

Scientific Review of the “Biological and Conference Opinion of the Eastern Collier Multi-Species Habitat Conservation Plan” [Emphasis on the Florida Panther]



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EXECUTIVE SUMMARY

This is a scientific review of the "Biological Opinion and Conference Opinion for the Eastern Collier Multi-Species Habitat Conservation Plan, under Section 7 (Consultation Code: 41420-2010-F-0297; Conservation Planning Activity Code: 41420-2008-FA-0786) prepared by the U.S. Fish and Wildlife Service (USFWS; South Florida Ecological Services Field Office in Vero Beach, Florida);" hereafter referred to as the BO. The USFWS has been working for several years with property owners in eastern Collier County in Florida (ECPO) on a multi-species habitat conservation plan (HCP). As part of this plan, the USFWS has conducted several analyses focused on the Federally endangered Florida panther (*Puma concolor coryi*). Specifically, they investigated the effect of roadway traffic on panther mortality and population dynamics. The USFWS presented their methodology in the BO and supplementary material. The "Applicants" requested Dr. Meghan Higgs of Critical Inference, LLC perform an independent review. Dr. Higgs's review was provided as a Technical Memorandum titled "Statistical review of Future Roadkill Estimation Method (FREM) used by USFWS South Florida Ecological Services Field Office staff" (65p. with Appendices). Dr. Higgs presented several of her concerns about the analyses performed by USFWS staff. The primary goal of this review, conducted by a U.S. Geological Survey scientist at the request of the USFWS, was to provide an independent assessment of the traffic impact analyses and vehicle-related panther mortality on the Florida panther population presented in the BO (particularly section 5) and associated appendices (Appendices B, C, H, I, J, and K). This review also covers analyses included in the Technical Memorandum authored by Dr. Higgs. This review is divided into the following sections: *Section 2: Interpretation of past work related to Florida Panther population dynamics and threats*; *Section 3: Population Viability Analysis (PVA) conducted by USFWS*; *Section 4: Future Roadkill Estimation Method (FREM) analysis*; *Section 5: Decision context for model developments and interpretations*; and *Section 6: Additional minor comments*. My comments focused primarily on interpretations of analyses and I pointed out aspects of the BO that would benefit from further clarifications. Particularly regarding the description of models and the limitations of the analyses presented in the BO. Based on my review, I found the analyses conducted by the USFWS useful, and the USFWS staff has clearly invested a significant effort in the development and implementation of their analyses. One difficulty for the USFWS is

the quantification of the magnitude of the effects that they have examined, such as the relationship between road traffic and mortality. Although the analyses presented in the BO are insightful and provide useful assessments about the potential impact of activities and changes in panther abundance (assuming that the analyses are correct), there is so much uncertainty with some of the processes involved that I would be cautious when it comes to the interpretation of any specific values (more systematically presenting measures of uncertainty such as confidence intervals and interpreting estimates in the context of that uncertainty would be helpful), particularly when important sources of uncertainty were not accounted for. Nevertheless, based on the information provided in the BO, there is support for the hypothesis that vehicle mortality represents a major threat to the Federally endangered Florida panther. Also, some of the recent reports of motor vehicle collision mortalities (between 2014 and 2018) indicated an increase in reported mortality compared to previous years, and these data may deserve more attention. The challenge is to assess more accurately the magnitude of this threat. As explained in the comments, until further model developments become available, the solution may be to better recognize the limitations of the analyses, better acknowledge uncertainty and provide more details about the methodology so as to improve transparency and reproducibility.

1. INTRODUCTION

This is a scientific review of the "Biological Opinion and Conference Opinion for the Eastern Collier Multi-Species Habitat Conservation Plan, under Section 7 (Consultation Code: 41420-2010-F-0297; Conservation Planning Activity Code: 41420-2008-FA-0786) prepared by USFWS (South Florida Ecological Services Field Office in Vero Beach Florida)," hereafter referred to as the BO.

The USFWS has been working for several years with property owners in eastern Collier County in Florida (ECPO) on a multi-species habitat conservation plan (HCP). As part of this plan USFWS staff have conducted several analyses focused on the Federally endangered Florida panther (*Puma concolor coryi*). Particularly, they investigated the effect of roadway traffic on panther mortality and population dynamics. The USFWS presented their methodology in the BO and supplementary material. The "applicants" requested Dr. Meghan Higgs of Critical Inference, LLC perform an independent review. Dr. Higgs's review was provided as a Technical Memorandum titled "Statistical review of Future Roadkill Estimation Method (FREM) used by USFWS South Florida Ecological Services Field Office staff" (65p. with Appendices). In her review, Dr. Higgs presented several of her concerns about the analyses performed by USFWS staff. The primary goal of this review, conducted by a U.S. Geological Survey scientist at the request of the USFWS, was to provide an independent assessment of the traffic impact analyses and vehicle-related panther mortality on the Florida panther population presented in the BO (specifically section 5) and associated appendices (Appendices B, C, H, I, J, and K). This review also covers analyses included in the Technical Memorandum authored by Dr. Higgs.

This review is divided into the following main sections:

- *Section 2. Interpretation of past work related to Florida panther population dynamics and threats*
 - In this section, I review the interpretations by USFWS staff pertaining to past studies relevant to the population dynamics and threats faced by the Florida panther. Some of these studies are highly relevant to the analyses conducted by the USFWS, and the staff used parameter values from some of these studies to inform the analyses in the BO.

- *Section 3. Population Viability Analysis (PVA) conducted by USFWS staff*
 - In this section, I reviewed the population projection model implemented by USFWS staff, also defined as population viability analysis (PVA) in the BO. The Future Roadkill Estimation Method (FREM) analyses have direct implications on the PVA, which is important for population status assessment and threat analyses.
- *Section 4. Future Roadkill Estimation Method (FREM) analysis*
 - This section reviews both: (i) the presentations and analyses provided by USFWS staff and (ii) the analyses presented by Dr. Higgs in her Technical Memorandum.
- *Section 5. Decision context for model developments and interpretations*
 - This concluding section discusses the context under which the analyses were conducted. By definition, models are simplifications of reality and inherently rely on assumptions. The question then becomes whether the models are useful in providing insights regarding a particular decision context.
- *Section 6. Additional minor comments.*
 - In this section I provide additional minor comments that did not fit in the previous sections.

2. INTERPRETATION OF PAST WORK RELATED TO FLORIDA PANTHER POPULATION DYNAMICS AND THREATS

The BO prepared by USFWS staff is a comprehensive document (draft is 382 pages long, plus appendices), which includes detailed information about the biology of several imperiled species. This review focuses primarily on the Florida panther for which the USFWS provided key references from the current scientific literature on topics relevant to the BO.

