm that focuses on prey depletion. Interest in opening trophy hunting of tigers in the Russian Far East (Kretchmar 2006) brings the threat of even greater human-caused mortality. Additionally, if the ban on tiger bone trade is lifted in China, as proposed by one economist (Mittra 2006), many believe there will be an even greater poaching pressure on all wild tiger populations, as bones of wild tigers could be easily 'laundered' into the government-sanctioned trade of farmed tiger bone, and because killing of wild tigers will always be cheaper than farming them (Bulte & Damania 2005; Dinerstein *et al.* 2007).

Evidence for the contention that tigers are resilient to high mortality rates, and that prey depletion is a more important factor determining the status of tiger populations, comes primarily from four sources:

1. A model developed by Karanth & Stith (1999), which concluded that prey depletion is a greater cause for concern than poaching, and even small, insular populations of tigers have a low probability of extinction due to the high reproductive potential;
2. Experimental verification that a close relative – the cougar *Puma concolor* (Linnaeus 1771) – can withstand high annual offtake (Anderson & Lindzey 2005; Lindzey *et al.* 1992, 1994), reinforcing the assumption that large solitary cats can withstand substantial mortality pressure (O'Brien, Kinnaird & Wibisono 2003);
3. Reports of quick recovery of tiger numbers after intensive hunting pressure in the Indian 'shikar' (colonial hunting) literature, as presented by Sunquist, Karanth & Sunquist (1999), supporting the contention that high reproductive rates buffer tiger populations from extinction; and
4. A quantitative analysis of long-term camera-trapping data (Karanth *et al.* 2006) reporting that despite yearly survival rate averaging only 77%, a population of Bengal tigers *P. t. tigris* in Nagarhole National Park, India, demonstrated positive growth over 10 years.

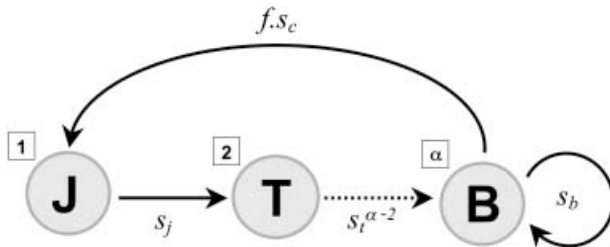
Our goal is to understand the impact on tiger population demography of high mortality rates associated with poaching, and to assess these four lines of evidence supporting the 'prey depletion paradigm'. Using a comparative approach to identify differences in life-history parameters between tigers, leopards *Panthera pardus* (Linnaeus 1758) and cougars – all large solitary felids – we develop population models parameterized with data from long-term field studies. We assess what impact species-specific differences may have on population persistence. We use known parameters of tiger spatial and reproductive ecology to discuss results of the Karanth & Stith (1999) model. We review evidence from the colonial hunting literature of India to consider alternative interpretations than those proposed by Sunquist, Karanth & Sunquist (1999). Finally, we conduct an analysis of heterogeneity in survival rate of different segments of a tiger population, which may explain apparent inconsistencies between theoretical results derived from our models and the empirical results of Karanth *et al.* (2006).

## Methods

### MODELLING APPROACH

We use comparative multi-type branching process models and deterministic models to assess the impact of high mortality rates, their relative impact on three solitary felids, and the impact of varying survival rates on different segments of a tiger population.

The stochastic analogue of a deterministic population model is a multi-type branching process. Branching process models have not been widely used in conservation demography yet provide a useful means of assessing probability of population persistence (e.g. Kokko *et al.* 1998). In such models, individuals survive and reproduce independently, with the life cycle of each individual characterized by the annual probabilities of survival, reproduction, changing age/social classes, and by the probability distribution of litter size for each reproduction event. The mean behaviour of the population is exactly the same as that predicted by the corresponding deterministic



**Fig. 1.** Pre-breeding life cycle graph for a large cat (J, juvenile; T, transient, and B, breeder). The upper-left square to each class is the age of individuals when entering this class and mathematical expression of transition probabilities are shown.

model, but also provides information on the probability of other outcomes. In particular, if the overall growth rate of the population is less than 1 (subcritical case), the population goes extinct with probability of 1 in both model types. However, when the growth rate of the population is greater than 1 (supercritical case), the deterministic model predicts that the population size will increase exponentially while the branching process will demonstrate that exponential growth happens *on average*, but other outcomes, including extinction, occur with a probability  $x$ , while the population is still small enough to be affected by demographic stochasticity. Therefore, branching process models provide an estimate of the 'eventual extinction probability', which is the exact probability that extinction occurs independent of fixed time periods.

