Elephant Population: A Linear Model

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Introduction

We use a matrix to model the effects of the darting on the population. Assuming that the age distribution was stable at the inception of darting, we:

- drop the birth rate by a chosen factor to simulate a percentage of the elephant cows being darted;
- manipulate this factor to model the waning effectiveness over time of the contraceptive used, thus obtaining an accurate estimate of how many cows to dart each year;
- assume the cost of darting to be comparable to current elephant contraceptives and compare this to the cost of removal; and
- model the effect of darting on populations drastically reduced following a disaster.

The resulting algorithm is sufficiently simple and fast and could be used by many different elephant parks.

Assuming that culling is not a viable alternative, removal appears to be a more effective solution, since darted elephants will need to be darted multiple times over their lifetime. However, this result does not take into account the increasing cost of removing elephants as humans encroach on their habitat. Also, since the relative number of older, bigger elephants will be greater, tourists revenue will increase. Thus, while removal is less expensive, it may not be the best alternative.

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Elephant Populations

Growth Rates for Elephant Populations

We first find the rate at which elephants can produce female offspring. Because of the assumed parity between males and females, we ignore the males and assume that the male population is equal to the female population. We feel that this is a safe assumption because the population growth is proportional to the number of females, not to the total number of animals.

Given that elephants produce offspring every 3.5 years, this gives us a starting rate of 1 elephant/3.5 years. Because 1.35% of births are twins, the birth rate is 1.0135 elephants/3.5 years. Finally, only half of the births are females, which gives the final birth rate of $\frac{1}{2} \times 1.0135$ female elephants/3.5 years, or an average of 0.1448 females born per cow per year. This is a good approximation because of the large number of elephants in the herd; any random variation tends to cancel itself out.

Given the unusually long gestation period, a further formula is needed to find the average birth rate per female during her first two years of maturity. Because elephants first conceive between the ages of 10 and 12, we assume that half conceive in the first year and the other half conceive in the second. Since the gestation period is not an integral number of years, one-twelfth of the elephants give birth during the ages of 11 to 12 (half of the elephants were able to conceive, one-sixth conceived during the first two months, so that 22 months later one-twelfth gave birth). The remaining five-sixths of the elephants that conceived during age 10 give birth when they are 12. Also, another one-sixth conceive during the first two months of their eleventh year, so they give birth at the end of their twelfth year. This means that $\frac{1}{6} + \frac{1}{2} \times \frac{5}{6} = \frac{7}{12}$ give birth in their eleventh year. From then on, we assume that elephants give birth yearly, always to 0.1448 cows each birth. This noninteger value reflects that we are dealing with averages, not individual cows.

It is a common practice in biological studies to view the age structure as a vector and the survival and birth rates as an appropriate square matrix. For the population vector, the ith element represents the current population that is between $i - 1$ and i years old. Multiplying the matrix by the vector gives an equal-size vector that represents the population in the next year.

The example below shows the age structure of a species that lives to the age of 8 years. Note that there is a 75% survival rate for the first year, after which the survival rate for any one year is β, except for the next to last year of the animal's life, when the survival rate is $\beta/2$. In the second year of the animal's life, it produces an average of 0.097 offspring. In the third through sixth years of the animal's life, it produces an average of 0.290 offspring per year; during years seven and eight, no offspring are produced. Next to the matrix, the age structure vector gives the relative ratios of the animal ages.

The first row consists of the birth rates. The product of this matrix with a population vector represents the passage of one year. Thus, multiplying the

$$A = \begin{bmatrix} 0 & 0 & 0.097 & 0.290 & 0.290 & 0.290 & 0.290 & 0 & 0 \\ .75 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \beta & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \beta & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \beta & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \beta & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \beta & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \beta & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \beta/2 & 0 \end{bmatrix}; \quad \vec{x} = \begin{bmatrix} x_0 \\ x_1 \\ x_2 \\ x_3 \\ x_4 \\ x_5 \\ x_6 \\ x_7 \\ x_8 \end{bmatrix}$$

matrix by a vector representing the population in one year, you get a matrix whose value in the first entry is the sum of all the female elephants, scaled by the number of births they had; this is the number of newborn elephants the following year.

By adding survival rates in the diagonal directly beneath the main diagonal, the entries other than the first become the population of the year before, scaled by this survival rate. All of the other entries are zero, since elephants can age only one year from the year before and can give birth only to newborns.