In the BO, USFWS staff conducted a thorough review of the ecological literature on life history, population dynamics, and the threats faced by the species considered. The articles cited in the BO included recent analyses (e.g., van de Kerk et al. 2019). Below I present specific comments regarding the synthesis and interpretation of these studies. My comments focus primarily on interpretations of analyses and I pointed out aspects of the BO that would benefit from further clarifications. Particularly regarding the description of models and the limitations of the analyses presented in the BO.

2.1 MODELS OF POPULATION DYNAMICS FOR THE FLORIDA PANTHER

In this subsection, I review some of the interpretations pertaining to recent models of population dynamics which were cited in the BO and used to inform the analyses in the BO. I discuss two types of models: (1) population projection models (matrix population models and individual based models [IBM]), which were used to project panther abundance into the future (Hostetler et al. 2013 and van de Kerk et al. 2019); and (2) statistical models for retrospective analysis, which were used to infer historical trends in panther abundance (McClintock et al. 2015).

- ***On line 3449, USFWS staff wrote: “Recent PVA models (Hostetler et al. 2013 and van de Kerk et al. 2019) confirm that the panther population grew rapidly through 2013 ($\lambda > 1$)”***

- *My comment:* I would suggest replacing “the population grew rapidly through 2013” with a more neutral statement by providing the actual estimates (with 95% confidence intervals [CI]), particularly given the large uncertainty. In fact, the hypotheses of a stable or declining population could not be conclusively rejected based on the results presented by van de Kerk et al. (2019) and Hostetler et al. (2013).

For example, “The annual estimate of stochastic population growth rate obtained with a matrix population model by van de Kerk et al. (2019) was 1.04 (95%CI: 0.72 to 1.41) and it was 1.03 (95%CI: 0.95 to 1.11) for Hostetler et al. (2013) (I note that Hostetler et al. (2013) presented several estimates of stochastic population growth rate, here I reported the one with “model selection included” presented in the Results section of their paper). Although the mean population stochastic growth rates (λ_s) from both studies would support the hypothesis of population increase with an annual rate of 3-4%, the confidence intervals imply that the hypotheses of (a) a decline (2.5th percentile: 0.72 [van de Kerk et al. 2019, this would be an extremely rapid decline]; 2.5th percentile: 0.95 [Hostetler et al. 2013]); (b) a stable population ($\lambda_s = 1$ within the 95%CI for both studies); or (c) a rapid increase (87.5th percentile: 1.41 [van de Kerk et al. 2019, this would be an extremely rapid increase]; 87.5th percentile: 1.11 [Hostetler et al. 2013]) could

not be conclusively rejected based on this analysis.” Although the analyses by Hostetler et al. (2013) and van de Kerk et al. (2019) were rigorous, it is worth mentioning that they did not appear to consider factors such as:

- Catastrophes, such as disease outbreaks (see <https://myfwc.com/wildlifehabitats/wildlife/panther/disorder/>, note that potentially more serious diseases could emerge in the future), which would likely reduce estimates of population growth rates and increase the probability of quasi-extinction. Runge et al. (2017) provided a framework for incorporating such catastrophes in PVAs.
 - Correlation among vital rates and correlated environments. A correlated environment would also potentially reduce estimates of stochastic population growth rates (Caswell 2001, Morris and Doak 2002).
 - As indicated in the BO these analyses did not consider other important threats (e.g., change in road traffic, sea level rise)
- ***L. 3450, USFWS staff wrote: “Recent PVA models (Hostetler et al. 2013 and van de Kerk et al. 2019) confirm that the panther population grew rapidly through 2013 ($\lambda > 1$) but that growth may be slowing (McClintock et al. 2015).”***
 - *My comment:* The structure of this sentence may give the impression that the population grew rapidly (see my comment above about inferring a “rapid growth” from van de Kerk et al. 2019) but then there was a stabilization in growth, which would be inferred based on the results obtained by Mc Clintock et al. (2015). I would interpret the results of these studies differently. First, I would make it clearer that these are two different types of analyses: (a) van der Kerk et al. (2019) is based on matrix population models (and an IBM) which project population growth using computer simulations, whereas (b) McClintock et al. (2015) use a statistical model (which combined motor vehicle collision mortalities [MVM] reports and radiotelemetry information) to estimate abundance over time. I addressed (a) with my previous comments, and indicated why alternative

hypotheses (e.g., stable) could not be conclusively excluded based on the estimates of 95%CI of λ_s alone. Regarding (b), although the estimates of annual abundance shown in the figure below (Fig. 1) do suggest some growth and then stabilization, the uncertainty is large (notice that the 95%CI of the abundance estimates overlap greatly). Therefore, the hypothesis of growth is best supported by the data based on McClintock et al. (2015), however, the hypothesis of very slow or no growth cannot be completely excluded based on this information alone. Also note that as explained by the authors, these estimates of abundance are larger than the actual population within the study area at any given point in time. This is because the authors used an *open population estimator*. Based on the estimates of uncertainty (particularly the 95%CI) the hypothesis of the abundance only being slightly higher than the counts (minimum number assumed alive, MNA) from McBride cannot be excluded (especially because the estimator is known to overestimate actual abundance at any given time) (Fig. 1). These same estimates also suggest that abundance could have been much greater (Fig. 1).

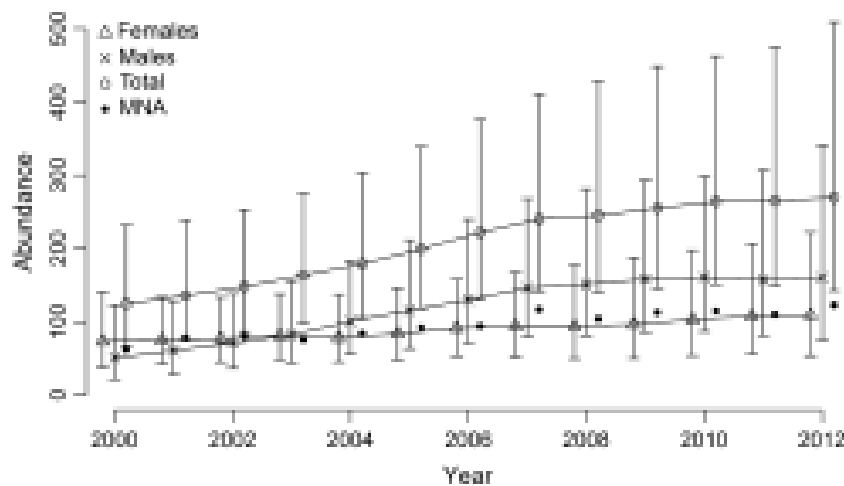


Figure 1. From McClintock et al. (2015) “Annual estimates for the subadults and adults (≥ 1 year old) Florida panther population size using the breeding range from 2000 to 2012. Separate estimates are provided for male and female populations. Total counts for the minimum number assumed alive (MNA) based on physical evidence (McBride et al. 2008) are included for comparison.”