We divide a female segment of a felid population into four classes based on age and reproductive status: cubs (C, 0–12 months), juveniles (J, 12–24 months), transients (T, > 24 months but non-breeding), and breeding adults (B, >  $\alpha$  years, when  $\alpha$  is the age at first reproduction). The life cycle (Fig. 1) is a pre-breeding one and hence does not show the cub class. We hypothesize that populations of tigers, leopards, and cougars contain the same classes, with only the transition probability between classes varying from one population to another. This approach allows us to compare species by varying the numerical value of parameters, with no change in the structure of the model itself.

Considering the life cycle (Fig. 1) as a multi-type branching process (see Supporting Information Appendix S1, for details), we can obtain the eventual extinction probability  $x$  of a population starting with 1 breeder only as the smallest solution of the equation  $h(x) = x$  for  $x \in [0, 1]$ , where

$$h(x) = (1 - s_b + s_b x) e^{f s_c s_j s_t^{\alpha-2} (x-1)}, \quad \text{eqn 1}$$

with  $s_c$  cub survival rate,  $s_j$  juvenile survival rate,  $s_t$  transient survival rate,  $s_b$  breeding adult survival rate,  $f$  fecundity with  $f = l/ib$  and  $l$  litter size,  $ib$  inter-birth interval.

Considering the same life cycle as a deterministic process and using transformation rules for life-cycle graphs (Caswell 2001), we can obtain the general characteristic equation of the transition matrix, where the sum of products of the terms for each loop is equal to 1:

$$1 = \sum_i \left( \prod_{j=1}^{i-1} S_j \right) \cdot F_i \lambda^{-i},$$

where  $S_j$ ,  $F_i$  and  $\lambda$  are survival rate, fecundity and asymptotic population growth rate, respectively. The general characteristic equation for a large felid population therefore becomes

$$\lambda^\alpha - s_b \lambda^{\alpha-1} - f s_c s_j s_t^{\alpha-2} = 0. \quad \text{eqn 2}$$

## MODEL PARAMETERS

Model parameters for survival and fecundity rates, were derived from long-term field studies (see Supporting Information Appendix S2, for details). Breeding adult and juvenile female tigers have the highest survival rates and transients typically suffer higher mortality rates than resident adults (Goodrich *et al.* in press). Cub survival rate is generally the lowest, as cubs are more susceptible to starvation, diseases and a greater variety of predators. Litter size at birth ( $l$ ) in the wild is extremely difficult to measure (e.g. Kerley *et al.* 2003), but there is no strong evidence that litter size varies significantly among the three species considered here. Therefore, we fix average litter size at 3, which appears to be close to the mean value for many large cat species (Logan & Swenar 2001; Smith & McDougal 1991), but since the model is female-only, we set  $l = 1.5$ , assuming an equal sex ratio at birth. Litter size and other generalized values (e.g. survival rate, sex ratio at birth), applied to all three species in the model no doubt vary among populations but such variation is likely to represent population-level responses to existing environmental conditions, and does not reflect life history characteristics that vary among the three species per se. In contrast, age at first reproduction  $\alpha$  and inter-birth interval  $ib$  appear to consistently vary among species, and hence these values are species-specific. For computations where  $\alpha$  and  $ib$  do not vary (see below), we used  $\alpha = 24$  months and  $ib = 18$  months for cougar,  $\alpha = 36$  months and  $ib = 20$  months for leopard, and  $\alpha = 48$  months and  $ib = 24$  months for tiger (see Supporting Information Appendix S2, for references).

