Female Peregrine Falcon at Grays Harbor, Washington, scanning prey on the beach. Photo by Diane Moore

Determining Resilience of Recovering North American Peregrine Falcons (*Falco peregrinus*) in the Pacific Northwest

Esther Guo, Chris Lindsey, Ryan Harer

UNR College of Agriculture, Biotechnology, and Natural Resources

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Introduction

North American peregrine falcons (*Falco peregrinus*) have suffered from the widespread use of deadly pesticides such as DDT in the 1950s-1970s (Barnes, 2011). This severely endangered most populations here in North America as their survival was greatly reduced by the harmful effects of DDT that interfered with female fertility, thinned eggshells, and poisoned their food sources. Their numbers were so low that they almost reached extinction in the 1970s. By 1976 in Washington, the main study area for this PVA, there were zero peregrines found occupying the 14 historical nest sites there (USFWS, 1999). However, when measures were taken to ban the use of DDT and reestablish peregrine populations, their numbers slowly rose again. Surveys in Washington found 17-45 known breeding pairs between 1991-1998 (USFWS, 1999). As peregrines rebounded from that devastating period of population decline, they were able to reach a stable population status that allowed them to be delisted from the Endangered Species List under the Endangered Species Act in 1999 (Barnes, 2011).

The successful conservation story of these resilient raptors should not end there, and it is important to continue monitoring how current populations of peregrine falcons are sustaining in the wild. In general, we are interested in projecting how peregrine falcons will grow or stabilize in the foreseeable future. We are particularly interested in simulating how another potential catastrophe similar to DDT might affect these once vulnerable populations, and if they are viable enough at their current size to overcome it. We define catastrophe as anything from inbreeding depression or genetic drift (stochastic threats affecting small populations), to habitat loss and pollution (deterministic threats affecting larger populations). We hypothesize that based on their current conservation status, peregrine falcon populations have grown past the stage of being vulnerable to stochastic threats and instead are at a size where they are more vulnerable to deterministic threats. We attempt to answer the question, which deterministic threat are recovering peregrine falcon populations in the Pacific Northwest most vulnerable to, habitat loss or pollution; and how will populations recover in the next few decades with and without these threats? We predict that given their intense history with DDT, pollution has the largest impact on the population compared to other deterministic threats like habitat loss. As for the second part of our research question, we predict that with or without these threats, peregrine falcon populations will continue recovering in a positive direction and are not likely to go extinct as they likely have surpassed a minimum viable population threshold.

Methods

In order to determine the current state of peregrine falcon populations we initially chose a population on the Washington coast that has been extensively studied for the past 20+ years by Varland et al. (2020). This population will serve as a representative population of a majority of the populations found in the Pacific Northwest. The peregrine falcons surveyed in this study area reside on three separate beaches (Figure 1). Varland et al. (2020) separates the population into three age classes: hatchlings (<1 y/o), juveniles (1-2 y/o), and adults (>2 y/o). At the time that they banded each individual there were 109 hatchlings, 85 juveniles, and 32 adults. This gave us a total population of 226 peregrine falcons with 148 being female and 78 being male (Varland et al., 2020). Due to the fact that females drive reproduction we

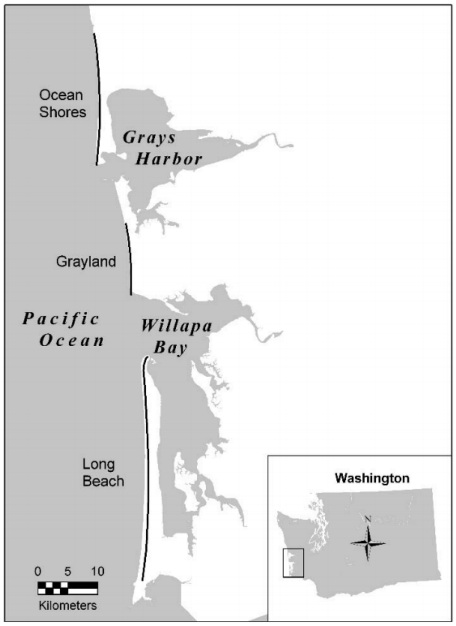

Figure 1. Location of three study area beaches in southwestern Washington (Ocean Shores, Grayland, and Long Beach) where we captured and banded Peregrine Falcons between 1995 and Feb 2018. Survey transects are indicated by black lines.

used the proportion of females in the population 148/226 to get 0.65. We then multiplied that by the number of individuals in each age class so each age class actually has 71 hatchlings, 56 juveniles, and 21 adults all of which are female. All three age classes were set up in Insight Maker with the appropriate number of individuals in each age class and were shown to transition from hatchling to juvenile to adult. All three age classes were added together to determine how the entire population was changing year over year.