We assume that the age ratios have reached an equilibrium; this is safe to say, provided that park management did not selectively hunt or relocate elephants based on age. Then the age vector of the next year is proportional to the age vector of the current year. In other words, $A\vec{x} = \lambda\vec{x}$, in which λ and $\vec{x}$ are an *eigenvalue* and an *eigenvector*. In this instance, λ gives the growth rate and $\vec{x}$ gives the age distribution of the current population, which can be scaled appropriately to fit the known population size.

Given a survival rate of elephants for their first year of between 70% and 80%, we set the first-year survival rate at 75%. The average elephant lives to 60, and the growth rate is 5% yearly [Douglas-Hamilton 2000]. This length of life leads to a survival rate is approximately 99% from one year to the next after the first year.

Because elephants do not live to 70, a lower survival rate is required during their last few years—a decrease from 99% at 60 to 0% at 70. Because these are average values, the survival function should be smooth; it should also be level during the first few years and then decrease more rapidly, much like a sine curve. We use

$$S(a) = 0.99 \sin\left(\frac{(a-48)\pi}{22}\right),$$

where S is the survival rate of an elephant a years old. While this curve may be a theoretical construct, any realistic death rate would have to be similar to this curve and thus have a similar effect on the rest of our math.

Age Structure and Growth Rate

We used a mathematical solver to investigate our 70×70 square matrix (which we do not display here); it has $\lambda = 1.043$. This means that the elephant population grows 4.3% each year. From the eigenvector, we found the age distribution of the elephants (**Figure 1**).

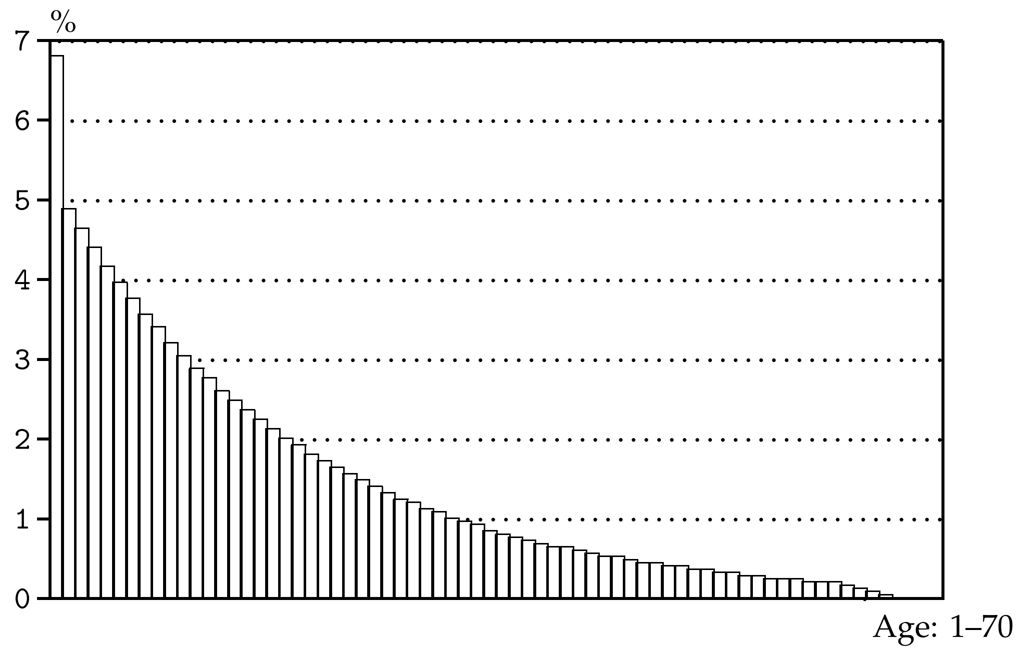

Figure 1. Current elephant age structure.

This growth rate does not agree with the data for removal of elephants from the park in the last two years (20% removed per year). The removal data do not take into account further elephants who may have been culled, so the numbers may have been even higher.

A second source [`www.africalibrary.org` 1999] confirms our estimates of birth and survival rates. Putting maximal values into the matrix, we could not obtain a growth rate of 20%; even with elephants giving birth every 22 months and a death rate of zero, the growth rate was never above 15%. So we decided that the data on removal were erroneous.