## COMPUTATIONS

### Minimum viable population size (MVP)

Based on the branching process model equation 1, the eventual probability of extinction of a population with  $N$  breeders is  $x^N$  ( $x$  being the probability of a population starting with 1 breeder only) and we can obtain the MVP, defined as a 1% extinction probability threshold, by solving  $h(x) = x$  and calculating:

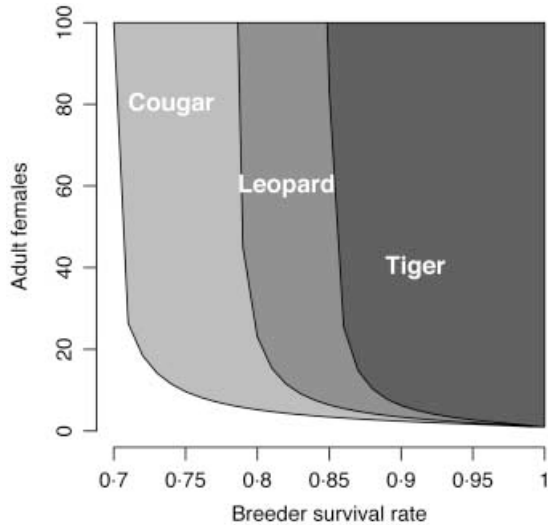
$$N = \frac{\ln(0.01)}{\ln(x)}$$

We compute  $N$  for the selected species and with breeding adult survival rate varying from 0 to 1 (having other class survival rates varying in the same proportion) and plot  $N$  for non-declining populations.

### Minimum parameters for population persistence

In equation 1, we can fix extinction probability  $x = 1$  and consider breeding adult survival rate as the unknown variable (with other class survival rates varying proportionally). We can then find the lowest required breeding adult survival rates for population persistence (i.e. non-certain extinction). For values of  $\alpha$  ranging from 20 to 60 months and for values of  $ib$  ranging from 12 to 30 months, we solve equation 1 for  $s_b$ , and we draw minimum breeder survival rate contour curves.

Since it has been argued that tigers can withstand mortality rates as high as cougars due to a high reproductive potential, we can fix  $s_b$  and other survival rates at values ensuring population persistence for cougar, and then consider litter size  $l$  as the unknown variable of equation 1, still maintaining  $x = 1$ . For the same range of values as above for  $\alpha$  (20 to 60 months) and  $ib$  (12 to 30 months), we solve equation 1 for  $l$  and develop minimum litter size contour curves.



**Fig. 2.** Number of adult breeding females required for population persistence (extinction probability < 1%), as a function of breeder survival rate for three large cat species – cougar, leopard, and tiger.

#### Asymptotic population growth rate

We solve equation 2 to find asymptotic growth rate  $\lambda$  for the selected species with breeder survival rate varying from 0 to 1, having other class survival rates varying by the same proportion.

#### Heterogeneity of survival rates among classes

Since survival rates for each class are likely to vary among populations and within a single population over time, we vary these rates across of a range of potential values for different segments of the population to assess their impact on population growth rates. We use equation 2 to determine whether a population can remain stable ( $\lambda = 1$ ) when either breeder survival rates or both juvenile and transient survival rates vary. With  $s_b$  varying from 0.5 to 1 and  $s_j$  varying from 0.5 to 1 ( $s_t$  being proportionally linked to  $s_j$ ), we solve equation 2 to find pairs  $(s_b, s_j)$  giving  $\lambda = 1$  and we compute iso  $\lambda = 1$  curves for the three cat species.

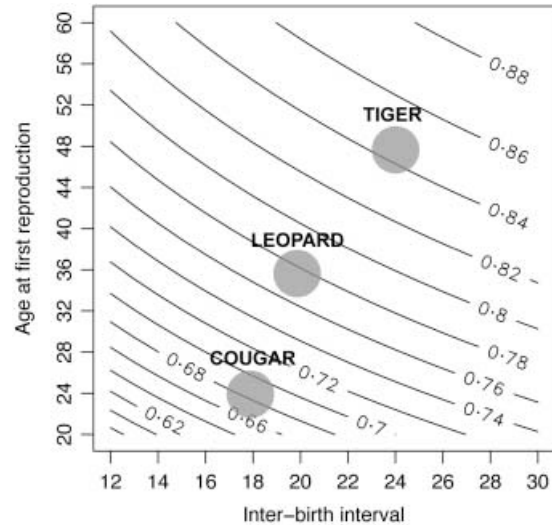
## Results

### MINIMUM VIABLE POPULATION SIZE

Computations of MVP (Fig. 2) show that when survival rates are less than 0.95, viable populations of tigers must be considerably larger than those of leopards or cougars. A viable population with  $s_b = 0.85$  would require 83 breeding female tigers but only 7 breeding female leopards, or 4 breeding female cougars. For any given population size, survival rate of breeding female tigers must be much higher than for the other species to ensure population persistence (Fig. 2).

