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Simulations of Cheetah Roaming Demonstrate the Effect of Safety Corridors on Genetic Diversity and Human-Cheetah Conflict

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Summary

Human-cheetah conflict is driving cheetahs (*Acinonyx jubatus*) into extinction. It is estimated that there are fewer than 7,100 cheetahs remaining globally, and encroachment from human populations has reduced their habitat to less than 9% of their historic range. Further pressure on cheetah survival comes from their poor genetic diversity, which leaves them susceptible to disease and genetic abnormalities. To reduce human-cheetah conflict and to increase the interaction between cheetah groups of diverse genetic backgrounds, we have proposed the development of "cheetah safety corridors," which connect different populations of cheetahs inside a protected strip of land. Computer simulations were developed to model cheetah roaming within a rural environment containing human populations of varying densities. Cheetah safety corridors were included in the simulations with a varying width of up to 90 km. Modeling of these safety corridors revealed a significant positive impact on cheetah lifetime, roaming range, and cheetah-cheetah interactions, which could lead to improved genetic diversity. Targeted investment in local communities inside the safety corridor had the biggest impact, with a 4-fold improvement in cheetah lifespan and a 20-fold increase in positive cheetah-cheetah interactions, compared to investment spread more uniformly across the entire simulated area. Engagement of the local population would be vital to the success of safety corridors so that communities regard cheetahs as an asset to the region rather than a threat.

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Introduction

Large predators like cheetahs are a vital part of any healthy ecosystem. The loss of cheetahs could lead to a top-down trophic cascade, which would have consequences far beyond an individual species (1). Cheetahs reduce sick or old prey, leaving the stronger ones to survive and thrive, and the remains of prey carcasses provide food for scavenging animals and birds. Without predation, herbivores, such as antelopes, overgraze vegetation, which can lead to soil erosion and desertification. Conservation is vital to protect not only cheetah populations, but to maintain the entire ecosystem and to preserve biodiversity.

Cheetah numbers have plummeted dramatically in the past century, mainly due to conflict with humans; it is estimated that there are fewer than 7,100 cheetahs remaining globally, which are confined to only 9% of their historic range (2, 3). Furthermore, most of the cheetah's range exists outside protected areas, which could have dire consequences for survival due to increased human-cheetah conflict. Cheetahs face additional challenges because of their lack of genetic diversity (4), which may have been triggered by at least one population bottleneck over the past 100,000 years (5). A recent study revealed that wild-born African cheetahs exhibit a 95% homozygous genome, compared to 24% in domestic cats (6), and that genetic diversity has declined further in the past 30 years (7). This leaves the cheetah vulnerable to certain diseases, since a genetic predisposition or susceptibility to a specific disease in one animal is likely to be present in all animals of the same genetic background (8, 9). This also may manifest itself through poor spermatozoa development and some genetic abnormalities (10).

Cheetahs come into conflict with humans largely due to the expansion of human activities into the cheetah's historic range. Many farmers regard cheetahs as pests that prey on their livestock, and they may shoot or trap cheetahs on their land. Recently, in an essay for the Cheetah Conservation Fund (CCF), we proposed the development of "cheetah safety corridors" to reduce human-cheetah conflict and to enhance the likelihood of cheetahs with more diverse genetic backgrounds interacting and breeding with each other (11). A "safety corridor" is a strip of contiguous land within the habitat of the threatened species, inside which they are both protected from humans and prevented from interfering with farms and livestock. Ideally, a safety corridor would be located to link up different groups of cheetahs that are more likely to exhibit genetic variability. Safety corridors have been used throughout the world for other species, to help connect tiger reserves to each other in Asia (12, 13), to protect jaguars in Central America (14), and to help wildlife in Canada avoid cars and other dangers (15). In this paper, we propose the establishment of safety corridors in Namibia and neighboring countries, designed to connect different sub-populations of cheetahs, with the aim of reducing conflict with humans and improving genetic diversity.