Darting Elephants—Now and Tomorrow

How Many and Which Ones?

To maintain a zero-growth population, we need to reduce the birth rate to 27.1% of its current value μ. This is a much more drastic change than the removal of the 600–800 animals that was required over the past 20 years. The main reason is that the birth rates are already low, so a much larger change is needed to affect the population. The survival rates, on the other hand, are high, so a much smaller reduction can affect a larger change.

We assume that the drug is 99% effective immediately upon injection and is still over 90% effective at the end of the first year; by the end of the second year, the drug drops to zero efficacy. A particular percentage of efficacy means that that percentage of the population is still under the effect of the drug and cannot conceive. Like the sine wave for survival rates, the drug efficacy should be concave downward, decreasing more rapidly as the second year ends. However, we feel that the sine wave decreases too rapidly for the first few months and too slowly in the end to model correctly the effects of the drug. We use instead a fourth-order polynomial:

$$E(t) = -.062t^4 + .99,$$

where E is the drug's effectiveness at time t years after injection.

This means that there is an average of 97.8% efficacy over the first year (implying a 2.2% chance of pregnancy) and 60.6% efficacy over the second year. This also means that a cow darted both years would have a 0.9% chance of pregnancy. Denote by γ the percentage of elephants darted; then in two years' time, the percentage darted both years is γ^2, the percentage darted only once is $2\gamma(1-\gamma)$, and the percentage not darted either year is $(1-\gamma)^2$. This means that the percentage able to get pregnant (and hence the factor by which the birth rate drops) is

$$\mu = 0.00883\gamma^2 + (0.3944 + 0.0224)\gamma(1-\gamma) + (1-\gamma)^2,$$

which simplifies to

$$\mu = 0.59203\gamma^2 - 1.5832\gamma + 1. \tag{1}$$

Setting this expression equal to the desired birth rate reduction (to 27.1% of the current value) gives the desired darting rate γ as 59% of all reproductive female elephants per year.

We also need to find the targets for the contraceptive. Should the park staff seek to drug whole herds? a certain percentage of each herd? or every animal in a certain age group? While seeking whole herds would be most cost-effective, this practice would decimate the herd by not allowing it to reproduce. Seeking out specific ages would be too expensive because of the difficulty in determining the ages of specific elephants. Therefore, we decided that we would target a random percentage based on the value of γ.

With the birth rates reduced by μ, the growth rate is 0.0%, as desired, and the stable age structure (achieved some time in the future) is shown in **Figure 2**.

Uncertainty in Derived Data

To find how the uncertainty in our given data affects our estimate, we could propagate the uncertainty through the functions involved. But error propagation through the process of finding the eigenvalue of a 70×70 matrix is tedious,

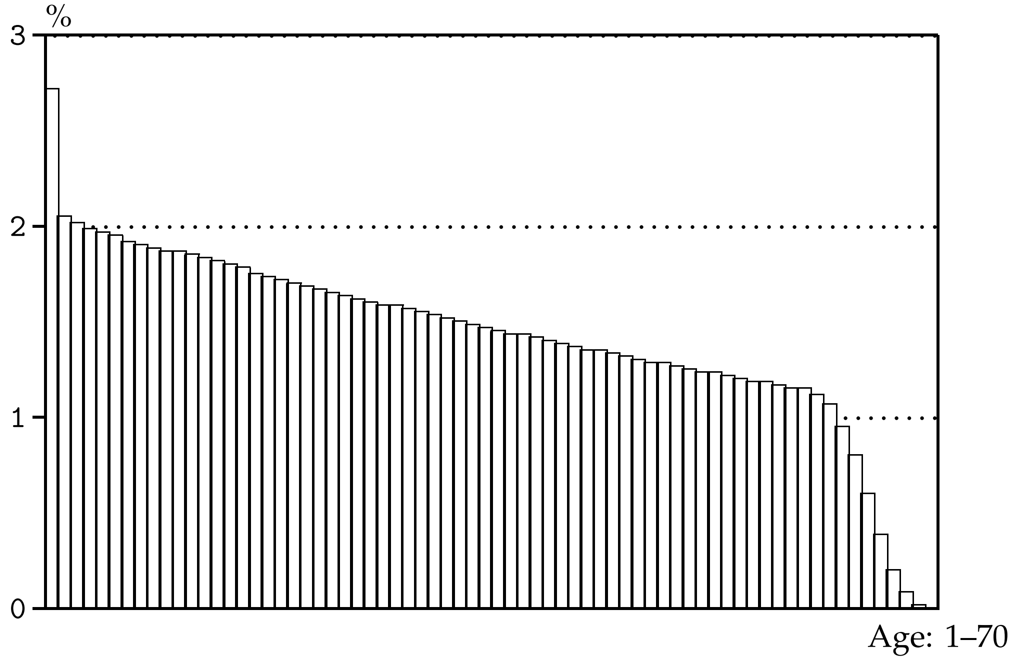

Figure 2. Equilibrium age structure with darting 59%.

