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A Call for Tiger Management Using "Reserves" of Genetic Diversity

Rachael A. Bay, Uma Ramakrishnan, and Elizabeth A. Hadly

From the Department of Biology, Stanford University, Stanford, CA 94305 (Bay and Hadly); and National Centre for Biological Sciences, Tata Institute of Fundamental Research, Bangalore 560065, India (Ramakrishnan).

Address correspondence to Rachael A. Bay, Hopkins Marine Station of Stanford University, 120 Oceanview Boulevard, Pacific Grove, CA 93950, or e-mail: rbay@stanford.edu.

Abstract

Tigers (*Panthera tigris*), like many large carnivores, are threatened by anthropogenic impacts, primarily habitat loss and poaching. Current conservation plans for tigers focus on population expansion, with the goal of doubling census size in the next 10 years. Previous studies have shown that because the demographic decline was recent, tiger populations still retain a large amount of genetic diversity. Although maintaining this diversity is extremely important to avoid deleterious effects of inbreeding, management plans have yet to consider predictive genetic models. We used coalescent simulations based on previously sequenced mitochondrial fragments (n = 125) from 5 of 6 extant subspecies to predict the population growth needed to maintain current genetic diversity over the next 150 years. We found that the level of gene flow between populations has a large effect on the local population growth necessary to maintain genetic diversity, without which tigers may face decreases in fitness. In the absence of gene flow, we demonstrate that maintaining genetic diversity is impossible based on known demographic parameters for the species. Thus, managing for the genetic diversity of the species should be prioritized over the riskier preservation of distinct subspecies. These predictive simulations provide unique management insights, hitherto not possible using existing analytical methods.

Key words: *carnivore conservation, coalescent simulation,* Panthera tigris

Like many large carnivores, the tiger (*Panthera tigris*) is heavily impacted by human activity. Severe habitat loss has contracted the species range to just 7% of historic estimates, the remainder of which is highly fragmented (Kitchener and Dugmore 2000; Sanderson et al. 2006). In addition, poaching continues to be a threat across the entire range of the species; a recent report by the wildlife trade monitoring network, TRAFFIC, estimates a minimum average of 104 tigers killed for their parts and derivatives each year since 2000 (Verheij et al. 2010). Recent surveys estimate only about 3600 tigers remain in the wild across the entire range of the species (GTRP 2010).

The current conservation objective of the Global Tiger Recovery Program, which comprises 13 countries with wild tiger populations, is to double the total census size by 2022, the next year of the tiger (GTRP 2010; Seidensticker 2010). Although ecological and demographic models have been considered in conservation efforts (Sanderson et al. 2006; Ranganathan et al. 2008), predictive models used to inform conservation decisions have not yet considered the importance of genetic diversity to tiger recovery. Conservation efforts for other top predators have shown that integrating genetic information along with ecological and demographic data is critical to the success of a conservation plan (Miller and Waits 2003; Leonard et al. 2005). Genetic diversity confers a highly significant advantage to the evolutionary fitness of species and has been advanced as an important determinant of International Union for Conservation of Nature (IUCN) designation of endangerment (Reed and Frankham 2003).

Although tigers have experienced an extremely severe recent bottleneck (Russello et al. 2004; Mondol et al. 2009) and 3 of 9 subspecies are extinct (Bali, Javan, and Caspian), the species retains a higher than expected amount of genetic diversity based on the census size. A large amount of this genetic diversity is harbored on the Indian subcontinent (Mondol et al. 2009) and there is little connectivity between subspecies, with each subspecies forming a distinct phylogenetic group (Luo et al. 2004). The level of diversity observed in the current population is a remnant of a much larger historic population size that has not yet been degraded by genetic drift. Because low genetic diversity can negatively impact the fitness of a species, and thus its survival (Roelke et al. 1993; Reed and Frankham 2003; Da Silva et al. 2005), it is critical that tiger population sizes increase before this "reserve" of genetic diversity is lost. Once lost, it will not be possible to regain for millions of years, even with higher population

sizes. Further, loss of genetic diversity has been implicated in decline of male fertility in many species (Fitzpatrick and Evans 2009), which will compromise attempts to increase tiger census size in demographic recovery efforts.