### MINIMUM PARAMETERS FOR POPULATION PERSISTENCE

As inter-birth interval and age at first reproduction increase, survival rates of adult breeding females must also increase if



**Fig. 3.** Minimal adult breeding female survival rate contour curves needed for population persistence, as a function of age at first reproduction and inter-birth interval for three large felid species.

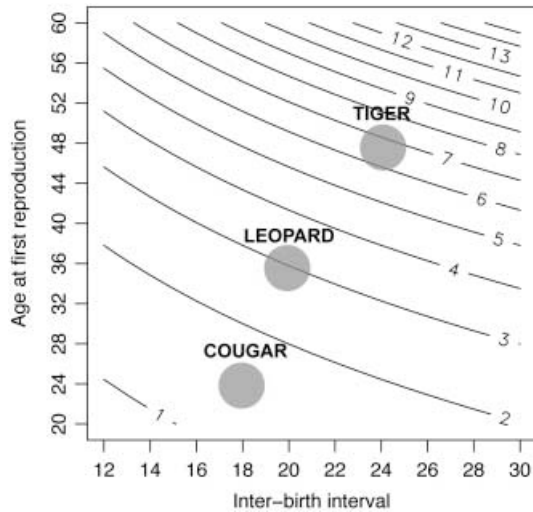
felid populations are to persist (Fig. 3). Hence, survival rate of breeding females in tiger populations must be higher than for leopard or cougar populations. For a tiger population to persist in the face of the minimal survival rate derived for cougars, it would require *both* a 50% decrease in age at first reproduction and a 25% decrease in inter-birth interval (this representing the shortest path from tiger coordinates ( $ib = 24$ ,  $\alpha = 48$ ) to the contour curve  $s_b = 0.69$  on Fig. 3), both of which are biologically highly unlikely. Cougar and leopard populations can persist in the face of high mortality rates due to short inter-birth intervals and an early age of first reproduction. If a tiger population were subjected to the lowest demographic parameters ensuring population persistence of a cougar population, our model suggests that it could persist through compensation in litter size only by producing > 6 females per litter (i.e. 12 cubs overall; Fig. 4).

### ASYMPTOTIC POPULATION GROWTH RATE

Computations of asymptotic growth rate suggest that a tiger population will decline if more than 15% of the breeding adult females die every year, whereas mortality rates of 22% and 31% are sustainable for leopards and cougars, respectively, with survival rate of other classes being proportional to survival rate of breeders. Under favourable conditions ( $s_b$  close to 1), tiger populations seem to be able to increase by 20% every year, whereas a cougar population can increase by 50%. However, with slightly lower, more realistic survival rates, high population growth rates are unlikely for tigers.

### HETEROGENITY OF SURVIVAL RATE AMONG CLASSES

When mortality rates are not distributed equally among classes, a high breeding adult survival rate can compensate for low survival rates of other classes (Fig. 5). For example, with low survival rate of juveniles ( $s_j = 0.5$ ) and transients ( $s_t =$



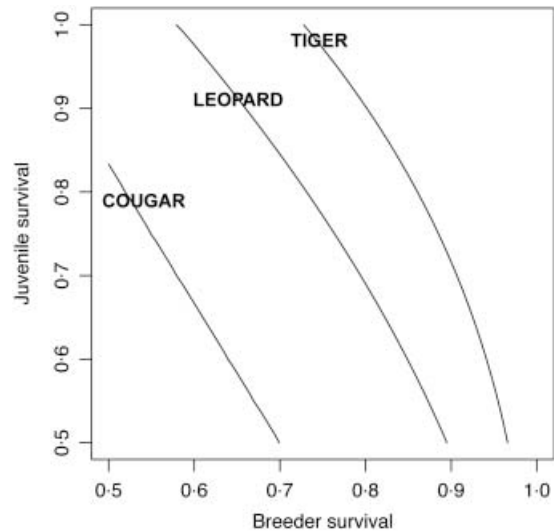
**Fig. 4.** Theoretical minimal mean litter size (females only), as a function of age at first reproduction and inter-birth interval, needed to ensure population persistence of large felid species if survival rates are set at a level that allows persistence of cougar populations (see Fig. 3).

