

Modeling and Control of the Peregrine Falcon Population

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Abstract

Peregrine falcons were recently removed from the endangered species list and there is a desire to harvest these birds for sport. The US Fish and Wildlife Service currently allows minimal harvesting in parts of the country. However, the question is how many can be extracted from the population before the future population will go into decline. My research utilizes a population projection matrix model that takes into account uncertainties in the population data while it analyzes the effect of harvesting on the population. I examine the future of the falcon population in order to help determine an optimal amount of harvesting that still ensures that the population will continue to remain stable or grow by a given amount. By successfully modeling this population, this simulation model can then be altered to describe other wildlife populations.

1 Introduction

In 1970, peregrine falcons joined the endangered species list [3] due to DDT, habitat loss, hunting, and other factors [4]. In addition to the ban on DDT, the implementation of fostering, hacking (young falcons are slowly reintroduced to the wild in stages), and release of over 6000 peregrines [3] helped populations recover[13].

DDT was used as an insecticide within the United States. At first there seemed to be no harmful effects from this substance. One of the earliest uses for DDT was during wartime when it

was spread over the soldiers to kill lice. Since so many people came into contact with it with very few harmful effects it was believed to be a safe chemical. However, DDT in powder form is not harmful but when combined with oil it exhibits toxic effects. If the chemical is swallowed then it will be stored within the body. The level of this chemical continues to accumulate and eventually side effects begin to occur. The food chain prolongs the life of this substance. If a predator eats something that had DDT it also begins to store the substance. DDT is also passed to offsprings. Thus the lifetime of this substance has continued despite the United States banning the use of DDT in the 1970s. While the abundance of DDT has gone down, other countries still allow the use of this substance so migrating animals still bring this chemical to the United States. [11]

The ban of DDT and other environmental efforts has positively affected the falcon population. With over 2000 breeding pairs in the United States, the population is again increasing, and falcons were removed from the endangered species list in 1999. There is renewed interest in harvesting peregrine falcons for falconry, and in May 2001 the US Fish and Wildlife Service allowed states west of the 100 longitude line (from North Dakota through Texas) to allow harvesting of up to 5% of their state's population [20].

In July 2005 there was controversy as to the number of falcons currently being harvested in Oregon. The Audubon Societies of Portland and Denver, the Center for Biological Diversity, and the New Mexico Audubon Council questioned the decision of the US Fish and Wildlife Service allowing up to 5% of the peregrine falcon population to be harvested. The plaintiffs claimed the US Fish and Wildlife Service's calculations were not valid, stating the way they considered the margin of error misrepresented the data. The concerns were dismissed and 5% of the population may still be harvested [8]. This study examines the percentage of birds that may be harvested while maintaining a steady or growing population.

2 Lifestyle of the Peregrine Falcon

The Peregrine falcon is adept for hunting with a strong, sharp beak, keen eyes, and sharp claws. The typical prey for falcons consists of pigeons, blackbirds, ducks, and pheasants. The falcon attacks its prey within the air. It stoops down from above and administers a blow from its claws to the smaller bird. The falcon can fly over 200 miles an hour during this stoop. Generally this blow is strong enough to kill the prey on contact and at the very least the bird is stunned. The falcon circles back around and catches the prey as it falls through the air. If the prey is still alive the falcon breaks the smaller bird's neck by striking the prey with its powerful beak. However, falcons are at the top of the food chain generally feeding on pigeons, gulls, ducks, herons, and small mammals or reptiles.[6] Due to the abundance of these lower trophic level species, prey is not a limiting factor for the Peregrine falcon population.

Falcons generally inhabit in mountainous country or near sea cliffs. They nest on ledges or in holes on a cliff's face. Habitat actually serves as a limiting factor for the peregrine falcon population [2]. The abundance of nesting sites affects whether two year old birds breed. This environmental component must be taken into consideration for the model of the falcon population since it serves as a limiting factor.

3 Model

My study is a continuation of work done in collaboration with Alyson Deines and Richard Ryan. The model that we implemented is described below.

The population is composed of three age components - birds less than one year old, birds one year old and less than two years old, and birds two years old or older. We refer to these as x_1 , x_2

and x_3 , respectively, and the population vector is

$$\vec{x} = \begin{bmatrix} x_1 \\ x_2 \\ x_3 \end{bmatrix}.$$

The population vector during year n is denoted \vec{x}^n , and $\{\vec{x}^n\}_{n=0}^{\infty}$ satisfies the discrete time equation

$$\vec{x}^{n+1} = A \vec{x}^n, \tag{1}$$

where A is the population projection matrix. The population projection matrix we use is a modification of the post-breeding model derived by Craig et al [13]. We conferred with Gary White, one of the author of *Survival, Recruitment, and Rate of Population Change of the Peregrine Falcon Population in Colorado*, [13], and he indicated that the matrix as published in this article has a typographical error in the matrix that represents the population model. Below, that error is corrected in the matrix in (2). The significant data include: S_0 , the survivorship from birth to age one; S_1 , the survivorship from age one to age two; S_2 , the yearly survivorship for all older birds. The fecundity F is assumed to be the same for all breeding pairs. Birds under one year old are assumed to not breed. The second age class exhibits a lower number of breeding pairs. We quantify this by letting B represent the percentage of birds in the second age class that breed. This varies based on circumstances. R denotes the percentage of birds that are female. In terms of these parameters, the population projection matrix is

$$A = \begin{pmatrix} 0 & FRBS_1 & FRS_2 \\ S_0 & 0 & 0 \\ 0 & S_1 & S_2 \end{pmatrix}. \tag{2}$$

We use values estimated from the peregrine falcons in Colorado, USA (see [13]) given in Table 1.