Here, we predict the amount of near-term population growth needed to preserve current genetic diversity in wild tiger populations. To address this question, we use coalescent-based simulations in an approximate Bayesian computation (ABC) framework. Using this framework to simulate future scenarios provides a less computationally expensive alternative to time-forward simulations (Hoban et al. 2011; Arenas 2012). Future population size for tigers is predicted based on the condition that current levels of genetic diversity are maintained. We use varying levels of migration between populations to determine the effect of gene flow on essential population growth. In addition, we address questions related to inter- versus intrasubspecies gene flow, by examining 3 scales 1) all tigers across the entire range, 2) 1 subspecies, and 3) 1 isolated population.

Table 1 Summary of samples used to estimate simulation parameters

Deme	*N*	*n*	Nucleotide diversity (π)
Siberian	360	11	
Sumatran	325	8	
Malayan	500	11	
Indochinese	377	27	
Bengal	2081	68	
Central India	506	14	
Andhra Pradesh	97	8	
Western Ghats	402	30	0.0014
Total (peninsular India)	1005	52	0.0026
Total (all)	3643	125	0.0043

All samples were from previous publications (Luo et al. 2004; Mondol et al. 2009). For each population, *N* represents the census estimate, whereas *n* indicates the sample size. Nucleotide diversity (π) was calculated using Arlequin v3.5 (Excoffier and Lischer 2010).

Methods

We used BayeSSC (Anderson et al. 2005), a coalescent simulation program, to model the evolution of tiger populations over 30 generations. Coalescent simulations allow for prediction of population history by comparing parameters from real genetic samples with those estimated by sampling populations simulated under different scenarios. BayeSSC, designed for use with ancient DNA samples, allows for sampling of simulated populations at multiple time points. Although the simulations are conducted in terms of generations as is appropriate for evolutionary modeling, for the purpose of our discussion herein, we convert to years, based on a tiger generation time of 5 years (Smith and McDougal 1991). We based our simulations on parameter estimates from 1263-bp mitochondrial fragments that include parts of the cytochrome b locus and have been sequenced in tigers across the range of the species (Luo et al. 2004; Mondol et al. 2009). These samples were used to calculate current nucleotide diversity (π) using Arlequin (Excoffier and Lischer 2010) (Table 1). Nucleotide diversity from these mitochondrial DNA (mtDNA) samples was compared with nucleotide diversity of samples from simulated populations in an ABC framework. We used rejection sampling with delta = 0.05, which allowed us to retain 0.1–5% of replicates. Based on these replicates, we determined a maximum likelihood estimate (MLE) for future census population size. Using this framework, we designed 3 sets of simulations to examine the need for population expansion and gene flow at different geographic and phylogenetic scales: 1) across the entire present geographic range of tigers, 2) within 1 region, and 3) within a single isolated population.

Simulation Scenarios

Simulation 1, which was based on samples from all extant subspecies (excluding the likely ecologically extinct South China subspecies), was designed to investigate how the larger effects of gene flow across the whole species range (including between subspecies) impact the amount and rate of population expansion needed to maintain current genetic diversity. For this simulation, 3 different conditions were used. For the first condition, we treated all samples as belonging to 1 panmictic population. In the other 2 conditions, we split the samples into either 2 populations (Bengal tigers from India and all others) or 5 populations (1 for each of 5 subspecies of tiger: Bengal, Sumatran, Siberian, Malayan, and Indochinese). Because populations are geographically distant and habitat is highly fragmented, very little gene flow currently exists between subspecies. For this reason, when multiple populations were simulated, we allowed only 1% migration per generation between any pair of populations.

As an extension to Simulation 1, we conducted an additional simulation to investigate the effects of delayed initiation of gene flow. First, we simulated 5 separate demes (representing 5 subspecies) with just 1% migration and constant population size for 25 years. These simulations were used to estimate loss of nucleotide diversity after 25 years with little crossbreeding. Because nucleotide diversity is not specified in the model, some simulated populations do not accurately reflect the diversity observed in the real data. For this reason, we discarded replicates in which current simulated nucleotide diversity was far (>1 standard deviation [SD]) from the observed value. Using the remaining replicates, we calculated the mean loss of nucleotide diversity over 25 years. This value, subtracted from observed nucleotide diversity, provides an estimate for nucleotide diversity 25 years into the future under constant population size and little gene flow between subspecies. We then continued this simulation as above, beginning 25 years into the future, under the assumption of panmixia to determine the population size essential for maintaining this new level of nucleotide diversity if crossbreeding of subspecies begins 25 years into the future.