so we use another method. We put into the population matrix all of the values that would cause a higher-than-calculated birth rate and use this to find the resulting error in μ.

First, we take the maximal scenario: 100% survival for adults, 80% for juveniles. Then the birth rate must be reduced by 82%, 9% more than the calculated value of 73%.

Taking the minimal scenario, we encounter a problem. We take the survival rate to be 99%, because anything lower causes the percentage growth to become unrealistically small. We solve this by taking the error in the growth rate of 4.29% to be $\pm 1\%$. This allows values as high as 5.29%, which is in agreement with the maximal scenario's pre-darting eigenvalue, and implies a growth rate of 3.29% for the minimal scenario. Assuming the juvenile survival rate drops to 70%, this implies a general survival rate of 0.984. Upon plugging these values into the matrix, we find that we need to reduce the birthrate μ only by 64%, again 9% away from the calculated 73%.

So, our estimates point to an error no larger than $\pm 9\%$.

Next, we want to find the error in how many elephant cows we need to dart. Our final goal is to estimate the error in the costs of darting and removing elephants.

Taking the derivative of both sides of **(1)**, we get:

$$\partial\mu = 0.59203 * 2\gamma * \partial\gamma - 1.5832 * \partial\gamma.$$

Solving for $\partial\gamma$ gives

$$\partial\gamma = \frac{\partial\mu}{0.59203 * 2\gamma - 1.5832}.$$

Taking the calculated value for γ to be 59% yields a value for $\partial\gamma$ of 0.0595, giving us the second step in our process: the uncertainty in how much we need to dart is $0.59 \times 0.0595 = 0.035$; therefore we need to dart $59 \pm 3.5\%$ of the elephants.

Sensitivity and Stability

The rather high uncertainties—3.5% for the percentage to dart and 15% for the cost (derived later)—point to low general stability.

Upon changing individual values in the population matrix, we find that the value for the survival rate is the most important. Changing that rate by only 1%, the growth rate changes by up to 1% and the number we need to dart by 9%. Birth rate and juvenile survival rate are insignificant by comparison, as was the gestation time.

Age Structures of the Future

What will the elephant population look like in 30 years? Assuming that the population was already at equilibrium without darting, we multiply the age vector by the new, adjusted matrix, yielding a vector that represent what the age structure would look like in the next year. Reiterating another 29 times, we find what the age structure would look like in 30 years (**Figure 3**).