2.2 THREATS AND FRACTION OF MORTALITY INFORMATION

Regarding the proportion of mortality, Figures 5.4 and 5.5 of the BO (Figs. 2-3 in this review) are instructive and have been updated with recent data (up to 2019). Although this is a common way to present proportion of mortality information for many species (e.g., sea turtles, manatees), it may be worth noting that these proportions do not account for uncertainty, particularly the uncertainty associated with “unknown causes.” Runge et al. (2017) have proposed an approach to address this source of uncertainty. Given that rigorous analyses to account for this uncertainty are highly complex and cutting edge, it may be reasonable to simply acknowledge this source of potential error.

FLORIDA PANTHER MORTALITY BY CAUSE, 1972-2019

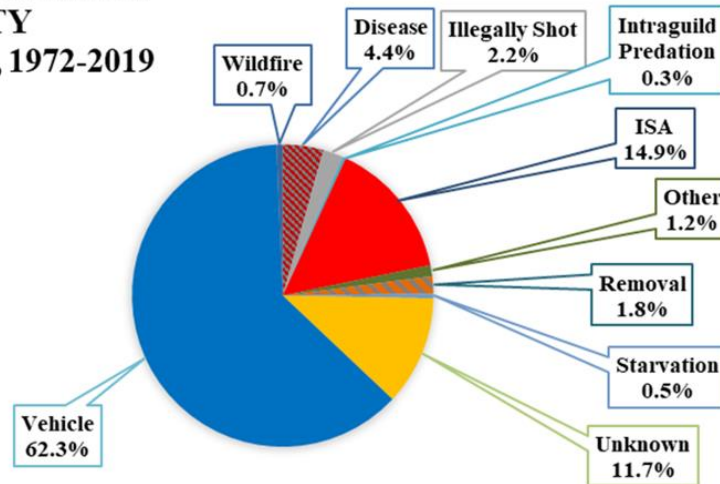


Figure 2. From BO “Percentage of Florida panther mortality from 1972 through 2019.”

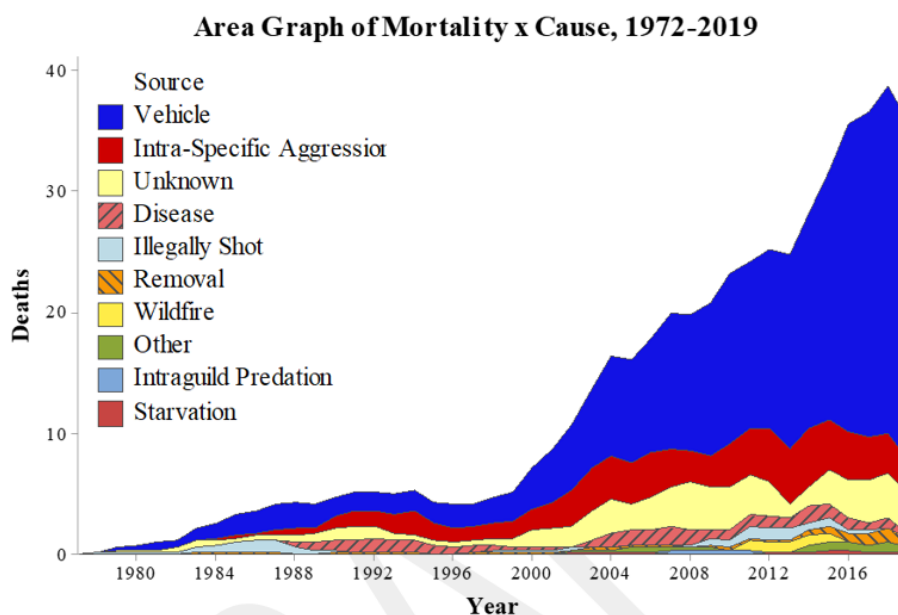


Figure 3. From BO “Magnitude of each source of Florida panther mortality over time from 1972 through 2019.”

3. POPULATION VIABILITY ANALYSIS (PVA) CONDUCTED BY USFWS STAFF

3.1 BENEFITS AND LIMITATIONS OF THE PVA PERFORMED BY USFWS STAFF

The population projection model developed by USFWS staff for the BO has several benefits:

- (a) Unlike previous analyses conducted by Hostetler et al. (2013) and van de Kerk et al. (2019), it considers the potential effect of changes in road traffic for several decades into the future.
- (b) It considers future threats related to habitat loss and the projected impact of sea level rise.

On the other hand, some limitations include:

- (a) It does not appear to consider correlation among vital rates and temporal autocorrelation of the environment. Unlike previous analyses, it does not appear to account for demographic stochasticity (source of uncertainty that describes the random fluctuations in abundance that occur because the birth and death of individuals is a discrete probabilistic event). This source of uncertainty is often important for small populations such as the Florida panther, and would tend to increase the probability of quasi-extinction and decrease the population growth rate.

(b) The USFWS used a female only model, and given the apparent bias in MVM (i.e., males appear to be more likely to die from vehicle related mortality than females, see section 5.1.6.4 of the BO), a two-sex model as implemented by Hostetler et al. (2013) would probably represent a better approximation of reality.

(c) It would be helpful to better clarify the quasi-extinction threshold used.

(d) As noted elsewhere, demographic stochasticity and the correlated environment would tend to reduce stochastic population growth rates. There is of course a positive relationship between the quasi-extinction threshold and probability of quasi-extinction. Also, it is not clear how parametric uncertainty was incorporated in the model. Runge et al. (2017) offered some insights on how to combine parametric and environmental uncertainty. Examples of parametric uncertainty include sampling variance (or standard error) of vital rates (e.g., survival and reproduction) and initial abundance.