Although Simulation 1 provides a general view of the effects of gene flow on maintaining genetic diversity, due to the extent of habitat fragmentation, it is unrealistic to treat each subspecies as an unstructured population. For this

reason, in Simulation 2, we focused on more realistic populations within a single region. Because India contains more genetic diversity (Mondol et al. 2009) as well as more individuals than any other country (GTRP 2010), simulated populations for Simulation 2 were based on 3 peninsular Indian populations: Central Indian Landscape (N = 506), Andhra Pradesh Landscape (N = 97), and Western Ghats Landscape (N = 402). These areas each contain multiple tiger reserves and combined are home to the majority of tigers in India (~1004 individuals) (Jhala et al. 2008). Equal migration between the 3 populations was 1) 1% (1% of individuals migrate each way between any 2 populations every generation), 2) 10%, or 3) complete (panmixia).

In Simulation 3, we used an even more localized approach to ask the question: What is the extent of population growth necessary for a single population if there is no connectivity between fragmented populations? Parameters for this simulation were based on samples taken from the Western Ghats in India (N = 402). We chose this population because it is one of the largest in a single area and we have a large sampling of real mtDNA data. Because the Western Ghats population is larger than most other populations and therefore less impacted by drift, the results likely represent a conservative estimate of the amount of local expansion necessary to maintain genetic diversity compared with an average-sized population. For this study, we also conducted an additional simulation to examine the loss of genetic diversity when population size remains constant. This additional simulation was run for 30 generations (150 years) and 100 000 replicates were simulated. Simulated replicates that accurately reflected current observed nucleotide diversity (<1 SD) were used to generate a distribution for the change in nucleotide diversity over 30 generations for this population.

The framework of Simulation 3 was also used to test the sensitivity of our analysis to different parameter choices. Simulation 3, based on a single isolated population, is the simplest of the simulation scenarios and therefore the easiest under which to test sensitivity to varying assumptions. We tested a range of mutation rates, population size estimates, and levels of genetic diversity to maintain (see Supplementary Materials).

Coalescent Simulations and Maximum Likelihood Estimation of Future Population Size

The basic simulation plan for a single deme is shown in Figure 1. Because simulations were based on mitochondrial sequences and thus represent only females, we assumed census size was double the female population size estimate. We used one-half of the census size estimates published in the GTRP (2010) for estimates of female population size. Working backward through time, we first chose a future deme size from a uniform prior distribution. The population expanded (or contracted) exponentially to reach current census size (see Table 1). We then simulated an increase backward through time at a rate based on a past census estimate of 100 000 individuals (Dinerstein et al. 1997) for 200 years (40 generations), which is the estimated timing for decline (Mondol et al. 2009). Although we do not sample at this time point, specifying this high historical population size in the model is necessary to achieve levels of diversity observed in present tiger populations. For each condition, simulations