0.39), a tiger population can still persist if breeder survival rates  $s_b = 0.95$ . Both leopard and cougar populations could persist with even lower breeding female survival rate in the face of such low survival rates for other classes (leopard  $s_b = 0.86$ , cougar  $s_b = 0.64$ ). However, for tigers, the relationship is not fully reciprocal; that is, even high survival rates of juveniles and transients cannot fully compensate for low adult survival rates.

## Discussion

### COMPARISON OF TIGER DEMOGRAPHIC MODELS

The results of our models, as well as those of both Kenney *et al.* (1995) and Karanth & Stith (1999) provide strong evidence collectively that high mortality rates are likely to quickly drive tiger populations to extinction. Kenney *et al.*'s (1995) individually based stochastic spatial simulation model assumed that all tigers over 2 years old are equally susceptible to poaching rates that ranged from 4.5 to 24% of the initial total population (cubs excluded), but because fixed numbers of animals were removed yearly, poaching rates (percentage of population) actually changed as population size changed. Karanth & Stith's (1999) two-sex and stage-based model computed the number of breeding males as a Poisson variate with a mean of one-third of breeding females. This nuance allows modelled populations to breed even when males have gone extinct in a previous time step, perhaps partially explaining their conclusion that tiger populations demonstrate high persistence even at low numbers. Kenney *et al.* (1995) computed extinction probability for simulations lasting from 3 to 9 years, Karanth & Stith (1999) used a 100-year timeframe, while our branching process model computes probability that extinction will occur, regardless of when it actually will. Hence, popula-



**Fig. 5.**  $\lambda = 1$  contour curves as a function of breeding female adult and juvenile survival rates. Transient female survival rates vary proportionally with juvenile survival rates in the cases of leopard and tiger.

tions not yet extinct, but in steady decline in Kenney *et al.* (1995) and Karanth & Stith (1999) will ultimately go extinct in our branching process model, making it more conservative.

The branching process modelling approach allows us to mathematically quantify the impact of simultaneous parameter changes on population growth and persistence. For example, we were able to demonstrate that minor variations in litter size have relatively little impact on demography in comparison to adult female survival rate. Female tigers would have to regularly produce litter sizes that are biologically unrealistic (12 cubs) for populations to persist when survival rates are as low as those under which cougar populations can persist.

Because our models are stage-structured and not individually based, they cannot account for all the potential impacts of poaching. The benefits of mathematical robustness are tempered by the requirement that such models must be relatively simple and cannot consider all nuances of tiger ecology. For example, our model is female only, as including males would have required defining the mating system, which would have led to a violation of a branching process assumption by introducing dependence between individuals. If poaching rates on male tigers were higher than other sex-age classes, our single-sex model would perhaps be inappropriate, but there is no evidence that poachers target a specific sex or age class of tigers (Goodrich *et al.* in press), and there is no evidence that males are a limiting factor for large felid populations (see Milner-Gulland *et al.* 2003 for the only known counter-evidence in mammals). Adult female survival has been identified as the key factor in population demography of other large carnivores (Eberhardt 1990; Mace & Waller 1998), suggesting a focus on the female segment of the population is justified.

However, a female-only model also prevents assessment of other factors. For instance, the impact of sexually selected

infanticide, which has been reported in a number of carnivores including tigers (Smith & McDougal 1991), could not be included in our single-sex model. Because an increase in infanticide rates by new males replacing poached residents may reduce cub production and population growth, as well as population persistence (Swenson 2003), tiger populations may be even more sensitive to high mortality rates than our results suggest.

We may have also underestimated the long-term consequences of high mortality rates by not including environmental stochasticity, as our models rely on solving equations and not simulations. Because large-bodied mammals such as tigers are more sensitive to environmental variation (Sibly *et al.* 2007), we may have underestimated the impact of increased mortality rates associated with poaching.

#### ASSESSMENT OF EVIDENCE SUPPORTING THE PREY DEPLETION PARADIGM

We now consider four lines of evidence, as outlined above, that seem to support the contention that tiger populations are highly resilient to high mortality rates, and hence, that prey depletion is a more important factor limiting tiger numbers.