The next most important thing for this model was the incorporation of survival and birth rates. The survival rates we found also come from Varland et al. (2020) and look as such; hatchling survival = 0.424, juvenile survival = 0.663, and adult survival = 0.738. Our model reflected these values and assumed that individuals who did not survive were going to die. Those who did survive would move on to the next age class with adults remaining in the adult age class if they survived. To incorporate some level of uncertainty on this parameter we used a random binomial distribution.

The next parameter we included was the birth rate which only applies to juveniles and adults. The mean birth rate of juveniles was 1.11 with a standard deviation of 0.11, which came from Wakamiya (2009). We halved the mean birth rate to 0.55 to account for our female only model. This mean birth rate was multiplied by the survival rate of juveniles (0.663) to account for a one year time step in fecundity. The mean birth rate of adults was 3.7 with a standard deviation of 0.7, which came from Ratcliffe 1993 and Palmer 1988. This mean birth rate was also halved to account for our female only model so our mean adult birth rate was 1.85. The mean birth rate was multiplied by the adult survival value (0.738) to account for a one year time step in fecundity. To incorporate uncertainty on these parameters we used a random normal distribution.

Density dependence was implemented on the births flow and assumes that carrying capacity is determined based on the number of available nest sites instead of a number of total individuals. This is because the number of nest sites would ultimately limit how many breeding individuals could occupy a given landscape. As of 2016, there have been 181 nesting sites documented throughout the state of Washington, shown in Figure 2 (Vekasy et al., 2016). To make this number more relevant to the coastal populations studied in Varland et al. (2020), we estimate that approximately 80% of the known sites (n=181) from Figure 2 are located on the western half of the state and could be occupied by populations surveyed on the Pacific coast, thereby making our carrying capacity 144.8. The density dependence equation takes into account the number of female juveniles and adults, or breeding individuals, and whether or not this number exceeds the number of nest sites available. The equation assumes that if the number of breeding individuals exceeds the number of available nest sites, then only the adults can breed because of reasons such as having already established territories or returning to sites they previously nested at (site fidelity) whereas juveniles may not have these advantages. We further assume that not all adults will be able to breed when carrying capacity is exceeded, and that only half the breeding adults can successfully breed. This results in population regulation in the model, where the population decreases when the population is above carrying capacity. On the other hand, if there are fewer breeding individuals than nest sites, then we assume that both juveniles and adults can breed at their normal fecundity rates and population would increase.

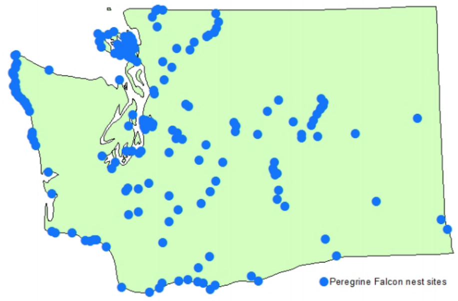

Figure 2. Distribution of peregrine falcon nesting territories in Washington, 2016.

Our initial simulation was run with all the parameters from above to give us a baseline to compare to the effects of habitat loss as well as extensive pollution on the population. All of our simulations were run for 50 years because when there is less than 5% chance of extinction over 50 years it can be considered a viable population. The second simulation was to determine the effects of habitat loss which would reduce the number of available nest sites. We represented this in Insight Maker as a 50% reduction in carrying capacity. To fully understand how peregrine falcons react to habitat conditions we ran a third simulation where we doubled carrying capacity, or doubled available nesting sites, to see how the population would change. Our fourth simulation was used to understand how this current population size would react to a pollutant similar to DDT which devastated peregrine falcon populations in the past. This was done by reducing hatchling survival from 0.424 to 0.212 to represent the low survival that would have been seen as a result of DDT causing their eggshells to be much thinner. Adult fecundity was also reduced to 1 which was a low seen during the height of DDT devastating peregrine falcons (Ratcliffe, 1993).