Developing a cheetah safety corridor in which humans are excluded entirely is not practical and would have a significant detrimental impact on the farmers living in the proposed area and on the local economy. Therefore, the concept of a safety corridor cannot necessarily imply relocating the human population out of the area. Rather, it would involve the education and engagement of the human population within the corridor, such that human-cheetah and cheetah-livestock interactions no longer lead to either cheetah or livestock death. CCF has pioneered projects to improve the relationship between humans and cheetahs, implementing livestock guard dog programs to scare the cheetahs away from farms, and actively engaging with the local community to promote cheetahs as an asset to the region rather than a threat (16, 17). With this level of engagement, a cheetah safety corridor becomes economically viable, since it requires neither the purchase of vast tracts of land nor the displacement of the local population. Instead, it requires the active participation of local farmers and the expansion of community outreach programs operated by CCF and other animal-welfare organizations.

However, until now, safety corridors have been proposed as a possible solution to some of the problems facing cheetahs, but with little or no evidence that they would actually work. In this paper, we have developed computer simulations of random populations of cheetahs and tracked their movement and interactions, both with humans and other cheetahs, and in the presence and absence of safety corridors. In this way, we can demonstrate that these proposed corridors should have a positive impact on multiple aspects of cheetah existence. We hypothesized that cheetah safety corridors would increase cheetah lifespan, reduce human-cheetah conflict, and increase the interactions of genetically diverse groups of cheetahs. In addition, we hypothesized that, given limited resources, investments targeted specifically at the community inside the corridor, rather than more generally, would have a significantly greater impact.

These simulations have demonstrated that the proposed cheetah safety corridors minimize human-cheetah conflict and improve genetic diversity, while maximizing the return on investment in the local community.

Results

The simulations were split into two parts: in the first we optimized the parameters used in the simulations by comparing simulated data against real data from southern Africa. Once the parameters were optimized, in the second part we simulated the effects of the safety corridors on human-cheetah conflict. A flowchart of the simulation process is shown in **Figure 1**.

We simulated cheetahs moving randomly inside a two-dimensional area of size 21,600 km^2. The human population was distributed randomly throughout the area, and interactions with humans occurred when the cheetah roamed close to a farm. When the cheetah was in close proximity with a farm, it had a certain probability of being detected and killed by the farmer. However, if that interaction occurred within the safety corridor, no harm came to the cheetah, representing the improved human-cheetah relationship.

We simulated two distinct groups of cheetahs, which were assumed to have two different genetic profiles. These groups were initially separated by 120 km, at opposite ends of the safety corridor. A meeting between two cheetahs from the same group was defined as a negative interaction, which could lead to offspring with

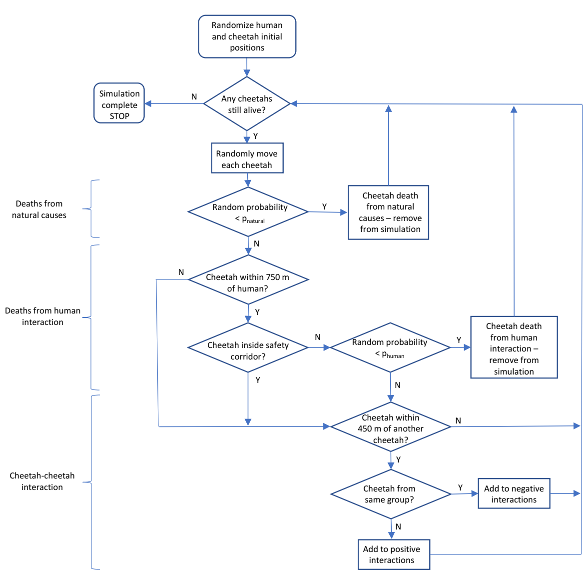

Figure 1. Cheetah Roaming Simulation. Flow chart describing a single run of the simulation – each set of data consists of 100 repetitions with different random starting conditions.

poor genetic diversity. Conversely, a positive cheetah-cheetah interaction was defined as one in which two animals from different genetic backgrounds interacted. Cheetah mating, the birth of cubs, and animal gender were not simulated; the cheetah interactions were recorded merely to indicate the possibility of genetic mixing, rather than to predict any resulting offspring.