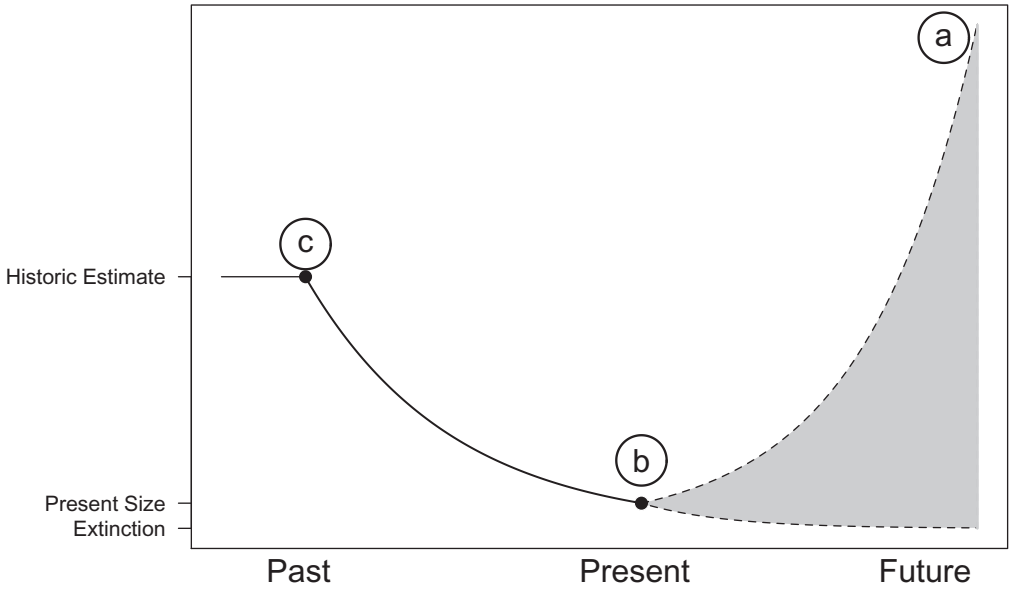

Figure 1. Simulation for a single population of tigers. Working backward through time: (**a**) a future census population size is chosen and the population undergoes exponential growth or decay to (**b**) current population size, then expands for 40 generations (200 years), then (**c**) remains constant. The past growth rate (from c to b) is based on a past total census size of 100 000 individuals.

were conducted in a stepwise manner. For example, the initial simulation began at 25 years after present (5 generations) and the next simulation, simulating 50 years after present was based on 25-year estimates for population size. A mutation rate of 2% per million years (Brown et al. 1979) was used for all simulations.

The rate of population growth, r, over time t generations was calculated according to the exponential growth equation:

$$r = \ln(N_P/N_F)/t$$

where N_F is the future female population size, and N_P is the present female population size (one-half of the census estimate). Because coalescent models work backward through time, a negative value for r indicates population expansion. Prior distributions for future population size were chosen in the first step of each simulation using Akaike information criterion (AIC) to compare the fit of the data under several possible prior distributions. For most simulations, future population size was chosen from a uniform prior distribution with a range of $[0,3*N_P]$. The only exception to this was when 5 populations were modeled in Simulation 1, where we found that using a maximum value of $5*N_P$ was necessary to achieve the rapid expansion needed for this condition (MLEs under a prior of $[0,5*N_P]$ had a better AIC score than those under $[0,3*N_P]$). We then used an ABC approach to determine and MLEs for N_F based on the true value for nucleotide diversity calculated from mtDNA sequences. The MLEs were used to create a future trajectory of the "essential population size," defined as the number of tigers needed to maintain genetic diversity.

Results

Simulation 1 was designed to investigate the impact of large-scale gene flow (i.e., between subspecies) on genetic diversity. Here, parameters were based on samples taken from the entire range of the species (Figure 2a) and simulations were compared with observed nucleotide diversity ($\pi = 0.0043$) estimated from all available samples. We simulated 3 different cases: 1) each of 5 subspecies as separate demes; 2) 2 populations (1 representing Bengal tigers, which comprise over half the total census size of the species, and another representing the remaining 4 subspecies); and 3) panmixia, where all individuals are able to interbreed with equal probability. A complete table of results for all simulations can be found in the Supplementary Materials. Our simulations indicate that maintaining genetic diversity in isolated populations will require a much more rapid population expansion than will 1 panmictic population (Figure 2b). Both the rate of population growth and the total necessary population expansion over 150 years are higher with multiple populations than in the case of panmixia. The trajectory under the assumption of panmixia is sigmoidal in shape rather than completely exponential; this case seems to approach a "stable" population size suggesting potential recovery, whereas the nonpanmictic cases continue to increase exponentially over the 150-year time scale covered in our simulations. However, based on simulated conditions, the "stable" population size is quite large: 60 800 individuals, which is still an extremely large increase from the current 3644.