(e) My main concern about the presentation of the PVA is that as written, it is hard to understand what was done exactly. Ideas to increase reproducibility include: (i) provide more details about the structure of the model (e.g., is this a post-breeding or pre-breeding census and why); (ii) be more explicit about the limitations and how the uncertainty was incorporated, as well as the vital rates used (date-range and sources of the data sets used, maybe even include the original data if available); (iii) given that program RAMAS was used for the analyses, A programming code, if available, or a video-record describing how to implement the PVA could be provided, and even published in outlets such as <https://www.jove.com/journal>.

(f) I did not find estimates of stochastic population growth rates (λ_s) (based on the models developed by USFWS), which is a common measure used for population status assessment (e.g., used in recovery plans of endangered species; used by the International Union for the Conservation of Nature as a criteria for classification). Estimates of stochastic population growth rates that would consider: demographic stochasticity, environmental stochasticity and parametric uncertainty have been suggested as desirable criteria as part of population status assessment (Caswell 2001).

(g) Similarly, showing a figure with statewide projected abundance over time (under alternative management scenarios) would be helpful from a communication perspective. As for the stochastic population growth rate, demographic stochasticity, environmental

stochasticity and parametric uncertainty would improve the reliability of the projections. Both in the case of stochastic population growth rate and abundance, providing estimates of uncertainty (e.g., 95% confidence intervals) would facilitate the interpretability of the results.

3.2 INCREASE IN REPORTED MOTOR VEHICLE COLLISION MORTALITIES (MVM)

One concern regarding the consideration of previous analyses (Hostetler et al. (2013), van de Kerk et al. (2019 and McClintock et al. (2015)) is that the annual survival probabilities end in 2013. This would have missed some of the highest MVM reports ever recorded; based on the file “AnnualCount_PVM_data.xlsx,” the average from 1995 to 2013 was 9 (variance: 32.1) and from 2014 to 2018, the average was 27.8 (variance: 17.2)

This of course does not account for the imperfect detection and reporting of MVMs. Yet, some insights can be gained with a simple implementation of the formula: $N_{t+1} = \lambda N_t - h N_t$, where h is the removal rate (from let’s say vehicle mortality) and N_t is the abundance at time t , λ in this case is the population growth rate without the removal. We can then compute h^* that would lead to a stable population (population growth rate [with removal] of one) under this simple deterministic model, with the minimum population size and stochastic population growth rates from van der Kerk (2019) 1.04 (95%CI: 0.72 to 1.41). As an illustration, assuming that $\lambda = 1.04$ and abundance (N) is ~150 (based on McBride, this corresponds to the minimum number of panthers known to be alive at the time of sampling [in 2015], see also McClintock et al. (2015)), $h^* = 0.04$ would lead to $N h^* = 6$. This would imply that removing more than 6 animals would eventually lead to a population decline under the conditions listed. If on the other hand $\lambda = 1.11$ (upper 95%CI from Hostetler et al. [2013]) and abundance (N) is ~230 (from BO), $N h^* = 25.3$. Of course, this is an oversimplification for several reasons: (1) in reality h is not equally applied to all age classes and gender, 2) uncertainty and potentially important sources of error are not considered (e.g., imperfect detection process for N [thus true N was probably greater; in addition the population may have grown since 2015] and MVMs), 3) carrying capacity, density dependence and other important considerations are not considered, see also Slade et al. (1998). Nevertheless, although this increase in MVMs is mentioned in the BO, it may deserve more attention. Evidence provided in the BO and in the literature point to an already highly vulnerable population, and the recent increase in MVM could be an important “signal” to consider.

For context, the calculation of the potential biological removal (*PBR*) which is included in stock assessment reports under the Marine Mammal Protection Act (MMPA) for marine mammals (including endangered marine mammals) by the National Oceanic and Atmospheric Administration (NOAA) and USFWS (but not under the Endangered Species Act), would also suggest that the recent MVM reports far exceed the *PBR*, based on the parameters presented above. I note, however, that the mean λ_s is probably not an ideal basis to compute R_{max} (“maximum theoretical or estimated net productivity rate of the stock at a small population size”).

$$PBR = N_{min} (R_{max}/2) F_r$$

F_r is a recovery factor (generally $F_r = 0.1$ for Federally endangered species), and N_{min} is the minimum abundance. Assuming $N_{min} = 150$ and $R_{max} = 0.04$ would lead to $PBR = 0.3$ (i.e., less than one individual). Again, this is given purely for explorative purpose, and I am not suggesting that *PBR* should be used (as more detailed analyses could be used), but it might provide a basis for awareness of a potential problem. For an example of a *PBR* (and associated references) for a stock assessment see: Federal Register, 79 FR 3856, Docket No. FWS–R4–ES–2012–0081.

I note that despite the low values of $N h^*$ ($h^* N = 6$, for $N=150$ and $\lambda = 1.04$) and *PBR*, it is possible that the population grew, nonetheless. Indeed, this could have happened if the true population was much greater than 150, or that the true λ was much greater than 1.04 (which would also imply a greater R_{max}) or both.

Thus, to conclude this section, the increase in mortality between 2014 and 2018 raises two important questions: (1) “Was the increase in PVM [panther vehicle mortalities] reports mostly a reflection of a growing panther population?” Or (2) “Does the increase reflect some changes in road traffic patterns (or other changes) that would lead to an unsustainable level of panther mortality?”. The level of uncertainty associated with the available information makes it challenging to conclusively exclude either of these hypotheses. Of course, the truth could be a mix of both hypotheses.

3.3 CHOICE OF SOFTWARE AND REPLICABILITY OF THE MODEL IMPLEMENTED BY USFWS STAFF

- ***USFWS staff wrote in BO: “To account for the possibility of future changes in habitat availability, new sources of mortality, and changes in existing sources of mortality, we started with the van de Kerk et al. (2019) PVA inputs. We chose to bring these into a commercially available platform (RAMAS Landscape) for ease of replicability in a platform familiar to Service biologists.”***
 - *My comment:* Generally, I do not have issues with the choice of the software used. While I do not use the RAMAS software for my own analyses, it is a well-known commercially available platform that has been used for peer reviewed studies. One downside is that it is expensive and therefore that could potentially reduce the replicability from non-RAMAS users (or owners of a license). If code or pseudo code are available for the analysis, it may be helpful to provide those for the sake of transparency. In that respect, the use of an easily accessible and free software such as R (R Core Team 2020) may have facilitated the replicability. With that said, some of the functions used by USFWS staff with the RAMAS Landscape software may have been hard to replicate with R (or other software). In addition, the fact that the USFWS has already developed a deep knowledge with this platform is another reasonable argument for using it. Finally, RAMAS has been around for a long time and has been designed to be a user-friendly software, which could help reduce the risk of programming errors (when compared to custom made models). As mentioned earlier, for the sake of reproducibility, programming code or a video-record of the process to implement the PVA could be provided, if available, and even published in outlets such as <https://www.jove.com/journal>.