##### 1. The model derived by Karanth & Stith (1999) indicates that prey depletion has a critical impact on population persistence

The effect of prey depletion in the Karanth & Stith (1999) model is simulated by depressing cub survival rate by 33%, 50%, and 67%. A fundamental assumption of this model is that when prey numbers are depleted, cub survival rate will be reduced, and stay at that lower level as long as prey numbers are low. In reality, home range size appears to increase with decreasing prey density (Miquelle *et al.* 2005a), so that the number of prey per home range is similar whether home range size is small (e.g. 20 km<sup>2</sup> in Nepal) or large (440 km<sup>2</sup> in Russia) (Miquelle *et al.* in press). Hence, it is more likely that cub survival rate would be reduced only during a period of instability as female home range sizes expand to adjust to lower prey densities. Hence, we feel that the assumptions used in this model to depict the impact of prey depletion are faulty, and therefore, the results are suspect.

##### 2. If other large solitary felids, such as cougars can withstand high annual offtake (Lindzey *et al.* 1992, 1994; Anderson & Lindzey 2005), so should tigers

Because age at first reproduction is greater, and inter-birth intervals are longer, our models suggest that tiger populations are not nearly as resilient to high mortality rates as cougar or leopard populations. While our model provides theoretical support for the contention that cougar populations can withstand and recover from high hunting pressures (Fig. 3), it illustrates the danger of developing conservation strategies based on results derived for other, even closely related species. Our comparative analysis does not include African lions

*Panthera leo* (Linnaeus 1758) because this species has a different social structure. Whitman *et al.* (2004) have demonstrated it is possible to sustainably hunt lions by targeting a relatively few males at the end of their reproductive life. Whitman *et al.* (2004) did not propose an acceptable harvest rate as a percentage of the population, but the level of harvest (3 males per year from a population of 10 prides or 80–110 lions) suggests that similar to tigers, lions can withstand only relatively light human-caused mortality rates.

##### 3. Reports of quick recovery of tiger numbers after intensive hunting pressure in the Indian 'Shikar' literature (Sunquist, Karanth & Sunquist 1999) seem to support the contention that high reproductive rates buffer tiger populations from extinction

Sunquist, Karanth & Sunquist (1999) cite one instance in which 77 tigers were killed in the Chitwan area, Nepal in 1935–1936, and 120 tigers were killed in the same area 3 years later (Smythies 1942), and use this report as evidence that tigers reproduce rapidly and recover from high mortality rates quickly. Assuming that a large proportion of the animals shot during these intensive hunts were adult females, it would be biologically impossible for reproduction of resident animals to account for recovery in just 3 years. At that time, the extensive terai forests and grasslands across southern Nepal and northern India provided a huge source population from which individuals could recolonize the Chitwan area after local populations were heavily harvested, and it is most likely that immigration played a major role in recovery of such populations. Subsequent research in Chitwan National Park (Sunquist 1981) and in Russia (Goodrich *et al.* 2005) demonstrates how quickly vacant territories are filled by dispersing tigers. However, those vast source populations no longer exist across most of tiger habitat due to habitat fragmentation and loss, and dispersal across marginal habitat, even when it can occur, often results in high mortality rates (Smith 1984; Goodrich *et al.* in press). Without the potential for dispersal, the impact of intensive human-caused mortality becomes a key factor in their survival. The loss of tigers in Sariska National Park (Check 2006) is apparently such an example in which high poaching rates, coupled with the absence of immigration, resulted in localized extinction.

##### 4. Karanth *et al.* (2006) reported that despite yearly survival rates averaging only 77%, a population of Bengal tigers in Nagarhole National Park, India, demonstrated positive growth over 10 years

'Mortality' in this analysis of camera-trapping data included both true mortality and emigration. Transient individuals and temporary immigrants represented a relatively large percentage of the population (10% and 18% of the total population, respectively), implying that movement into and out of this study population was high, and consequently, actual emigration probably represented a large percentage of the value termed 'mortality' as estimated via camera-trapping.