Results

The results produced from entering all of the initial parameters before the scenario tests demonstrated that the peregrine falcon population along the Pacific coast of Washington are indeed growing at a steady rate as we expected. In individual runs of the model, all three age classes were projected to increase over the next 50 years, making the total population growing as well. From running 100 simulations of our model for the total abundance (all age classes combined), we found that the current population exhibits logistic growth under conditions of our model with density dependence, environmental stochasticity, and demographic stochasticity (Figure 3). The median total abundance over 50 years stabilizes around 250 individuals, with 95% of the 100 simulations falling between 150 and 400 individuals by the end of the 50 years

(Figure 3). Total abundance for 95% of the runs never fell below 1 in all simulations across all years, therefore this current population meets the criteria of being a viable population, where less than 5% of the population is at risk of extinction.

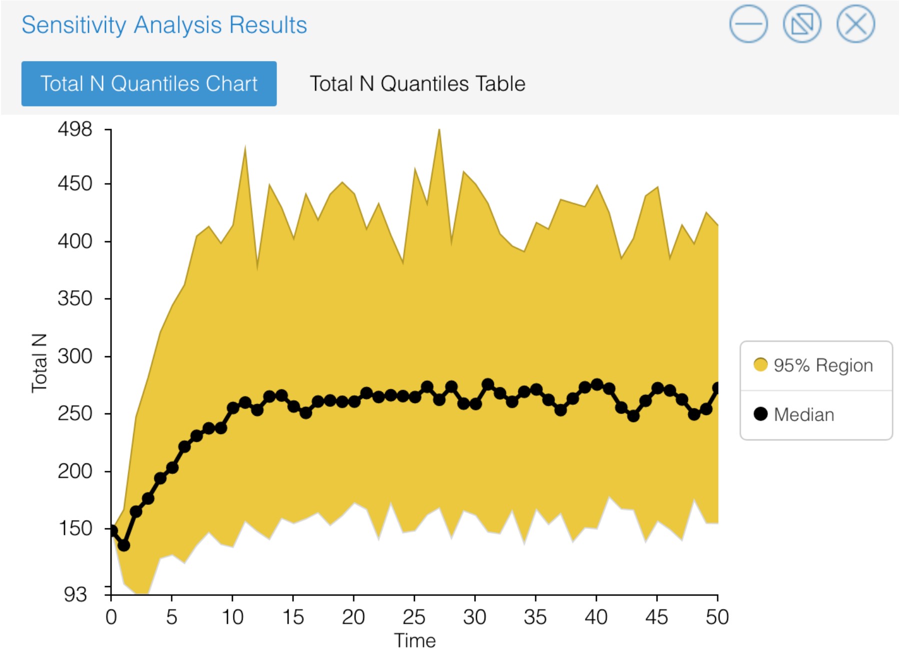

Figure 3. Projection of total female peregrine falcons *(Falco peregrinus)* on the Washington coast over 50 years, produced by running 100 simulations in a stochastic population simulation model. The shaded yellow region represents 95% of the simulations. The dotted black line represents the median total abundances out of all simulations. The trend demonstrates logistic growth, where the population (n=148) decreases then increases at the start because it is slightly above carrying capacity (K=144.8), and eventually levels out around 250 individuals due to density dependence.

When we simulated a scenario that would represent habitat loss by cutting the carrying capacity, or nesting site availability, in half, the total abundance stabilized at a lower equilibrium over 50 years compared to the first scenario with the absence of threats (Figure 4). By the end of year 50, the median total abundance declined slightly from its initial abundance of 148 to about 138 individuals, which is where the population abundance tended to level off around starting from year 4 (Figure 4). There is large variability accounted for by the 95% quantile upper and lower bounds, however, with the possibility of the population growing to as high as 225 individuals or dropping to 82 individuals in 50 years. The median trend line suggests that this population may not be particularly vulnerable to habitat loss because it does not react in a particularly strong, negative way when half of the available nest sites are reduced and can still stabilize at a decent population size relatively close to their initial abundance. The lower bound of the 95% region suggests that habitat loss could potentially cause some population decline, but it would not cause risk of extinction within 50 years because the abundance stays well above 1 for all 50 years and is therefore viable. The upper bound suggests that there may even be chances of population growth under conditions where 50% of habitat is lost.