4. FUTURE ROADKILL ESTIMATION METHOD (FREM) ANALYSIS

4.1 FREM ANALYSIS PERFORMED BY THE USFWS

The FREM analysis is based on a simple equation and attempts to link projected Average Annual Daily Traffic (AADT, a proxy for road traffic) to panther mortality. This is an important

objective because previous analyses (such as Hostetler et al. 2013 and van de Kerk et al. 2019) had not sufficiently considered this major source of mortality (Figs. 2-3) in their long-term projections. Although the approach is simple, it captures the fact that potential collisions are likely to increase as a function of vehicle density. The rationale behind the FREM formula (i.e., an increase in collision growing proportionally with traffic volume), while simple, can be justified with the theory of encounter probabilities (Koopman 1956; Gerritsen and Strickler 1977, Gurarie. And Ovaskainen 2013) which has been applied to vehicle-wildlife collisions (Wilson et al. 2007, Van Der Hoop et al. 2012, Martin et al. 2016, Rockwood et al. 2017, Crum et al. 2019). Several of these scientific publications have demonstrated or applied the principle that, generally, everything being equal, there is a linear increase between encounter probabilities (e.g., potential collisions) and moving agent (e.g., animals and motor vehicles) densities. The process behind panther vehicle mortality is complex, and some nonlinearity may arise. Nevertheless, the hypothesis of a linear relationship is not unreasonable. Therefore, examining its impact on the population dynamics of the Florida panther is justified. A major benefit of the approach is that it provides a mechanistic link between vehicle density (indirectly through AADT) and potential deadly collisions. More explicitly considering the growth in panther population as part of the collision process would be helpful in future developments. Ideally, the relationship between road traffic and panther mortality could be inferred from statistical models. There is, however, some major hurdles to that approach. Given (a) the complexity and large uncertainties associated with the deadly collision process, and (b) the relative rarity given the uncertainty (from a sample size perspective), it would be extremely difficult to quantify or even detect the “signal” (relationship between AADT and deadly collisions) from the “noise” (e.g., uncertainty associated with road kills reporting among other things). Thus, again, a more mechanistic approach seems appropriate, particularly if the proper caveats and sources of errors are explained. On that latter point I agree with Dr. Higgs, that more context and explanations would be helpful for the interpretation of the results.

There are additional limitations to the analyses and the presentation of the methods, results, and interpretations.

- Improving the notation would help the reader better understand what was done. Dr. Higgs provided a detailed review of that aspect, which clarifies how the FREM analysis is implemented.
- Given the simplicity of the FREM analysis, many sources of uncertainty are not considered. But properly incorporating important sources of uncertainty is not straightforward.
- The analysts from the USFWS also tried to account for the fact that as panther abundance grows, the expected panther-vehicle-mortality (PVM) would also grow in the population model. This aspect of the model could be improved and better explained and included in the BO (most of the explanations are in external documents).

4.2 TECHNICAL MEMORANDUM PROVIDED BY DR HIGGS

In this section, I provide comments about the Technical Memorandum provided by Dr. Higgs, titled "Statistical review of Future Roadkill Estimation Method (FREM) used by USFWS South Florida Ecological Services Field Office staff" (65p. with Appendices).

Dr. Higgs wrote:

- ***“Based on the information available about FREM and my review based on my statistical expertise, I find inadequate justification for using the FREM approach for predicting PVM in 2060, particularly if the predictions are to guide decision-making. This conclusion is based on the following points, which are described previously in the report:”***
 - My comment: I agree with Dr. Higgs that the presentation of the methodology could be improved. Dr. Higgs provided a summary with her own notation for the FREM formula, see below.

From Dr. Higgs report:

Critical Inference LLC – TECHNICAL MEMO

November 10, 2020

Appendix A – FREM Notation and Definitions

Description of the FREM approach

Prepared by Megan Higgs, Critical Inference LLC

Introduction

The following reflects my current understanding of the Future Roadkill Estimation Approach (FREM) adopted in 2018 by staff at the U.S. Fish and Wildlife Service (US FWS) South Florida Ecological Services Field Office. The approach uses a simple formula to predict future PVM over a 5-year period for an individual road segment using a past 5-year PVM, the reported AADT value for the midpoint year, and a future year's AADT projected by FDOT traffic models. The goal of this document is to increase transparency of the method by making mathematical definitions, details, and assumptions of the approach explicit.

Key information about inputs:

- The predictions are obtained at the level of each road segment and then summed over all road segments to be included in a larger regional prediction.
- AADT = annual average daily traffic is a common measure of traffic volume. As indicated in the name, it is meant to summarize yearly traffic volume while aggregating over within year changes (diurnal, daily, seasonal, etc.). AADT can be estimated or calculated based on data collected at monitoring stations and/or FDOT traffic modeling. Uncertainty in an estimate is expected to depend on methods used to obtain it. AADT values for the future are obtained as predictions from FDOT traffic models.
- Sources of uncertainty in estimated AADT and projected AADT are not quantified or discussed qualitatively.
- A 5-year average PVM is used as a baseline to predict an annual average PVM for a future year, by assuming the ratio of past to future 5-year PVM is equal to the ratio of past to future AADT values.
- As part of FDOT modeling of future AADT, attributions of future AADT for a road segment to a particular development included in the model is also provided. These proportions of future AADT attributed to a particular development are then translated directly into a proportion of future PVM through the FREM formula
- Predictions are made for road segments of interest with at least one PVM since year 1971. Given the FREM formula, any road segment with a baseline 5-year average of 0 PVM will have a prediction of 0 PVM in the future regardless of the projected increase in AADT.

Notation and definitions

Define quantities

$AADT_{j,t}$ = estimated AADT on road segment j in year t in the past

$\widehat{AADT}_{j,t}$ = predicted AADT on road segment j for year t in the future

$PVM_{j,[t_1,t_2]}$ = total observed PVM on road segment j over time period from year t_1 to year t_2 (inclusive)

$\widehat{PVM}_{j,[t_3,t_4]}$ = total predicted PVM on road segment j over time period from year t_3 to year t_4 (inclusive)

$\overline{PVM}_{j,[t_1,t_2]}$ = average annual PVM on road segment j over time period from year t_1 to year t_2 (inclusive)

$\widehat{\overline{PVM}}_{j,[t_3,t_4]}$ = predicted average annual PVM on road segment j over time period from year t_3 to year t_4 (inclusive)

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The formula

Future 5 year annual average PVMs are predicted based on the assumption that the ratio of a projected future year's AADT to a past year's AADT is equal to the ratio of a future 5-year PVM (average or total) to a past 5-year PVM (average or total), where the year associated with the AADT is the midpoint year of the 5-year period. Using the proportional relationship, the future 5-year PVM is solved for given values of the other three quantities.