The simulations of cheetah roaming exhibited a pattern very similar to those found in nature, from animals fitted with GPS tracking collars (18, 19). To optimize the parameters used in the model, we compared simulations against demographic data from one of the largest and most comprehensive studies of cheetah populations in Namibia (20). Specifically, the cumulative survival of Namibian cheetahs was compared against the simulated survival data, while the probabilities of death from human interaction and natural causes were varied. The mean-square error between the simulated cumulative survival curves and the demographic data from the Namibian study (20), were plotted as a function of the annualized probabilities of death from natural causes ($p_{natural}$) and from a single human interaction (p_{human}) (**Figure 2**). The curves reached a minimum mean-square error for $p_{natural}$ = 9%/year (y), and p_{human} = 0.1%/interaction. These values were used in additional simulations, which compared the percentage of deaths from natural causes in Namibian cheetahs against simulated deaths. Demographic data of combined male and female cheetahs indicated that 36% of cheetahs die from natural causes in the wild (20). We generated simulated curves showing the percentage of deaths from natural causes, as a function of the probability of cheetah death from both natural causes and human interaction (**Figure 3**). The curve for p_{human} = 0.1% crossed the 36% line at $p_{natural}$ = 9%/y, in agreement with the cumulative survival data.

Once the model parameters were optimized, we added the safety corridor to the simulations. The impact of a safety corridor on the cumulative survival is shown in **Figure 4** for a corridor of width 50 km. The survival curve is right-shifted to longer lifespans in the presence of a safety corridor. For example, 50% of cheetahs die in the wild by age 2 y without a safety corridor, while this increases to 5 y with a 50 km corridor.

The mean cheetah lifespan, as a function of the width of the safety corridor and over a range of human population densities, is shown in **Figure 5A**. Without the safety corridor, the mean lifespan of the cheetah was typically < 1 y for the highest population densities. With the cheetah safety corridor, the life expectancy increased dramatically, and was related strongly to both the width of the corridor and to the human population density. For the widest corridor, at 90 km, the cheetah's expected mean lifespan was 5 – 6 y, depending on the human population.

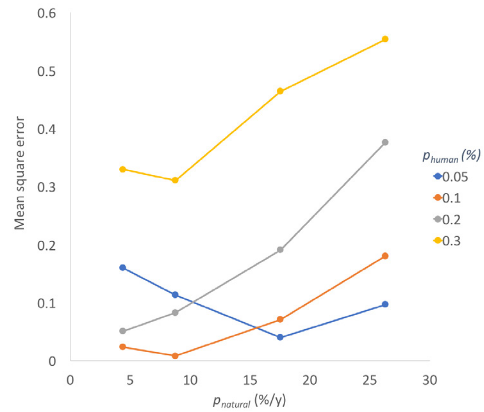

Figure 2. Simulated versus Demographic Lifetime Data. Mean-square error between the simulated cumulative survival curves, and real demographic data from cheetahs in Namibia (20), plotted as a function of the annualized probability of death from natural causes ($p_{natural}$), for a range of values of the probability of death from a single human interaction (p_{human}). The minimum mean-square error gave values of $p_{natural}$ = 9%/y, and p_{human} = 0.1%/interaction, which were used in all subsequent simulations.

The mean roaming distance of the cheetahs is shown in **Figure 5B**. In this graph, we simulated the distance a cheetah will travel in its lifetime, with varying corridor widths and human population densities. The shape of the roaming curve was very similar to the lifetime curve, which was not unexpected, since a cheetah that lived longer would travel further. If the cheetah safety corridor widened, then the cheetah had more space to roam without getting harmed. With no corridor, at the highest human population density, cheetahs roamed a mean distance of only 15 km before death. When the cheetah safety corridor had a width of 90 km, roaming distance increased to 100 km.

The number of positive cheetah-cheetah interactions, expressed as a percentage of the total number of interactions, both positive and negative, is shown in **Figure 6**. At the highest human population densities, in the absence of a safety corridor, there were no positive interactions at all; cheetahs from one group simply could not reach the other group without lethal human-cheetah conflict occurring first. Only when the corridor size exceeded 10 km was there any likelihood of the two groups meeting. Above this figure, the percentage of positive interactions increased significantly and appeared to approach a peak for the largest corridor size. Similar to the correlation between mean lifetime and roaming distance, the cheetah-cheetah interaction data suggests that increasing the size of the corridor beyond about 60 km gave little improvement in positive interactions, with a peak value of approximately 18%.