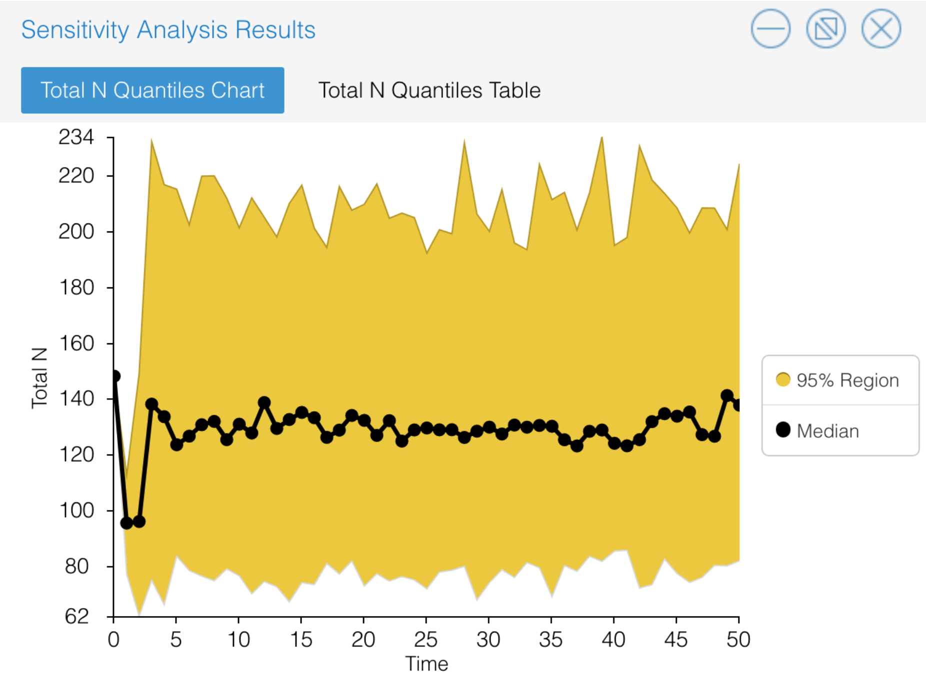

Figure 4. Projection of total female peregrine falcons *(Falco peregrinus)* on the Washington coast over 50 years under habitat loss conditions. Produced by running 100 simulations in a stochastic population simulation model. The shaded yellow region represents 95% of the simulations. About half the region represents possible population decline. Habitat loss appears to have minimal effects on median total abundance, as there is only a slight downward shift before reaching a relatively stable abundance near the initial abundance.

To check the impact of habitat availability, not just the loss of it, we also doubled the carrying capacity to see what increasing habitat, or nest sites, might do for the population. To no surprise, the population exhibited increased logistic growth under this potential management scenario (Figure 5). The median total abundance stabilizes at a higher equilibrium of around 500 individuals starting from year 19 to the end of the 50 year simulation (Figure 5). This median total abundance is precisely double the median total abundance of the population seen in Figure 3, where threats were absent. The results from this presents an interesting relationship between habitat availability and median total abundance that the habitat loss result did not show. In this scenario, doubling the number of nest sites effectively doubles the median total abundance. Whereas, in the habitat loss scenario, cutting the number of nest sites in half did not cut the median total abundance in half, and instead only slightly lowered it below its initial abundance. This tells us that habitat loss may have minimal impacts on the population since halving habitat does not halve the population size, while doubling habitat doubles the population size.