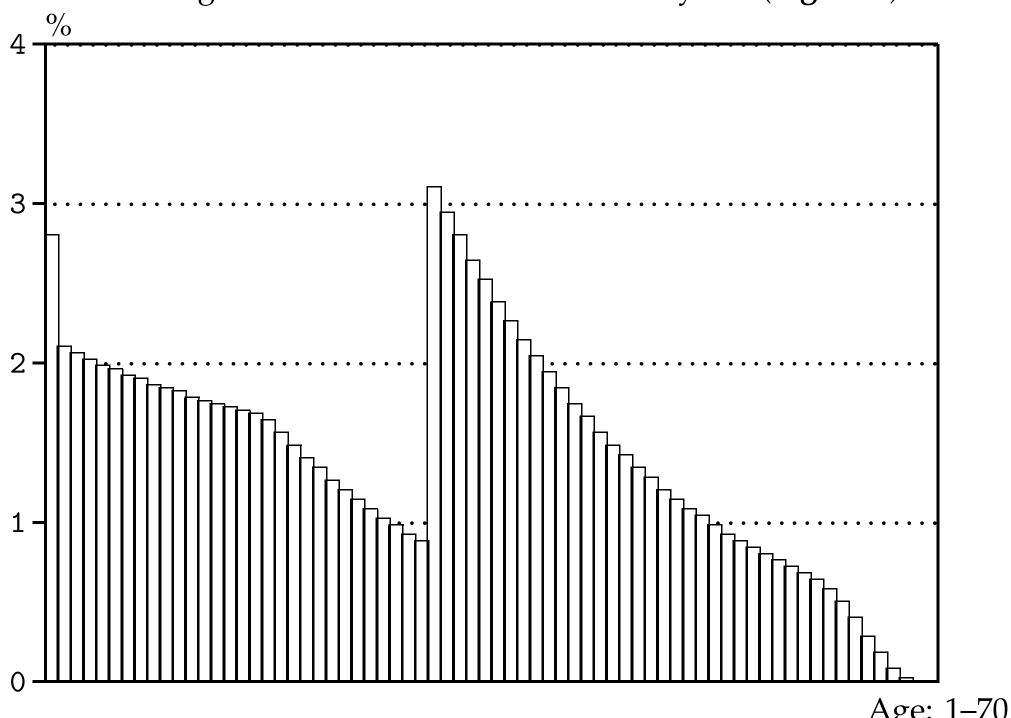

Figure 3. Age structure in 30 years.

The most notable aspect is the sharp peak that occurs at 30 years. At first glance, this may seem troubling because of the unexpected discontinuity; however, this is to be expected, because it represents the sharp drop in births when the contraceptive program began 30–31 years earlier.

Another interesting detail is the spike in the zero-year-old range. This is a result of many of these elephants dying off before they reach age one, as reflected in the value of 0.75 for their survival rate.

Repeating another 30 times allowed us to find the age structure 60 years after the darting process (**Figure 4**).

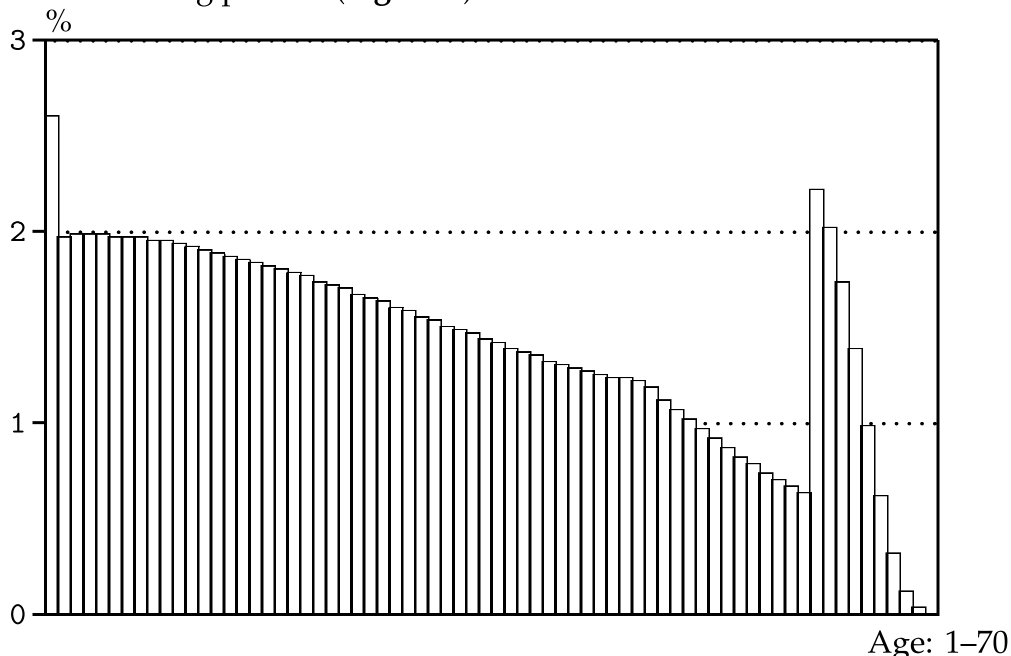

Figure 4. Age structure in 60 years.

The aspect of this situation that is most troubling at first is the large jump in the population structure in the elderly age range. However, this is to be expected once again, as it points to the last year that the elephants were not darted. A more interesting aspect of the graph is the slight increase of the two- and three-year-olds as opposed to one-year-olds. The reason is that the elderly group that we were examining a moment ago contributed to this slight increase; then they were no longer able to contribute to the current one-year-old population because they had reached the age of 61, at which point elephants no longer bear young. The population dip at the one-year mark is a result of this effect.