We conducted an additional simulation to determine the effects of a delayed initiation of gene flow between subspecies, using all samples across the entire range (as in Simulation 1). For 5 demes at constant population size, the mean change in nucleotide diversity is -3×10^{-5} over 25 years. Although this only represents a 0.7% decline in nucleotide diversity over 25 years, it is sufficient to increase population expansion needed to maintain diversity (Table 2). The overall growth rate to maintain genetic diversity is 44% higher when panmixia is delayed for 25 years. This leads to an essential population size after 150 years of ~98 000 individuals compared with ~60 000 individuals when panmixia is achieved immediately.

Because existing tiger populations are more fragmented than populations covered in Simulation 1, we designed Simulation 2 to explore the effects of migration among more realistic populations within a single subspecies, basing this simulation on 3 populations within peninsular India for which we have empirical data ($\pi = 0.0026$, $N = 1005$) (Figure 2c). In this case, we simulated 3 different levels of migration: panmixia, 10%, and 1%. Here, when less gene flow is allowed between the 3 populations, more rapid population expansion is required to maintain the current diversity of peninsular Indian populations (Figure 2d). As in Simulation 1, when panmixia exists, a stable population size can be achieved. However, in this simulation, the stable population size plateau does not require an unfeasibly large or rapid population expansion (2260 individuals after 150 years compared with a current population of 1005).

Increasing habitat fragmentation may ultimately lead to isolated populations with no connectivity whatsoever. Thus, for Simulation 3, we simulated a single population based on parameters from samples taken in the Western Ghats ($\pi = 0.0014$, $N = 402$), a region of India that contains a number of tiger reserves (Figure 2e). Results indicate that to maintain current genetic diversity of the Western Ghats population without immigration, growth must be rapid, reaching 18 000 individuals (from a starting population of 402) in 150 years (Figure 2f). In this case, we do not see a stabilizing effect, suggesting that essential growth would continue even after the 150-year time frame covered by our simulations. Our sensitivity analysis suggests these results are not substantially impacted by realistic changes in mutation rate, census estimate, or the use of effective population size in simulations (Supplementary Materials). The need for an increase in population size is further supported by the likely loss of genetic diversity when population size is held constant (see inset in Figure 2f). The mean change in nucleotide diversity is −0.00023, indicating that, on average, nucleotide diversity declines by about 18% in 150 years.

Discussion

Coalescent simulations have proved a useful method for understanding population level evolutionary processes