For example, for the ECMSHCP analysis, a prediction was desired for year 2060. The baseline period used for PVM was the 5-year period from beginning of March 2014 through end of February 2019, and the past AADT was taken from 2017. The predicted 5-year annual average PVM technically applies to beginning of March 2057 through end of February 2062.

The formula for road segment j , assuming t_0 is the midpoint of the baseline 5-year time interval (e.g., 2017 in the previous example) and t_f is the midpoint of the future 5-year time interval.

$$\widehat{PVM}_{j,[t_f-2,t_f+2]} = \widehat{PVM}_{j,[t_0-2,t_0+2]} \times \frac{\widehat{AADT}_{j,t_f}}{\widehat{AADT}_{j,t_0}}$$

To obtain a predicted PVM for a collection of J total road segments in region of interest (region), the individual segment predictions are summed:

$$\widehat{PVM}_{region,[t_f-2,t_f+2]} = \sum_{j=1}^J \widehat{PVM}_{j,[t_f-2,t_f+2]}$$

Accounting for contribution from specific development

Based on FDOT projections of AADT, percent contribution of projected AADT for each road segment attributed to a particular development is also modeled. Continuing with the assumption of a direct proportional relationship between AADT changes and changes in PVM, the fraction of AADT attributed to a potential development is then taken as the fraction of future PVM for each segment attributed to the potential development. The percent attribution varies by road segment and therefore the attribution calculation for 5-year average PVM is performed at the level of the individual road segment before aggregating to a regional prediction.

The percent of projected 2060 Total AADT for segment j in year t attributed by the FDOT traffic model to development k is denoted

$$propAADT_{k,j,t}$$

The predicted 5 year annual average PVM for segment j attributed to potential development k is calculated as:

$$\widehat{PVM}_{k,j,[t_f-2,t_f+2]} = \widehat{PVM}_{j,[t_0-2,t_0+2]} \times \frac{\widehat{AADT}_{j,t_f}}{\widehat{AADT}_{j,t_0}} \times propAADT_{k,j,t_f}$$

The individual segment predictions are then summed, as described above before accounting for attribution to a development.

For a segment, the predicted 5-year average PVM attributed to development k plus the predicted 5-year average PVM *not* attributed to development k is equal to the future predicted 5-year average PVM provided previously.

- My comment: I found the notation provided by Dr. Higgs (see above) useful, and I agree that a more detailed description would be helpful. I also agree that ideally uncertainty would be accounted for. Dr. Higgs provided programming code and a R shiny app that may be helpful for exploratory purposes. I examined both the R shiny app and R programming code provided by Dr. Higgs. I found the app and code clear and easy to use. Even though providing models that account for uncertainty is preferable when possible, the results from the deterministic FREM analysis (as supportive evidence for the impact of road traffic on the population dynamics of panthers) are still useful until better information becomes available. As noted in the introduction, models simplify reality and inherently rely on generalized assumptions. The question then becomes whether a model with its many imperfections can provide useful insights. Nevertheless, whenever possible developing models that account for uncertainty and providing estimates of uncertainty is a preferable approach.

Dr. Higgs wrote:

- ***“Documentation of the development and application of the approach is inadequate transparency, utility, and objectivity. There is no documentation providing definitions, notation, and assumptions, or describing how the approach was developed. The information provided regarding predictive accuracy refers to two examples of successful predictions, but it lacks adequate detail for evaluation and/or reproducibility. The small prediction errors reported for the two examples beg questions about how the scenarios were chosen and what data were used to develop FREM initially. The available documentation does not meet the standards outlined in the USFWS Information Quality Guidelines and Peer Review.”***
 - My comment: I agree that the notation and presentation of the assumptions could be improved, which would help with transparency and reproducibility.

Dr. Higgs wrote:

- *“Source of uncertainty in predictions are ignored, both quantitatively and qualitatively. As described previously in this document, there are many sources of uncertainty associated with the FREM approach that are expected to affect predictions. From a statistical perspective, (at least) two such sources that are not justifiably ignored are (1) uncertainty in the AADT values used as inputs, and (2) uncertainty based on extrapolation beyond the observed range of AADT values for a segment. Based on the investigations in this review, the potential range of predictions resulting from the two aforementioned sources are expected to be large relative to the decision contexts the predictions may be used for. That is, after incorporating some uncertainty, the range of potential PVM predictions for a road segment are large enough to potentially change decisions regarding the predicted PVM in 2060). At the very least, the potential variability in the predictions for the same inputs should be acknowledged and considered in any decision making, rather than following the FREM approach to obtain a single number with no explicit discussion of associated uncertainty. The ignoring of uncertainty in inputs and predictions is a substantial limitation because it leaves serious questions as the practical usefulness of the predictions.*
 - *My comment:* I agree that the consideration of uncertainty would be helpful, but it also depends on the goal of the analysis. Indeed, deterministic analyses and stochastic analyses may serve different purposes. Deterministic analyses have several benefits; they are easier to interpret, easier to run, and sometimes more generalizable. If the purpose is to simply assess the relationship between AADT and population growth rate, the deterministic analysis can still be useful until more elaborate analyses become available. A stochastic extension that would incorporate uncertainty would be a valuable improvement, particularly if the inclusion of that uncertainty significantly affects the ultimate decisions. In other words, although, both deterministic and stochastic analyses can be useful and provide complementary insights, whenever possible it is generally preferable to account for uncertainty. Of course, there is a “cost” associated with additional analyses in terms of allocated staff time. The cost of additional analyses include

(1) diverting resources (in terms of staff time) from other priorities, and (2) potential delays in decision making which may induce an “opportunity cost.” Thus, a common question in the conservation literature is “To what extent would the ultimate decision be affected by new analyses?” This may help determine the value of new information, and how much decision makers might be “willing to pay” (e.g., in this case diverting resources from other priorities) for that new information and for prioritizing future monitoring programs. Until a more elaborate model that accounts for uncertainty becomes available, it appears reasonable to provide the results of the deterministic analysis, and provide the adequate caveats (e.g., that uncertainty was not accounted for). Dr. Higgs provided useful exploratory analyses that could be referenced, and some of these concepts could also be considered for future model developments and extensions.