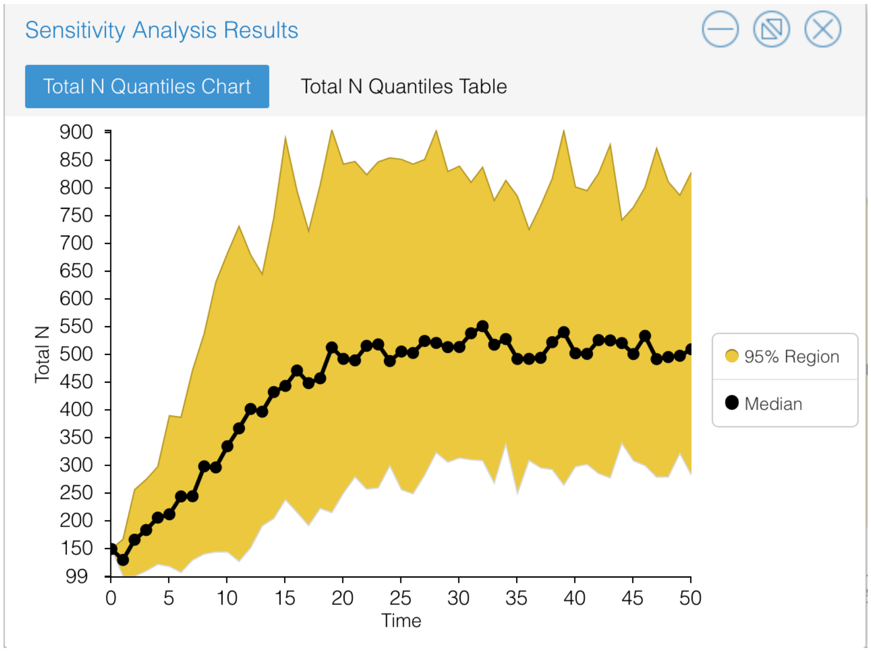

Figure 5. Projection of total female peregrine falcons *(Falco peregrinus)* on the Washington coast over 50 years under nest site supplementation scenario. Produced by running 100 simulations in a stochastic population simulation model. The shaded yellow region represents 95% of the simulations. The dotted black line represents the median total abundances out of all simulations. The trend demonstrates logistic growth, where the population (n=148) increases at the start because it is under carrying capacity (K=289.6), and eventually levels out around 500 individuals due to density dependence.

The population reacted in a much different manner when pollution was simulated as a threatening force. With a decrease in hatchling transition rate and adult fecundity representing the effects of pollution, we found that the population is not able to grow and was even at risk of extinction. The initial total abundance of 148 females declines exponentially to a median total abundance of about 10 individuals around year 20 and remains around this low abundance for the rest of the 50 year simulation (Figure 6). There were no cases of total extinction observed. However, there were multiple years where the lower bound values of the 95% region reached a critical low of 1, meaning more than 5% of the population is susceptible to extinction and therefore makes the population not viable when pollution is presented as a threat.

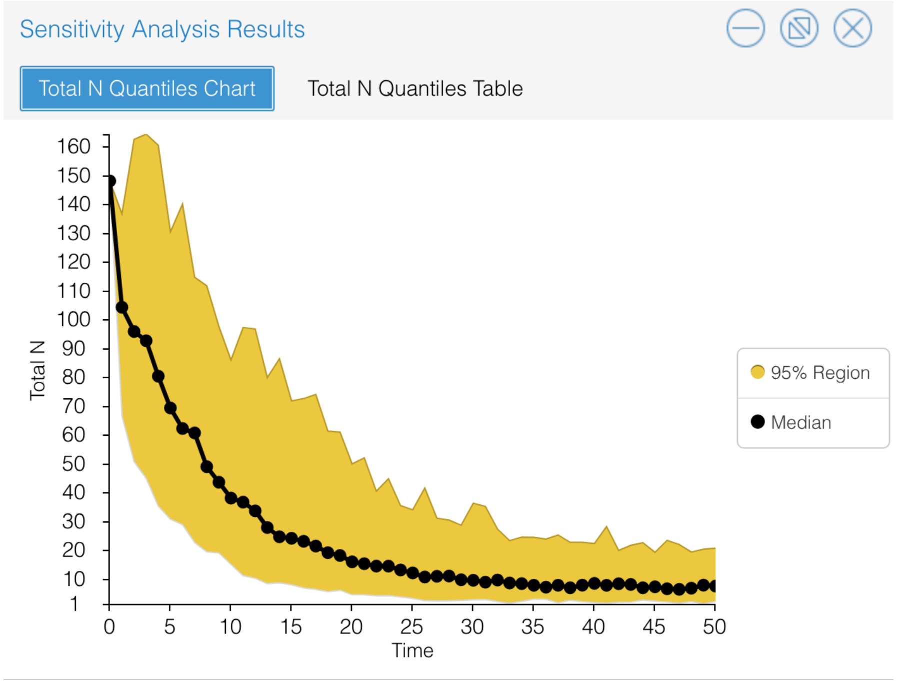

Figure 6. Projection of total female peregrine falcons *(Falco peregrinus)* on the Washington coast over 50 years under pollution conditions. Produced by running 100 simulations in a stochastic population simulation model. The shaded yellow region represents 95% of the simulations. The lower bound of this region reaches a critically low abundance of 1 in multiple years. The trend shows severe exponential decline once hatchling survival was halved and adult fecundity was reduced from 1.85 to 1, with possible risk of extinciton.