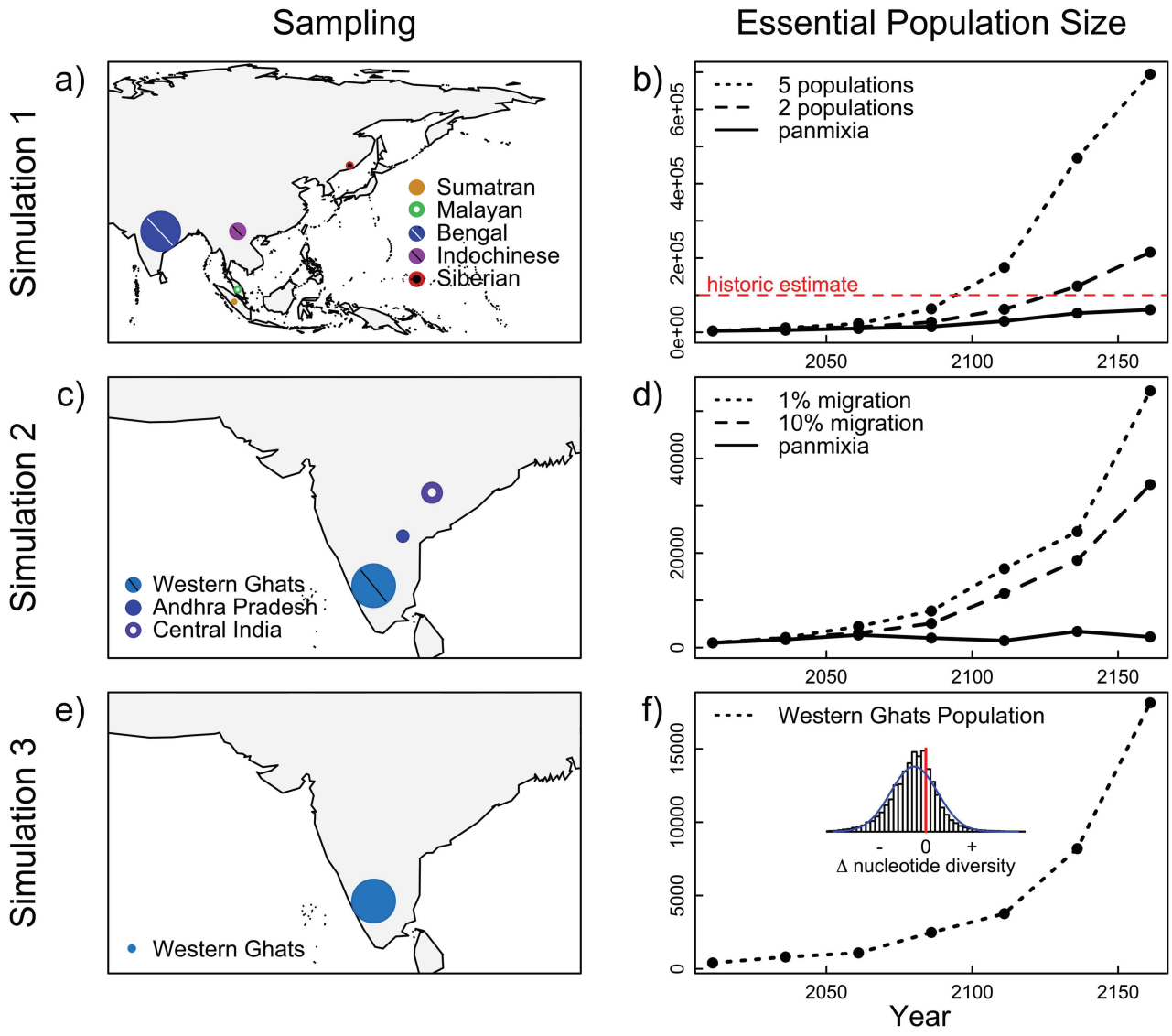

Figure 2. Sampling and results for simulation studies. Samples used to measure parameters for each simulation study are represented on a map (**a**, **c**, and **e**) where the area of each point is proportional to the number of samples for a given population. Results corresponding to maps are shown in panels (**b**), (**d**), and (**f**), respectively, and represent census population trajectories based on MLEs (b, d, and f) for future population sizes. The dotted horizontal line in (b) represents a historic census estimate of 100 000 individuals. The inset in (f) shows a distribution for the change in nucleotide diversity over 30 generation when population size is constant.

Table 2 Results from coalescent simulations comparing immediate and delayed commencement of gene flow across 5 subspecies

Time		Essential population size (N_F)		Growth rate (r)	
Generations	Years	Immediate	Delayed	Immediate	Delayed
0	Present	3644	3644	—	—
5	25	5860	3644	0.10	0
10	50	10 440	8620	0.12	0.17
15	75	15 360	19 880	0.08	0.17
20	100	30 000	43 400	0.13	0.16
25	125	51 600	70 600	0.11	0.10
30	150	60 800	98 200	0.03	0.07
			Overall	0.09	0.13

Time is represented by the number of generations and years into the future. Growth rate, r, is per generation.

(Hoban et al. 2011). We demonstrate that modeling future population dynamics using coalescent simulations is valuable when formulating conservation plans for threatened species. Coalescent simulation is less computationally expensive than forward-time simulation, but because the 2 types of models have been known to yield slightly different results (Arenas 2012), it is perhaps most prudent to use them in conjunction with one another. For tigers, current conservation plans have considered both ecological and demographic models (Sanderson et al. 2006; Ranganathan et al. 2008), but predictive genetic models have yet to be utilized in plans for the recovery of the species. The current goal of the Global Tiger Recovery Program is to double census size by the next year of the tiger, 2022. However, our simulations show that facilitating gene flow, both naturally and through assisted migration programs, may be more effective to preserve the genetic diversity of the species than simply encouraging local population expansion. In fact, allowing for gene flow would minimize the amount of population growth needed to maintain diversity.