Perhaps more importantly, survival rate of different components of the population was not possible to estimate. Our modelling exercise suggests that survival rate of adult breeding females is a key factor in population persistence. Our simulations suggest that in a population in which breeding adults are largely protected from poaching, as appears to be the case in Nagarhole (K. U. Karanth, personal communication), high breeder survival rates ( $s_b = 0.95$ ) ensures a population can persist even with low juvenile ( $s_j = 0.5$ ) and transient ( $s_t = 0.39$ ) survival rate (Fig. 5). However, poaching of breeding females can have a major impact: even if juvenile and transient survival rates are remarkably high ( $s_j = 1$ ,  $s_t = 0.77$ ), adult female survival rate must be greater than 0.74 (Fig. 5). Thus, the difference between our model results, and the field data presented by Karanth *et al.* (2006) probably reflect a difference in which portion of a population incurs the majority of poaching pressure.

#### CONSERVATION IMPLICATIONS

The primary intent of this modelling exercise was to assess the idea that tiger populations are inherently resilient to high mortality rates by assessing the impact of varying mortality rates on tigers, comparing these results to other large felids, and determining the relative importance of varying mortality rates on different segments of a population using a mathematically robust approach. The results of this exercise suggest that existing tiger conservation strategies focusing on landscape planning (Wikramanayake *et al.* 1998; Miquelle *et al.* 1999b), or prey recovery (Karanth & Stith 1999) alone may not be sufficient if total mortality rates (i.e. poaching and other sources) exceed 15% of the adult female population, and indicate that determining conservation priorities via extrapolation from other species, even though ecologically similar, can have dangerous repercussions.

We agree that prey recovery efforts are essential for recovery of tiger populations across much of the remaining suitable habitat in Asia (Karanth & Stith 1999; Karanth *et al.* 2006), and it is clear that, in the absence of high rates of human-caused mortality, tiger density is directly related to prey abundance (Karanth *et al.* 2004; Miquelle *et al.* 2005a). However, our results suggest that the threat of high human-caused mortality should not be underestimated in ensuring the long-term survival of tiger populations. Reduction of human-caused mortality is the most essential short-term conservation effort that must be made. Instead of eliminating support, new initiatives to improve anti-poaching efforts should be pursued. In addition, any management policy that has the potential to increase mortality rates should be firmly avoided. Discussions of sport hunting of tigers in the Russian Far East as a mechanism to generate conservation funds seem completely inappropriate in light of the fact that the true level of poaching is unknown and stochastic. Although some may argue that trophy hunting may decrease poaching because it would provide economic incentives to protect tigers, economic benefits are unlikely to reach local people at least in Russia, and it is more likely that condoning any type of hunting would stimulate even greater levels of poaching. Similarly, relaxation of laws relating to

trade in tiger bone within China could spur another poaching episode across Asia, which could have severe implications for tigers range-wide. If poaching reaches critical levels, efforts to recover prey populations will not be sufficient to ensure a future for tigers.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Branching process model

**Appendix S2** Model parameters

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## Appendix S1, Supplementary Material

Chapron, G.; Miquelle, D.G.; Lambert, A.; Goodrich, J.M.; Legendre, S. & Clobert, J.

**The impact on tigers of poaching versus prey depletion**  
*Journal of Applied Ecology*

## Branching process model

We define  $q_i$  as the extinction probability of a population with only 1 female individual from the  $i^{th}$  class in the population. With a population that consists of a single individual which is a cub (0 month old),  $q_0$  is the extinction probability for the entire population. Over a single time step (1 year), this cub can die or survive to become a juvenile and a population with only 1 juvenile has an extinction probability of  $q_1$ .

With  $s_c$  being the probability of cub survival,  $q_0$  is the probability that the cub survives  $s_c$ , itself multiplied by the extinction probability of a population with 1 juvenile only, plus the probability that the cub dies (equivalent to  $1 - s_c$ ):

$$q_0 = s_c q_1 + 1 - s_c$$

With reasoning the same for classes  $q_0$  to  $q_k$ , we get, with  $s_j$ ,  $s_t$  and  $s_b$  being the probability of survival for juveniles, transients and breeding adults:

$$\begin{aligned} q_0 &= s_c q_1 + 1 - s_c \\ q_1 &= s_j q_2 + 1 - s_j \\ q_2 &= s_t q_3 + 1 - s_t \\ q_3 &= s_t q_4 + 1 - s_t \\ &\cdot \\ &\cdot \\ q_{\alpha-1} &= s_t q_\alpha + 1 - s_t \end{aligned}$$