Finally, we analyzed simulation data to study the impact of targeting the investment of resources on the

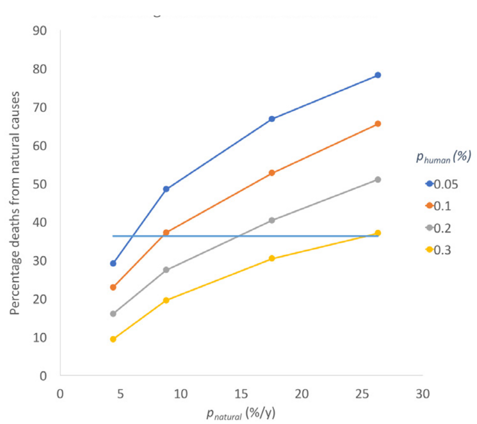

Figure 3. Simulated versus Demographic Data on Cheetah Deaths. Comparison of the percentage of deaths from natural causes in Namibian cheetahs (20), against simulated deaths. Real demographic data of combined male and female cheetahs indicated that 36% of cheetahs die from natural causes in the wild, represented by the horizontal line. Simulated curves showed the percentage of deaths from natural causes, as a function of the probability of cheetah death from both natural causes, $p_{natural}$, and human interaction, p_{human}. Where these curves crossed the 36% line indicated the optimum parameter values.

community inside the cheetah safety corridor, rather than spreading a similar level of investment randomly throughout the entire region (**Figure 7**). This modeled the same number of "safe" farms, where cheetahs would not be killed by farmers, but instead of being concentrated in a safety corridor, they were spread randomly throughout the entire region. For a corridor width of 60 km and a human population density of 0.05 km^{-2}, focused investment inside the safety corridor led to cheetahs living 4 times longer, roaming 3.5 times further, and being involved in 20 times more positive cheetah-cheetah interactions.

Discussion

The concept of a cheetah safety corridor was first suggested in an essay we wrote for CCF in 2016 (11). The idea was to provide a means to reduce human-cheetah conflict and to increase the opportunities for cheetahs with different genetic backgrounds to interact. To validate this hypothesis, this paper has described computer simulations of the effect of safety corridors on cheetah populations and has demonstrated that they have a highly significant, positive impact on cheetah lifespan and genetic diversity. While simulations can only ever approximate reality, the parameters driving the model have been derived from real demographic data of Namibian cheetahs (20).

If the area of the roaming range is assumed to be the square of the linear distance, then, without a safety corridor, the cheetah's range would be 400 – 3600 km^2, depending on human population density. For the average population density in Namibia, this would give a mean roaming area of about 1600 km^2, which compares very favorably with the calculated range of 1713 km^2 derived from camera trap data (21).

The cheetah safety corridor caused a significant reduction in human-cheetah conflict and extended the lives of those cheetahs moving through it. With no safety corridor, the cumulative survival distribution exhibited a rapid drop, which was like that observed in Namibian cheetah populations (20). Introducing a safety corridor had a dramatic impact on the cumulative survival (**Figure 4**) and mean lifetime (**Figure 5A**). The mean lifetime increased from a low of < 1 y in the absence of a corridor to a high of 6 y for the widest corridor simulated. Increasing the corridor width beyond about 60 km appeared to have a diminishing impact, particularly on genetic diversity, which suggested that the width was beginning to exceed the size of the cheetah range. This could have an important impact on the cost of developing cheetah safety corridors, as, above 60 km in width, there would be a diminishing return on the investment. At that point, it might make more sense to build the corridors longer, encompassing a more genetically diverse population of animals, rather than make them any wider.

The cheetah safety corridor had much more of an impact at higher human population densities, which suggests that targeting corridors to those regions with a greater concentration of humans would have the biggest impact. The shape of the lifetime curve indicated that, at the largest corridor widths, the benefit from the corridor was starting to reach a maximum, and further corridor growth would produce a diminishing return.

Probably the most significant effect of the safety corridor was the establishment of safe lanes of passage

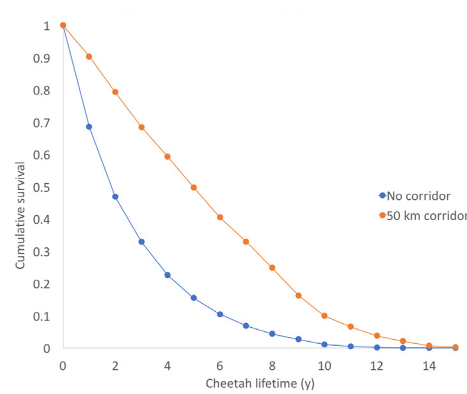

Figure 4. Normalized Cheetah Survival Distribution. Survival curves for a human population density of 0.02 km^{-2}, without a safety corridor, and with a corridor of width 50 km.