Could we have arrived at these predictions for the genetic future of tiger populations without serial coalescent simulations? We could, for example, use a simple, back-of-the-envelope population genetic calculation to calculate the effective size that is consistent with observed genetic diversity in current populations. We could estimate effective size from current nucleotide diversity (a measure of $\theta(2N_e\mu)$, where μ is the mutation rate) and target population growth to reach that effective size. However, if we used such an approach, we would underestimate the required population size growth in some cases (Simulation 1, N_e estimate ~21 500) because existing population structure is high. Similarly, we might overestimate population size (Simulation 2, N_e estimate ~13 000) when the existing population structure is low. BayeSSC allows us to combine the effects of drift and gene flow and look at them in the context of population growth, something that is not trivial to calculate through analytical formulae. This analysis hence provides unique insight into the genetic future of populations.

Although analysis based on mtDNA sequences has provided valuable insights for conservation in a number of contexts, this type of analysis is not without limitation (for reviews, see Moritz 1994; Ballard and Rand 2005). Because mtDNA is inherited maternally, the effective population size and evolutionary trajectory are different from that of nuclear DNA. In addition, higher mutation rates and lack of recombination in mitochondrial genomes can lead to different coalescent times than for nuclear markers. However, although estimates of population size from mitochondrial data may not be extremely accurate, it is generally agreed that qualitatively, the inferences from mtDNA are robust (Moritz 1994). Most cases in our data set indicate a need for exponential growth in order to maintain genetic diversity. Although the exact number of individuals may change depending on which genetic marker is modeled, our overall conclusions are likely to remain the same.

Several case studies have illustrated that loss of genetic diversity can lead to negative fitness effects, as deleterious variants can become fixed in a population (Reed and Frankham 2003). For example, the Florida panther (*Puma concolor coryi*), a subspecies of the puma, experienced a dramatic decrease in its range and a subsequent decrease in population size down to 30 individuals in the early 1990s. This demographic reduction led to inbreeding, lowering the genetic diversity of the subspecies, which in turn led to conditions such as lowered reproductive capacity, cardiac defects, and an increased prevalence of infectious disease (Roelke et al. 1993). As with the Florida panther, severe habitat fragmentation has led to isolation of tiger populations from one another. However, unlike the Florida panther, effects of inbreeding do not seem to yet be apparent in wild tigers. This is likely because, until recently, tigers occupied much larger and contiguous habitats, suggesting a recent and large historic effective population size (Mondol et al. 2009).

The necessity of a large population to house genetic diversity for tigers means that in the absence of gene flow, an unrealistic increase in population size would be necessary. Simple calculations based on the population sizes generated by our simulations indicate that the required rates of population growth, assuming panmixia, are 1.8%, 0.5%, and 2.5% for the whole species, peninsular India, and the Western Ghats, respectively. Contrastingly, with only 1% gene flow, the required growth rates are 3.5% for the entire species and 2.6% for peninsular India. Are such growth rates reasonable for tigers? Landscape-based models indicate that current tiger reserves may be able to support up to 3 times current population sizes (Wikramanayake et al. 2011). In nearly all cases, the necessary growth to maintain genetic diversity exceeds this limit.

Even given sufficient space for such population expansion, these growth rates are unattainable. Tigers are highly dependent on the numbers of prey in their territories (Karanth and Nichols 1998). A long-term capture–recapture study in the Western Ghats (Karanth et al. 2006) indicates that tigers can grow at rates of 3% annually, but only given a high prey density on the order of 57 prey/km^2. Karanth et al. (2004) suggest that only 3 out of 15 tiger reserves in India have ungulate prey density above this threshold value, whereas a more recent estimate by the NTCA (Jhala et al. 2008) suggests that with the exception of the Terrai landscape in Uttarakhand, no protected areas have prey densities that are this high. Taken together, these data suggest that it will be very difficult to increase tiger numbers at biologically realistic rates to meet the simulation criteria in the absence of gene flow between populations in India. In fact, even with the added benefits of gene flow, essential population sizes often exceed realistic limits. Results from an additional simulation, in which we required only 95% or 90% of genetic diversity to be maintained (Supplementary Figure 4), show that lowering our goals for the amount of genetic diversity maintained reduces the essential population size—5980 individuals are required to maintain 90% of genetic diversity after 30 generations compared with 18 140 individuals required to maintain current levels of diversity in the Western Ghats population. However, the population trajectories are still exponential, suggesting that after 30 generations, continued increases in population size would still be required. We therefore conclude that even in cases where it may not be feasible to maintain all

current genetic diversity, local expansion and increased gene flow will maximize the amount of genetic diversity we are able to preserve.