Variable	Value
S_0	0.544
S_1	0.670
S_2	0.800
F	1.660
R	0.500
B	0

Table 1: The nominal data from the Colorado study, [13]

We need to incorporate harvesting into the population projection matrix. We introduce the variable h , which represents the percentage of nestlings harvested, so the term $(1 - h)$, denoting the percentage of nestlings remaining in the wild population, is included in the matrix A by multiplying this term by the fecundities [12]. The amount of harvesting is assumed to be the same in both age classes since for many birds the age cannot be determined.

$$A_h = \begin{pmatrix} 0 & (1-h)FRBS_1 & (1-h)FRS_2 \\ S_0 & 0 & 0 \\ 0 & S_1 & S_2 \end{pmatrix} \quad (3)$$

Harvesting can effect the nesting habits of the parents and the survivorship of the remaining nestlings. Peregrine falcons are known to re-nest (lay another clutch) if a clutch is lost early. However, by US Fish and Wildlife Service regulations, nestlings may not be harvested prior to 10 days of age [20]; thus removing nestlings will not cause the parents to re-nest. We were also concerned that by removing a nestling the survivorship of the remaining nestlings would increase due to less work for the parents. However, removing nestlings only minimally affects the survivorship of the remaining young [10], thus, in modeling the worst case we may ignore this.[14]

4 Sensitivity and Error

Deines et al present a systematic method to consider the uncertainty in the peregrine data while determining what percentage of falcons may be removed from the population without damaging population growth. This study utilized robustness, developed by Hodgson et al [17]. Robustness allows us to look at the growth rate while considering how much tolerance the system has to changes in individual or multiple values, while maintaining desired characteristics.

A robustness and sensitivity analysis done by Deines et al determined that the lower right entry of the matrix, the term S_2 in the position $A_{3,3}$, was the most sensitive to the outcome of the leading eigenvalue. The original values for the variables and the Sensitivities in Table 2 were taken from Craig et al[13].

Symbol	Meaning	Estimate	Sensitivity	Elasticity
F	Nestlings fledged per pair	1.66	0.134	0.222
R	Proportion of female nestling	0.5	0.445	0.223
S_0	Survival of nestling to age 1	0.0544	0.409	0.223
S_1	Survival of 1 year old birds	0.670	0.332	0.222
S_2	Survival of bird ≥ 2	0.800	0.569	0.165
B	Proportion of 2 year old birds taht breed	1	0.058	

Table 2: The estimates and sensitivities are from [13]. The lower bound elasticities were determined by setting the leading eigenvalues to 1 which leaves elasticity to be determined by multiplying the estimate value of the variable times the sensitivity of each variable.

This table suggests that the S_2 term is the most sensitive. Deines et al created a visual representation that demonstrates the intensity of the differences in sensitivity of the variables in Figure 1.

I continued my investigation at Wittenberg by examining the model further in order to determine if an altered model would be more accurate. The S_2 term represents all birds older than two years old. The average lifespan of a bird in the wild is eight years [5]. Since this term denotes a large portion of the population, the expansion of the model to more than three age classes offered a possibility of decreasing the uncertainty within the matrix and creating a more accurate model.

Figure 1: The growth rate of the population vs. the perturbation of the variables.

The matrix was expanded to eight age classes. The assumption was made that the survivorship and the fecundity of each of these age classes remained the same as the S_2 age class. However, modeling the population distribution for eight age classes produced the same model as for three age classes. In order to make certain that this alteration to the model did not create the desired effects, some of the parameters were varied. The B term was manipulated from 0 to 1 and the S_2 (in the original model) and the S_2 - S_8 terms (in the altered model) from 0.3 to 0.8. These changes were implemented both individually and simultaneously. The two models still remained identical. Expanding the model at the most sensitive position did not change the uncertainty of the population distribution.

5 Control of the Falcon Population

Various methods of harvesting were implemented in order to determine a good method that allows the population to increase but also incorporates harvesting. Since the falcon population is

believed to be around 2000 breeding pairs my initial population vector is below.

$$\vec{x}^0 = \begin{bmatrix} 500 \\ 500 \\ 3000 \end{bmatrix}$$

A control mechanism was utilized in order to achieve the goal of determining the largest number of birds that could be harvested at the end of fifty years while still causing the population to be growing. The projection was made for fifty years because this amount of time provides a good indication of the behaviors of the population projection. It is long enough that one will not be thrown off by initial behavior but it also is not too long which is a reminder to take into consideration that ecological systems can change and the population must be continuously examined.