From these results, we see that the population is much more vulnerable to pollution compared to habitat loss, which answers our research question and supports our first prediction. Our second prediction about the population recovering in a positive direction regardless of these threats was not supported, as we found in this last scenario that they are barely at a viable population size and may not be able to overcome the detrimental effects of pollution on the species' vital rates.

Discussion

Looking at the results produced by our PVA model with the initial parameters we can see that the peregrine falcon populations on the Washington coast are increasing at a constant rate. We can see in Figure 3 that running 100 simulations over a 50 year time period that 95% of the simulations fell between 150 and 400 individuals with a median abundance of about 250. Examining deeper into the data we can see that the total abundance of this population never dropped below 1 which means this is a viable population that is unlikely to go extinct under conditions like density dependence, environmental stochasticity, and demographic stochasticity. We then looked at what would happen to this population if an event caused habitat loss.

To model habitat loss we cut the carrying capacity, or nesting sites, in half. Looking at Figure 4 the median total abundance had a slight decline from the initial abundance of 148 to around 138 individuals. At around year 4 we see that the median total abundance stays around this value of 140 individuals. After running the sensitivity testing tool, we can see a wide variability in the 95% upper and lower quantiles. The upper value was around 225 individuals while the lower value was as low as 82 individuals by the end of the 50 year simulation. Looking at the median total abundance during the 50 years we can assume that this population is not very vulnerable to habitat loss. The lower bound may suggest a potential decline, but it does not show this population being at risk of extinction because the abundance stayed above 1 for the whole simulation which means this is a viable population when exposed to 50% habitat loss. We then wanted to see how the population reacted to habitat availability.

To do this we doubled the carrying capacity, or nesting sites, and we found that this produced a similar increasing population that was also seen in Figures 3 and 4. This time the median total abundance was around 500 at the end of the 50 year simulation. In Figure 5 we can see that the upper bound value was around 900 and the lower bound was about 100 individuals. Looking at this figure we can see that doubling the number of nesting sites will double the median total abundance. After looking and comparing the plots of Figure 4 and 5 we concluded that this also represents a viable population even though habitat was the potential threat. This prompted us to consider a more threatening force, pollution.

As we can see in Figure 6 the population declined over the 50 years because this pollution resulted in a decrease in hatchling transition rates and adult fecundity. This population is not able to grow and is at risk of extinction. Our initial abundance of 148 declined exponentially to a median total abundance around 10 individuals at year 20 and slowly decreased for the rest of the 50 year simulation. In our observations we never encountered a case of total extinction, but there were multiple years where the lower quantile of the 95% region reached a low of 1 which means that more than 5% of the population is vulnerable to extinction. This means that this population when exposed to pollution as a threat is not viable.

After the completion of our PVA model we answered our research question and found that Peregrine Falcon populations are more vulnerable to a catastrophic event like pollution compared to a scenario like habitat loss, which supports our first prediction. As we saw in our final scenario, Figure 6 showed that the population was not able to recover in a positive direction which did not support our second prediction that a population would recover regardless of the threat present. Figure 6 produced a population that was barely viable and was at risk of extinction because it was not able to overcome the damaging effects of pollution on the species' vital rates.

The scenarios tested in this PVA more closely resembled natural processes rather than actual management strategies, with the exception of the nest site supplementation scenario, so more research would need to be done to see what strategies could best help this population in cases of greater threat. Although they were observed to be increasing for the most part even under stochastic and catastrophic conditions in the habitat loss scenario, our findings from the pollution scenario raises concerns about modern peregrine falcon populations that nest within cities, alongside human development and exposed to contaminants. Although proven to be very successful and resilient birds, peregrine falcons are not yet at a stage where they can fully recover from another disastrous event comparable to DDT or the like. Further research should be done to see what management practices would ensure that these birds stay away from polluted areas and reduce their chances of being exposed to contaminants that would be life-threatening and potentially population-threatening.

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