Although local population expansion is indeed necessary for tigers, the only way to alleviate the potential loss of genetic variation in the species is by facilitating gene flow. Our simulations based on the empirical data for 3 populations within peninsular India demonstrate that gene flow is necessary between populations within each subspecies, but it is also vital between subspecies, which are presently separated by national boundaries. For this reason, gene flow between species will be much harder to promote as a conservation strategy. Although subspecies of tigers do have morphological and behavioral differences that are likely to be locally adaptive, the question is whether conservation of the individual subspecies is practical, or even possible. Indeed, crossbreeding with another subspecies may have saved the Florida panther; after introduction of individuals from a closely related subspecies in 1995 (Seal 1994; Hedrick 1995), the population has risen to 104 individuals as of 2008 and deleterious genetic disorders are less common, genetic diversity has increased, and overall fitness is higher (Land et al. 2002; Johnson et al. 2010; Benson et al. 2011). Results from our simulations show that crossbreeding subspecies may also be a valuable conservation tool for tigers. Based on our simulations, global census sizes would have to be extremely large, much larger even than historic estimates, in order to maintain current genetic diversity without crossbreeding subspecies.

Genetic rescue—when immigrants increase the fitness of a population—has the potential to alleviate harmful effects of inbreeding but poses its own risks. Outbreeding depression occurs when offspring of individuals from different populations have reduced fitness, either due to masking of adaptive genetic variants or noncompatible genetic backgrounds (Allendorf et al. 2001). These fitness effects may not be visible in the F1 generation, making experimental studies of possible outcomes even more difficult. Although a growing body of literature suggests that genetic rescue is possible and even beneficial in species ranging from prairie chicken (Westemeier et al. 1998) to wolves (Ingvarsson 2003), factors such as life history and divergence between populations can influence the effectiveness of such a plan. It is important to closely consider these possible negative impacts when forming a management plan (Tallmon et al. 2004; Edmands 2007; Hedrick and Fredrickson 2010).

In addition to showing that both gene flow and population expansion are essential to retain current genetic diversity, our results suggest that a delay in implementing a conservation plan that includes gene flow between subspecies will only serve to decrease nucleotide diversity and increase the rate of population expansion needed over the same time interval. Our simulations show that, even in one of the larger natural populations (the Western Ghats), nucleotide diversity will substantially decrease if population sizes do not increase and gene flow is not facilitated within the next 25 years. We expect this effect to be more pronounced in smaller populations, where drift is even stronger. We also show that even a small decrease in nucleotide diversity (<1%) over just 5 generations greatly increases the essential future population size. Combined, these results illustrate the urgency of the situation; it is imperative that a plan to increase gene flow be implemented immediately, before genetic diversity declines.

Although we have modeled a restrictive set of gene flow conditions to exemplify its effect on the future genetic diversity of tiger populations, an alternative is to use this approach in a more realistic context. We know, for example, that some populations are potential sources (higher tiger population density) and could provide dispersers. If we could allow dispersal from some populations, how much natural dispersal would be adequate to offset loss of genetic variation in the future? Although using coalescent simulation in a more population-specific way to plan management strategies for population growth and gene flow in the peninsular Indian landscape might be feasible, subspecific-level gene flow between national boundaries will be much harder to promote as a conservation strategy. Every tiger—including those in zoos, which presently outnumber those in the wild—is important as a potential reserve of the genetic diversity of the species. Research efforts should aim to estimate ongoing gene flow between protected areas, and immediate efforts toward cross-boundary tiger breeding should be considered.

Supplementary Material

Supplementary material can be found at http://www.jhered.oxfordjournals.org/.

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