Given the age structure some number of years after the darting began, we find the difference between that year's expected age structure and the calculated equilibrium age structure. After weighting each age vector to have the same total population (their sum), we find the difference between the two and calculate the length of the difference vector. Plotting this length over time, we were able to find the difference from any age vector to the expected equilibrium value (**Figure 5**).

A large hump occurs at about 60 years. This happens because up to this point the large spike that was prevalent in the age distributions at 30 and 60 years prevents the age vector from getting closer to the equilibrium vector. At about 60 years into the future, however, this large spike begins to die off as the elephants in that age group reach age 60 and begin to leave the population.

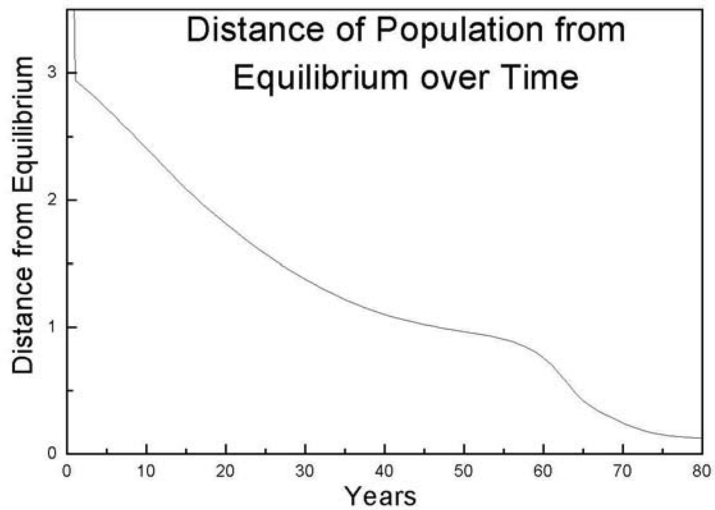

Figure 5. Difference between projected age vector and projected equilibrium value.

Effects of Darting on Tourism

Contraceptive darting is conducive to increased tourism, not simply because it means an end to killing but also because of the changes it creates in the age structure. By shifting the population distribution to favor older elephants and keeping the total population size the same, darting assures a higher number of older elephants in the future. Older elephants are not only bigger, but smarter; a herd led by an experienced elephant is much more stable and tourist-friendly than one led by an inexperienced elephant [Mullins 1997].

Removal of elephants, while cheaper, may not be best when one takes tourism into account. The increased tourism due to bigger, calmer elephants may bring in revenues that far exceed the extra spending. Here a model cannot help us, only time can tell which method is cost-effective.

Relocation vs. Darting

Our model shows that it is possible to rely completely on darting female elephants to control the growth rate and keep a stable population, by darting roughly 59% of the fertile cows yearly.

If we simply remove elephants each year, we are paying a flat cost to remove them from the population forever; removal can be modeled by increasing the death rate of the elephants. When we dart elephants, however, we are not removing them, so the population still increases unless we reduce the birth rate to be as low as the death rate. We also have to re-dart the females every year to keep this birth rate lower, meaning that we are darting more females than the total number of elephants that we would be transporting. Depending on the costs of darting, this could become a more expensive endeavor than simply removing several elephants every year.

It costs \$800 per elephant [Shaw 1999] to move an elephant out of the park, and the cost of darting a single wild horse with the same contraceptive is \$25 [Bama 1998].

How much would it would cost to dart an elephant with this contraceptive? The contraceptive works by stimulating the immune system of the mammal to produce antibodies that bind to the sperm receptor sites of the oocytes [www.wildnetafrica.com]. This means that when the sperm attempt to bind to the eggs of the mammal, there are no places for them to bind to, and hence the sperm do not fertilize the egg. The immune system needs to be triggered by a sufficient concentration of the antigen, so the dosage should depend on the total mass of the animal in question. With this information, and the fact that the average mass of an elephant (3250 kg [Estes n.d.]) is 9.7 times the average mass of a wild horse (335 kg [www.agric.nsw.gov.au]), it should take 9.7 times as much contraceptive to have the same likelihood and strength of a result. At \$25 per horse, the cost for an elephant should be about \$242.53, or after costs of the helicopter fuel and maintenance, about \$250.