The work done with Deines et al examined the largest percentage of the population that could be harvested yearly without causing the population to go in to decline. This method determined that 17.41% of the falcon population could be harvested and the population would still remain steady. After fifty years 4760 falcons will be in the wild population. The birds that were harvested for the sport of falconry that are still alive will sum to 996. The survivorship of the birds was assumed to remain the same when they are in captivity even though their lifespan most likely will be lengthened.

Another method of harvesting examined was harvesting in periodic years. Figures 2, 3, 4 demonstrate harvesting once every year, once every three years, and once every five years. Each of these graphs demonstrate the projection of the population over 50 years with harvesting 0%, 5%, and 17.41%. As demonstrated by these graphs the population drastically increases if harvesting is done periodically. Figure 3 and Figure 4 have jagged curves because in the year harvesting is done the population size experiences a decline but then quickly recovers in the following years.

Since the population recently came off of the endangered species list, building up the population a little before harvesting to a large extent was desirable. The final model incorporates the idea of

Figure 2: Population projection if harvesting is done every year. The bottom line represents the population projection if 17.41% of the population is harvested every year. The middle line demonstrates the growth of the population if 5% of the population is harvested every year. The top line shows the population if 0% is harvested every year.

increased iterated harvesting. In order to determine the amount of harvesting in a specific period the following was defined.

$$harvest = maxharvest * \frac{currentperiod}{maxperiod} \quad (4)$$

The first step to using this method was to determine the largest *maxharvest* that would not put the population in to decline after 50 years. This percentage was determined to be 19% by examining when the population will begin to decrease at exactly the fiftieth year. By setting *maxharvest* = .19 in (4) the maximum harvest percentage from the population was established to be 18.62%. Using this new percentage, after fifty years 1012 birds that had been harvested would still be alive and the wild population would include 10454. This method appears to fulfil the goals of my model the best.

Then the population was modeled out 100 years with the first 50 years harvesting with the increased iterated harvesting as described above, then the next fifty harvesting a steady 18.62%. After 100 years there would be 10715 birds in the wild populations.

Figure 3: Population projection if harvesting is done every three years. The bottom line represents the population projection if 17.41% of the population is harvested every three years. The middle line demonstrates the growth of the population if 5% of the population is harvested every three years. The top line shows the population if 0% is harvested.

6 Pre-breeding vs. Post-breeding Model

The harvesting of some populations may not be restricted to only young of that species as it is in the falcon model. Thus in order to transition the falcon model into a model that can be used for other species the pre-breeding model was converted into a similar post-breeding model. The pre-breeding falcon model is defined as

$$A = \begin{pmatrix} 0 & FRBS_1 & FRS_2 \\ S_0 & 0 & 0 \\ 0 & S_1 & S_2 \end{pmatrix}. \quad (5)$$

Since the birds will be counted immediately after birth we make the assumption that the first age class of the post-breeding model has survivorship of 1 because the birds are counted a few days after birth. Other than for the first age class the birds are counted a few days after they would have been in the pre-breeding model one can assume that the survivorships of the subsequent age classes remain the same. However, this model must be converted to a four age class model because

Figure 4: Population projection if harvesting is done every five years. The bottom line represents the population projection if 17.41% of the population is harvested every five years. The middle line demonstrates the growth of the population if 5% of the population is harvested every five years. The top line shows the population if 0% is harvested.

with the addition of the initial survivorship the now fourth age class represents the subsequent age classes of the species in question. The fecundities also experience a shift. The first two age classes do not breed because these age classes represent the newborns and the birds that are one year old, which was previously stated do not breed. The transition between a pre and post breeding model can be represented by the map (6). This mapping suggests that the correlation between the pre and post breeding models is be unique and the relationship between the models is well-defined.

$$\phi \begin{pmatrix} 0 & a & b \\ c & 0 & 0 \\ 0 & d & e \end{pmatrix} = \begin{pmatrix} 0 & 0 & a & b \\ 1 & 0 & 0 & 0 \\ 0 & c & 0 & 0 \\ 0 & 0 & d & e \end{pmatrix}. \quad (6)$$

The post-breeding falcon model is

$$\begin{pmatrix} 0 & 0 & FRBS_1 & FRS_2 \\ 1 & 0 & 0 & 0 \\ 0 & S_0 & 0 & 0 \\ 0 & 0 & S_1 & S_2 \end{pmatrix}.$$

These models are very similar but not exactly equivalent. Depending on when the population is counted the population is a little different. In order to exhibit the closeness of these models, the population distribution over thirty years was examined, this time period gives sufficient indication of the similarity of the population projections. Two initial population vectors, one with three age classes and one with four, were created. Each of these vectors contains 720 birds however the distributions are different since there are different numbers of age classes. Due to this inconsistency in the distribution the population projections vary a little, however they demonstrate similar population sizes.

Figure 5: Population Distribution over thirty years. * represents the pre-breeding model and o represents the post-breeding model.

This connection between a pre and post-breeding model is the first necessary step to expand this harvesting model to other populations.

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