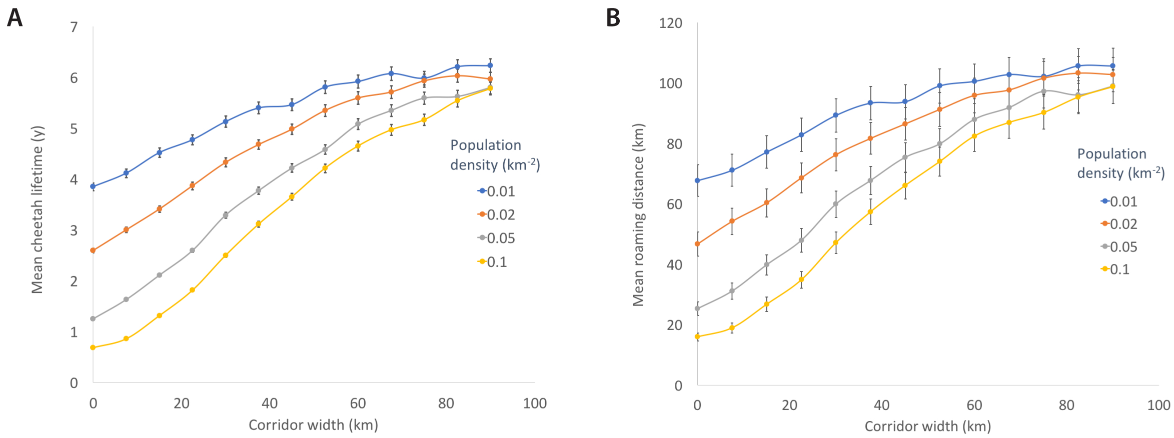

Figure 5. Simulated Cheetah Lifetime and Roaming Distance with a Safety Corridor. (A) Mean cheetah lifetime as a function of safety corridor width, for a range of human population densities. (B) Mean cheetah roaming distance as a function of safety corridor width, for a range of human population densities.

between cheetah groups, allowing cheetahs from one group to interact with animals from the second group without human conflict (**Figure 6**). With no corridor, the two groups of animals, initially separated by 120 km, were unable to reach each other at all before being killed by farmers. As the corridor widened, the percentage of positive interactions, which had the potential to produce more genetically diverse offspring, increased. While these simulations did not track cheetah breeding or the birth of cubs, any increase in the fraction of positive cheetah-cheetah interactions almost certainly would lead to an increase of births with improved genetic mixing.

The type of bushland contained in the cheetah habitat was not simulated, which could have an impact given the widespread occurrence of invasive thorn bush. Due to a number of factors, including over-grazing by cattle farmers, loss of native browsing herbivores, and suppression of natural fires, thorn bush has become a serious problem in countries like Namibia (22). These shrubs grow at high densities and could have an impact on visibility for the cheetah population. Thorn bushes could limit cheetahs' natural hunting methods, which rely on expanses of open savannah, and also block potential routes for cheetah-cheetah interaction (19). Invasive thorn bush could be included in the simulations by adding regions on the map that are impassable for the cheetahs. Organizations like CCF are developing programs to remove thorn bush from cheetah habitat, and convert it into biofuel, with the active involvement and participation of the local population (23).

While deaths from natural causes were included in these simulations, the birth of cubs was not simulated, so the population could never increase. Births would impact the overall population of cheetahs within a given region but would not have any effect on this specific group of animals. The purpose of these simulations was to measure the impact of safety corridors on human-cheetah and cheetah-cheetah interactions within a pre-existing cheetah population. Similarly, coalitions of cheetahs were not modeled, since these typically only occur between small numbers of male cheetahs and would have no impact on genetic diversity.

The cheetah safety corridors described in this paper were assumed to exist in partnership with the local population rather than at their expense. Farmers still live and work inside the safety corridor; it is the responsibility

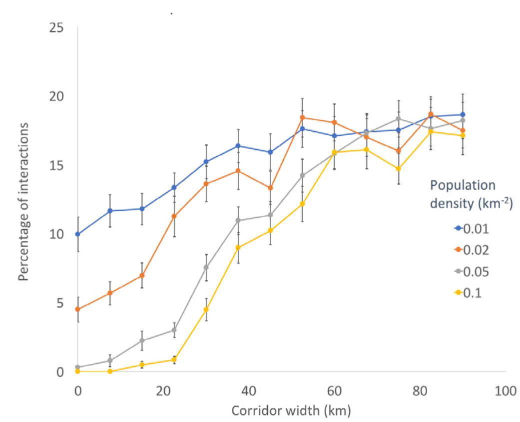

Figure 6. Positive Cheetah-Cheetah Interactions. Expressed as a percentage of the total number of interactions, both positive and negative. A positive interaction was defined as one in which cheetahs from different groups, and, hence, with different genetic backgrounds, interacted. A negative interaction was between cheetahs from the same genetic group.