We want to determine the total costs for various levels of removal and darting. The difficulty is that the more elephants we remove from the park, the fewer elephants we need to dart, and we cannot easily tell how one changes with the other. Random darting can be simulated by scaling all the birth rates down by a fixed amount and removal by a change in the death rate. Both rates are measures of how the population, and more specifically the age groups, change from one year to the next. If we assume that the rangers remove animals regardless of age, then we can create a fixed value for the removal rate and multiply it times all of the death rates.

The two variables that we can control are the darting ratio γ and the removal number ρ. The proportion not removed in a given year is $\sigma = 1 - \rho/C$, where C is the (varying) total number of fertile cows in the population.

We test two extreme cases, $\rho = 0$ and $\rho = 300$, to see how they affect C. We tested $\rho = 300$ under the assumption that C does not change from year to year. This results in a variation in C of 2% and the same in σ. This tells us that both C and σ can be treated as constants.

We alter our original model population matrix by multiplying all of the survival values (that is, the values in the diagonal directly below the main diagonal) by σ. We choose a value for ρ and get a value for σ from it. We place this in our matrix accordingly, and then test the positive real eigenvalue. If it is greater than one, then we try a value of μ and manipulate it until we achieve $\lambda = 1$. At this point we have a stable equilibrium value. We repeat this process several times for the different values for ρ and recorded.

The last step is to find the costs. We solve for γ and multiply by \$250 per cow to get the cost of darting. We get the cost of removal by multiplying the ρ value by \$800 per cow. The sum of these values is the total cost, shown in **Figure 6**.

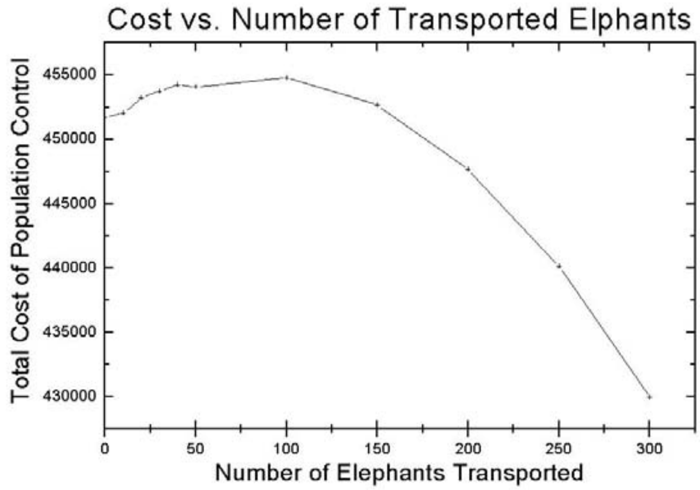

Figure 6. Cost of control as a function of number of elephants removed.

Recovery from Drastic Loss

Our model takes advantage of the fact that for large populations, fluctuations tend to cancel each other out. That is why the birth and death rates are so constant. For example, if 50 cows die due to an epidemic of flaccid trunk disease, out of a population of 100 this is a catastrophic 50% loss! However, if the population is 10,000, this is merely 0.5%. Thus, a variation that is a disaster for a small population is negligible for a larger one.

Therefore, for modeling the effect on the population due to a catastrophic loss, a different model is needed, since the assumption that birth and death rates are constant is no longer valid. This model must be flexible enough to account for differing death rates for a given year.

Since the only thing we need to know is how the darting affects the outcome, we can use marginal analysis. Thus we can start with a loss of 90% and see how much of a death rate it would take for the population to die out.

A certain minimum number of a given species is needed for viability. For this minimum value, we choose 20 elephants, about the size of a single herd.

Applying this analysis to our specific case, if 90% of the 11,000 elephants die off, we have only 1,100 left. To address the effect that darting might have on the situation, we consider two different cases: if the elephants are being darted, and if they are not.

No Darting

For initial population p_0, the population one year later is $p_1 = p_0 + p_0(b-d) = p_0(1+b-d)$, where b is the birth rate and d is the death rate. For the sake of simplicity, we set the birth rate to be the average value of 0.1448, assuming that any change will be illustrated by an appropriate change in the death rate.

Then, doing algebra to turn the recursive function into a general one, we find $p_n = p_0(1 + b - d)^n$.

Solving for d, given $b = 0.1448$, $p_0 = 1{,}100$, $p_n = 20$, and $n = 10$ years, we find (after discarding the unrealistic solution) that for the elephants to be doomed in 10 years after a 90% loss, d would have to be 47% on average! This is an extraordinarily high number, especially when one notices that this was the worst-case scenario.