Dr. Higgs wrote:

- ***“The FREM equation implies a strong association between 5-year PVM and midpoint year AADT value. However, evidence for such an association to support the fundamental assumption of the approach is missing in the exploratory analysis performed for this review. On the other hand, there is evidence of a strong, positive association between panther annual counts (as a surrogate for changes in population size) and PVM at the regional level. The reliance of FREM on estimates and predictions of AADT (as a measure of traffic volume) implies a strong relationship between the two variables, over space and/or time. The lack of evidence for such a relationship observed in the data investigated for this review is surprising given the FREM formula. This suggests a main motivation for adopting the FREM approach may be the relative ease of obtaining the inputs, particularly future projections of AADT from FDOT traffic models.”***
- My comment (Note: this was also discussed in section 4.1): Processes governing deadly collisions between panthers and vehicle are complex particularly when trying to make predictions over decades. It involves animal behavior and movement, changes in density of both vehicles and panthers, the probability of avoidance, among

other things. Nevertheless, the assumption that there is a positive relationship between traffic volume and panther mortality seems reasonable. The rationale behind the FREM formula (i.e., an increase in collisions grows proportionally with increased traffic volume), while simple, can be justified with the theory of encounter probabilities (Koopman 1956; Gerritsen and Strickler 1977, Gurarie. And Ovaskainen 2013) which has been applied to vehicle-wildlife collisions (Wilson et al. 2007, Van Der Hoop et al. 2012, Martin et al. 2016, Rockwood et al. 2017, Crum et al. 2019). Several of these scientific publications have demonstrated or applied the principle that everything being equal, there is a linear increase between encounter probabilities (e.g., potential collisions) and moving agents (e.g., animals and motor vehicles) densities. The process behind panther vehicle mortality is complex, and therefore some nonlinearity may arise. Nevertheless, the hypothesis of a linear relationship is not unreasonable. Also, given that collision events are relatively rare events (from a statistical point of view), it makes rigorous statistical inference from these data extremely challenging. Given the large uncertainty associated with this problem, finding an ecological signal (even if in reality there was a strong positive relationship between road traffic and panther mortality) from the data available would be difficult. Therefore, a more mechanistic approach may be warranted in this case. I would also caution about the interpretation of the results presented in Figure 4 (Fig. 9 in the Technical Memorandum by Dr. Higgs) because the PVM counts do not account for the imperfect detection process and some of the relationships are based on very few points.

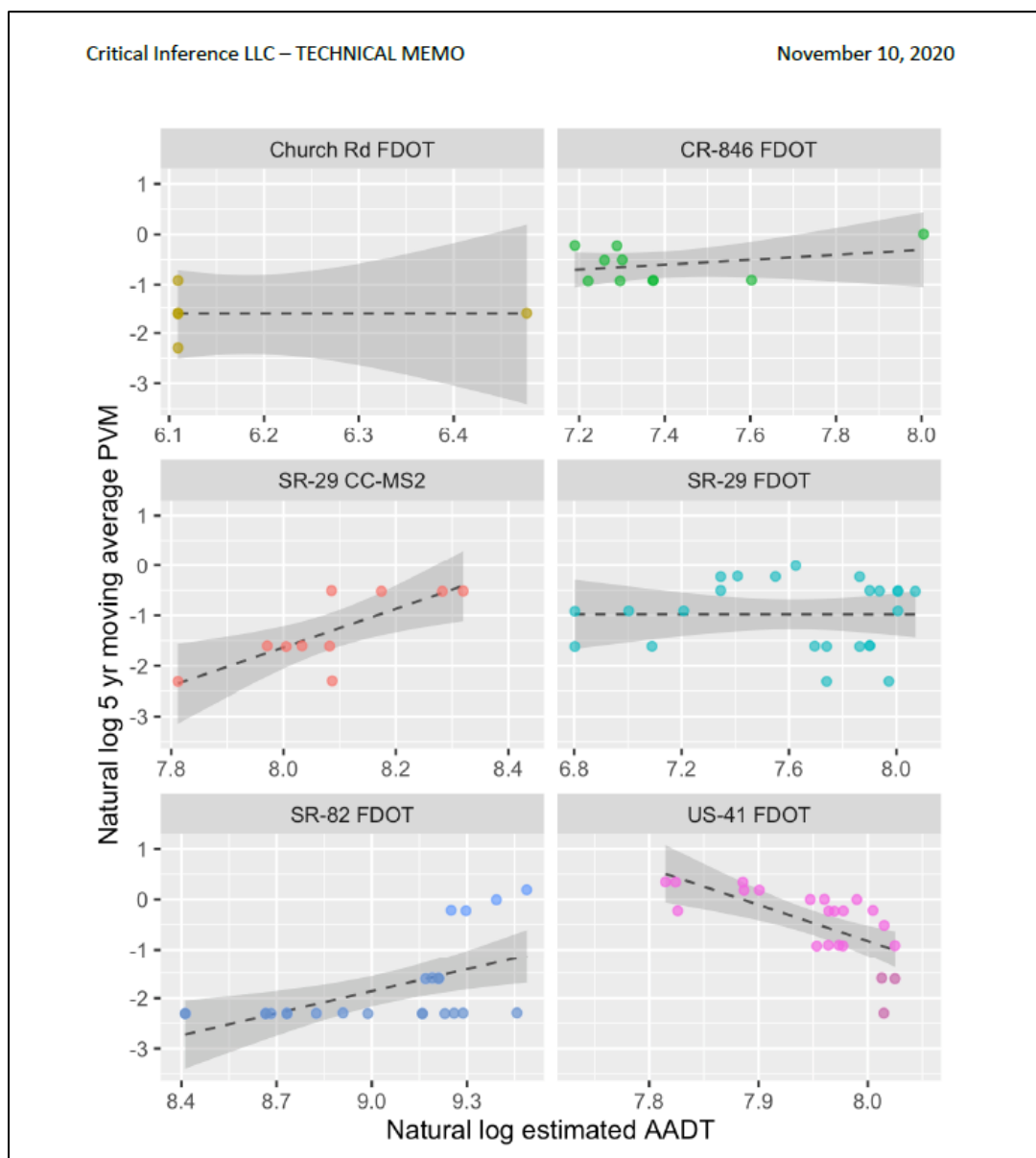


Figure 4. From Dr.Higgs Technical Memorandum, in the figure legend Dr. Higgs says: “Scatterplots, simple linear regression fitted lines, and 95% pointwise confidence bands investigating the relationship between the natural log estimated AADT and the natural log of the 5-year moving average PVM (0.1 was added to the moving average PVM of 0 before log transforming so points associated with zeroes are plated at -2.3). Note x- and y-axis scales differ by panel (see Figure 9 [in the Technical Memorandum] for common scales). Assumptions of linear regression are violated by use of moving averages and confidence should be interpreted as understating the statistical uncertainty in the relationship.”