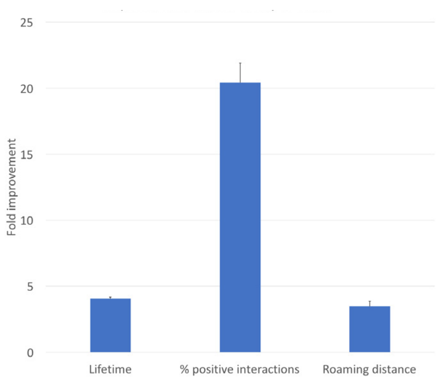

Figure 7. Improvement Due to Corridor. Improvement in cheetah lifetime, roaming range, and positive genetic interactions, as a result of targeted investment in communities within the safety corridor, rather than distributing that investment randomly across the entire simulated human population. The graph shows the fold improvement for each property.

of the corridor designers to ensure the engagement and involvement of the farmers as partners in this venture. This will require financial investment in programs such as livestock guard dogs, in addition to education and outreach to the local community. The question then becomes how that investment should be realized, given that there are limited resources available, and how those resources should be put where they will do the most good. These simulations have demonstrated that a targeted approach, where investment is put primarily into communities inside the safety corridor, and in areas of higher human population density, would have the biggest impact. Indeed, this type of targeted investment could lead to a 20-fold increase in the likelihood of cheetah-cheetah interactions between genetically diverse groups, and a 4-fold improvement in cheetah life span.

While safety corridors have not been used with cheetah populations, they have been applied extensively for other species, such as jaguars and tigers (12-14). Empirical data do not exist to determine at what width corridors lose their functionality. However, corridors less than 10 km in width were identified as "corridors of concern" in dispersing jaguar populations (14). Tiger dispersal corridors in the Terai were modeled, based on dispersal cost contours, and those data suggested that viable corridors would be approximately 50 km in width (12). The Ocala to Osceola corridor in Florida ranges from 10 – 30 km in width and provides a greenway for large predators, such as bears and black panthers (24, 25). While it is difficult to compare corridors in completely different locations with varying habitats and across different species, it is clear that corridors are a valuable method to improve animal survival and dispersal. Our simulations provide an indication of the required corridor size to maintain viable cheetah populations and are consistent with corridors utilized across the world to protect other species. While it is likely that cheetahs still will be killed by humans inside safety corridors, these results represent a "best case scenario," in which corridors are 100% effective.

The maintenance of healthy cheetah populations within countries like Namibia relies on the natural dispersal of cheetah genetics, such that widespread groups of animals are able to intermingle and breed. The proposed cheetah safety corridor promotes this genetic mixing, while minimizing human-cheetah conflict and maximizing the return on investment in the local community.

Methods

Computer simulations of cheetah roaming were written in BASIC for testing, then transferred into C for faster execution. A flowchart describing the simulation steps is shown in **Figure 1**. The parameters used to simulate cheetah and human populations were based on real data, obtained from a variety of sources. A small portion of southern Africa was simulated in two-dimensions, consisting of 21,600 km^2, inside which a number of farms and cheetahs were randomly located (see **Table 1** for a list of simulation parameters). The density of the human population was varied between 0.01 km^{-2} and 0.1 km^{-2}, spanning the likely density in rural Namibia, as reported in demographic data (26). The simulations were performed with a time step of 1 hour, over a two-dimensional matrix of unit cell size 150 m × 150 m, and were run until all cheetahs simulated had died.