Darting

For a worst-case scenario, let the first 5 years have a birth rate of 0. After that, the rest of the $n - 5$ years have a normal birth rate, taken again as 0.1448. Thus one gets the general equation $p_n = p_0(1 + b - d)^{n-5}(1 - d)^5$.

Taking $n = 10$ again, $p_n = 20$, and $p_0 = 1{,}100$, we find that the 10-year "doom" value for d becomes 40%.

Conclusion

We conclude that the effect on survival of darting ($d = .40$ vs. $d = .47$) is minimal.

Other Park Populations

The matrix method that we have applied to the herd can be used with other populations, of elephants or nonelephants. Difficulties arise only if the park is too small, when small variations in data might be amplified and the model possibly lose stability and accuracy.

Report to Park Management

While at first glance modeling may seem quite abstract, in reality it is an extremely useful and practical tool. The universe contains patterns that may be studied and used to make predictions. These patterns are everywhere: human beings need to eat and breathe, a thrown ball will eventually return to the ground, ice cubes never form spontaneously in a cup of coffee. It is this underlying order that a model takes advantage of to make predictions about the future.

For all the complexity in elephant populations, there are many patterns to it. Most of these are simply common sense. Take the elephant gestation period, for example; it can be used to make an estimate of the maximum elephant fertility.

Other patterns are the nearly constant survival rate after age 1, the constant birth rate, and negligible migration. They allow us to make predictions about the behavior over the elephant population as a whole.

It is easier to model the behavior of the whole preserve than that of an individual elephant. For larger, more complex systems, patterns become even easier to see and understand, because random variations cancel each other out. There is no such thing as a statistical certainty; but the larger a group, the fewer fluctuations due to random chance, and the surer one can be.

We took advantage of these facts in making our model of the elephant populations in your park. Random chance effects tend to cancel each other out in so large a population. Thus, we are able to use a uniform and constant value for the birth and death rates of the elephants.

Given these rates, we modeled the changes in the population over time by putting them into a matrix. This matrix, when multiplied with a list of elephant populations for every age in a given year, returns a list of how many elephants would be that age the next year.

We assume that the age distribution of the elephants has become constant over time. In essence, this says that as elephants get older, younger elephants also get older and replace them. Some of the younger ones die before they can get older, however, so the population numbers remain the same.

Without culling, removal, or darting, the population would tend to grow but the proportion of each age would remain the same.

Such details as twins, gestation, and gradually increasing death rates can also be accounted for. These details can be simulated by slightly altering a few of the numbers in the matrix.

Once we can model the population, simulating darting becomes simple. We make the rather safe assumption that darting the elephants drops the birth rate to a uniform degree. We find that the growth rate of the elephants needs to be reduced to 27% of the natural reproductive rate. To accomplish all of the reduction through darting, 59% of females would need to be darted each year.

But the darting will also affect the age structure of the elephants, and our model easily simulates this over any number of years.

However, for smaller systems, our approximations of constant, average values are no longer valid. This is not to say that we cannot model smaller systems, only that the larger the system, the more effective a model can be.

We modeled a much smaller elephant population subjected to catastrophic loss. Take the worst disaster you can think of—say 90% of the elephants dying—and then say that somehow the death rate experiences a continual "random fluctuation" upward constantly, for 10 years. Even with darting it would take a constant death rate of 40% per year to kill off the elephants. Hence, use of contraceptive darts would have no effect upon whether or not the unlikely event of a sudden loss would cause an extinction of the park's elephant population.

The data for the last two years are startling: 20% of the elephants were removed each year! This seems to imply that the population is growing at 20% per year. However, such a rate is unrealistic.

Much of our confidence in our model comes from testable predictions that it makes. When we plot the age structure 30 years after darting, we see a graph that gradually dies down until it reaches the number of 30-year-olds, where there is a sudden spike, corresponding to elephants born before darting. Furthermore, the graph of the 60-year-olds shows not only this spike but another bump about 10 years later, reflecting the formerly larger number of elephants having given birth to a larger number of calves. These effects are predicted by the model without any manipulation by us.

With common sense, a little data, and some mathematics, an excellent predictive model can be made. Our model should be a useful tool in your making well-informed decisions.

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