By combining left and right terms we get:

$$\begin{aligned}
q_0 &= s_c q_1 + 1 - s_c \\
s_c q_1 &= s_c s_j q_2 + s_c (1 - s_j) \\
s_c s_j q_2 &= s_c s_j s_t q_3 + s_c s_j (1 - s_t) \\
s_c s_j s_t q_3 &= s_c s_j s_t^2 q_4 + s_c s_j s_t (1 - s_t) \\
&\cdot \\
&\cdot \\
s_c s_j s_t^{\alpha-3} q_{\alpha-1} &= s_c s_j s_t^{\alpha-2} q_\alpha + s_c s_j s_t^{\alpha-3} (1 - s_t)
\end{aligned}$$

then by simplifying:

$$q_0 = (1 - s_c) + s_c (1 - s_j) + s_c s_j (1 - s_t) (1 + s_t + \dots + s_t^{\alpha-3}) + s_c s_j s_t^{\alpha-2} q_\alpha$$

which is:

$$1 - q_0 = s_c s_j s_t^{\alpha-2} (1 - q_\alpha)$$

A population with only 1 reproducing female (class  $\alpha$ ) has an extinction probability  $q_\alpha$  that depends on the probability this adult dies and on the probability its offspring dies:

$$q_\alpha = (1 - s_b + s_b q_\alpha) \sum_{i=0} P_i$$

where  $P_i$  is the probability this female will give birth to  $i$  cubs that will ultimately die. Suppose that cub production follows a Poisson distribution with fecundity  $f = l/ib$ , where  $l$  is litter size, and  $ib$  is the inter-birth interval, then:

$$q_\alpha = (1 - s_b + s_b q_\alpha) \sum_{i=0} \left( e^{-f} \frac{f^i}{i!} q_0^i \right)$$

We therefore get:

$$q_\alpha = (1 - s_b + s_b q_\alpha) e^{-f(1-q_0)}$$

Since we found previously that:

$$1 - q_0 = s_c s_j s_t^{\alpha-2} (1 - q_\alpha)$$

we finally get:

$$q_\alpha = (1 - s_b + s_b q_\alpha) e^{f s_c s_j s_t^{\alpha-2} (q_\alpha - 1)}$$

The eventual (infinite) extinction probability  $x$  of a population starting with 1 breeder only is the smallest solution of the equation  $h(x) = x$  for  $x \in [0, 1]$  where:

$$h(x) = (1 - s_b + s_b x) e^{f s_c s_j s_t^{\alpha-2} (x - 1)} \quad (1)$$

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**Model parameters**

Parameters for models (Tables 1 & 2) were based on data from long-term field studies (Sunquist 1981, Martin & de Meulenaer 1988, Smith & McDougal 1991, Lindzey et al. 1992, 1994, Bailey 1993, Smith 1993, Logan & Sweanor 2001, Kerley et al. 2003, Goodrich et al. 2005).

Table 1: General demographic parameters for the branching process and deterministic models

Parameter	Value
Cub survivorship	0.6
Juvenile survivorship	0.9
Transient survivorship	0.7
Breeding adult survivorship	0.9
Litter size (female-only)	1.5

Table 2: Specific parameters (age at first reproduction and inter-birth interval) for three large felids.

<b>Species</b>	Age at first reproduction $\alpha$ (months)		Inter-birth interval $ib$ (months)	
	Literature	Model	Literature	Model
Tiger	41-81 (Smith & McDougal 1991) 42-54 (Kerley et al. 2003)	48	24-30 (Sunquist 1981) 20-24 (Smith & McDougal 1991) 22 (Kerley et al. 2003)	24
Leopard	<u>Africa:</u> 36 (Martin & de Meulenaer 1988) <u>Asia:</u> 24-36 (Sunquist 1983, Pikunov & Korkishko 1989)	36	<u>Africa:</u> 15-24 (Martin & de Meulenaer 1988, Bailey 1993) <u>Asia:</u> 20-21 (Nowell & Jackson 1996)	20
Cougar	20-24 (Lindzey 1987) 26 (Logan & Sweanor 2001)	24	12 (Robinette et al. 1961) 18-24 (Lindzey 1987) 17.4 (Logan & Sweanor 2001)	18

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