Simulations were performed to optimize the main parameters that were used to define the interactions of cheetahs with humans, and deaths from natural causes, by comparing simulated data against real cheetah demographics obtained from one of the largest studies of the cheetah population in Namibia (20). The main parameters that were optimized were the probability that a single human-cheetah interaction would result in the death of a cheetah (p_{human}), and the probability per year that a cheetah would die of natural causes ($p_{natural}$). These probabilities were drawn from a uniform, or rectangular, distribution, and were varied over a range of values (p_{human} = 0.05 – 0.3%; $p_{natural}$ = 4 – 26%), and the cumulative survival distribution and the percentage of cheetahs that died of natural causes were calculated. The survival distribution was compared against real data from Namibian cheetahs (20), and the mean-square error between simulated data and real data was calculated. The minimum of the mean-square error was assumed to provide the optimum values of p_{human} and $p_{natural}$. As a confirmation, the optimized value of p_{human} was used in simulations to derive the percentage of animals which died from natural causes, and the optimum value of $p_{natural}$ was compared against the demographic data.

Once the parameters for the simulations were optimized, a safety corridor was introduced, to determine the impact on cheetah survival. Two groups of cheetahs (N = 20 per group) were simulated, each within an area of 900 km^2, at a population density of 0.02 cheetahs/ km^2, based on GPS tracking and survey data (18, 20, 27), and the two groups were separated by an initial distance of 120 km. These two groups were assumed to come from distinct genetic populations. The groups did not represent any kind of social interaction – cheetahs generally are solitary animals, but do form small social groups, particularly between male siblings (28). However, social groups were not included in the simulations, since all-male groups will have no impact on genetic diversity. Consequently, there was no preferential interaction between cheetahs of the same group – the group structure merely represented geographic location, and assumed that animals in a specific group were derived from a common gene pool.

The cheetahs in the first group were moved randomly, while the second group of cheetahs did not move, and required the first group to migrate over to them to interact. If a cheetah moved within 450 m of another cheetah, that was considered an interaction. If a cheetah from one group met a cheetah from the other group, that was considered a positive interaction, as it may have led to an improvement in genetics. However, if two cheetahs from the same group interacted, that was considered a negative interaction, which may have contributed to poorer genetic diversity. The nature of the interaction was not simulated, and there were no assumptions about mating or the birth of cubs. This was merely an indication that some kind of cheetah-cheetah interaction had occurred, and that interaction may have positive or negative consequences on genetic diversity. The number of positive interactions was recorded as a percentage of the total number of interactions, both positive and negative.

A safety corridor was simulated extending across the entire area, and the width of the corridor was varied between 0 km (baseline condition with no corridor) and 90 km. Outside the safety corridor, it was assumed that any human-cheetah interaction, defined as a cheetah coming within 750 m of a farm, had a certain probability of leading to the death of the cheetah, given by p_{human}. However, inside the safety corridor, this was assumed to be 0%. Death by natural causes, such as age, disease, or interaction with other animals like lions, was simulated, based on a probability of death per year, given by $p_{natural}$.

The impact of targeted investment in communities inside the safety corridor was studied. Simulations were performed to look at cheetah survival, roaming range, and positive cheetah-cheetah interactions, using a representative safety corridor of width 60 km, and human population density of 0.05 km^{-2}. The safety corridor was then removed, but the same fraction of "safe" farms were then simulated again, except this time they were scattered randomly throughout the land area, rather than concentrated inside a corridor. These farmers were assumed to be tolerant of cheetahs, and would not kill a cheetah if it came in close proximity to the farm. The relative difference between cheetah survival with the safety corridor, and without the corridor, but with the same number of "safe" farms, was measured. In this way, the effects of investment in farms and communities inside the safety corridor, compared with similar investment spread throughout the entire region, could be determined.

All graphs were plotted in Excel, and error bars represented ± 1 standard error.

Parameter	Value or range simulated
Area of land	21,600 km^2
Human population density	0.01 – 0.1 km^{-2}
Cheetah population in each group	20
Starting cheetah population density	0.02 km^{-2}
Starting cheetah range	50 km^2/cheetah
Initial separation between cheetah groups	120 km
Cheetah corridor width	0 – 90 km
Human-cheetah interaction range	750 m
Cheetah-cheetah interaction range	450 m
Optimized probability of human killing cheetah outside safety corridor (p_{human})	0.1%/interaction
Probability of human killing cheetah inside safety corridor	0%
Optimized probability of death from natural causes ($p_{natural}$)	9%/y
Number simulation runs per data point	100
Simulation time step	1 h
Grid unit cell size	150 m × 150 m

Table 1. Initial parameter values, or value ranges, used in simulations.

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