Dr. Higgs wrote:

- “On the other hand, there is evidence of a strong, positive association between panther annual counts (as a surrogate for changes in population size) and PVM at the regional level.”
- On page 5 of her report she also says, “Data analysis reveals evidence for a strong, positive association between annual panther counts and annual PVM counts in the region. Using the natural log scale for both variables, the estimated correlation coefficient is 0.94 (see Section 3.3.5).”

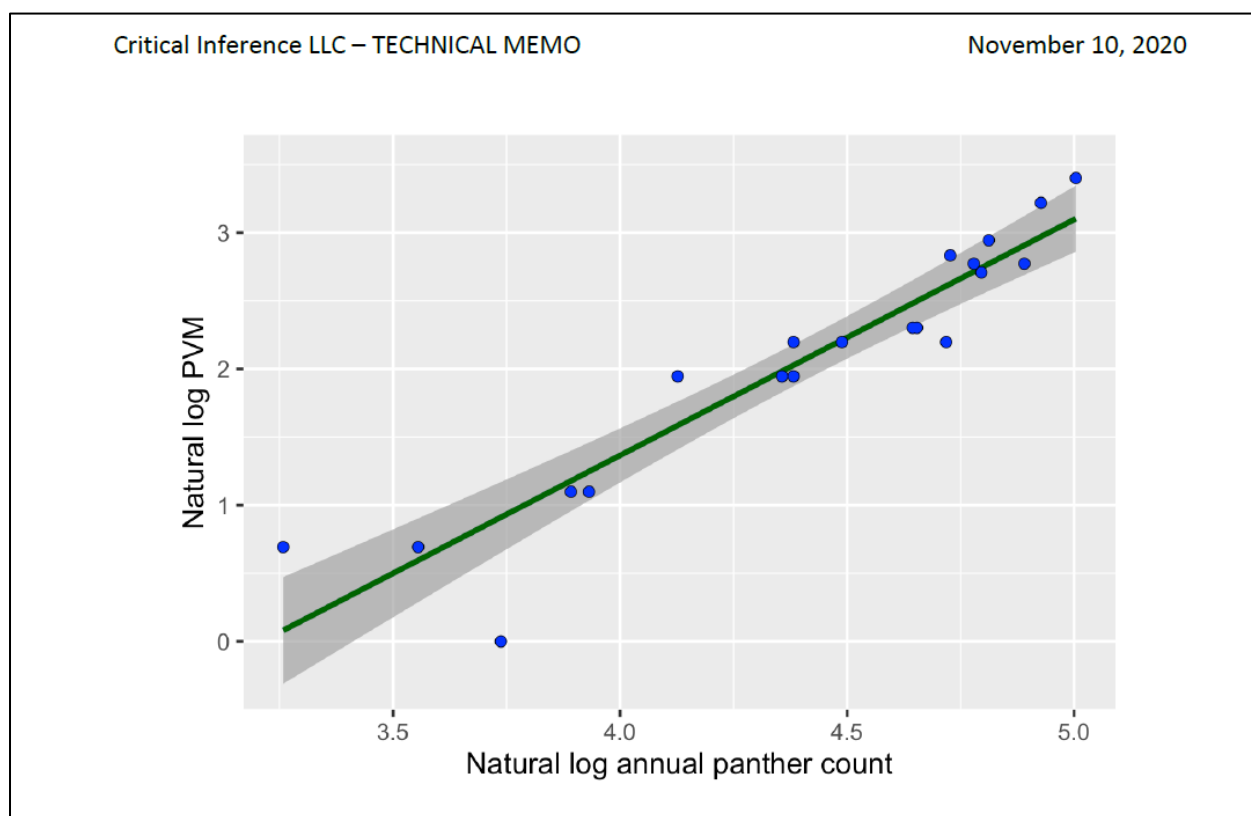


Figure 5. From Dr.Higgs Technical Memorandum, in the figure legend Dr. Higgs says: “There is clearly a strong relationship on the log-log scale; the observed correlation coefficient is 0.94. The bands around the regression line are 95% point-wise confidence bands”.

- My comment: I would interpret this relationship (i.e., “between panther annual counts (as a surrogate for changes in population size) and PVM at the regional

level.”, see Fig. 5 [which is Fig. 12 in Dr. Higgs Technical Memorandum) with caution given that neither of the measures used by Dr. Higgs in her analysis accounted for imperfect detection (nor properly accounted for uncertainty). Indeed, neither the index of abundance nor the number of reported panther deaths properly account for imperfect detection (a potentially important source of error) (Williams et al. 2002). For example, it is possible that the counts would increase because of an increase in detectability (e.g., due to potential improvement of the skills from the staff in charge of monitoring [as staff gain more experience after each field season]; or other confounding factors) or that an increase in traffic would also increase the probability of detection of road kills (because of “more eyes on the road,” among other potential factors). Thus, this positive relationship could be spurious. This is not to say that part of the observed increase in panther mortality is not linked to an increase in panther abundance (the increases in panther counts until 2015 and in PVM until 2018 provide some support for that hypothesis [Fig. 11 from Dr. Higgs Technical Memo]), but simply, that the inference that can be made based on that relationship alone is weak. If the panther population did increase, we would indeed expect some increase in mortality. The question then becomes “what is the magnitude of that increase?” (and “what fraction is due to changes in traffic patterns?”). A stronger argument would be based on models of population dynamics such as the ones developed by Hostetler et al. (2013), van de Kerk et al. (2019), McClintock et al. (2015), and the PVA from the USFWS. For the same reason that an increase in vehicle traffic would increase the chance of potential collisions, an increase in panther density would also increase the probability of potential collisions. Note that the analyses from Hostetler et al. (2013), van de Kerk et al. (2019 and McClintock et al. (2015) did not consider the increase in reported MVM between 2014 and 2018 (see section 3.2.).

5. DECISION CONTEXT FOR MODEL DEVELOPMENT AND INTERPRETATIONS

In this section, I provide perspectives from the literature and other case studies involving imperiled species which may help with respect to the choice of models and the interpretation of the analyses discussed in the BO for decision making. Models are approximations of reality, and are therefore always based on simplifications and often rely on strong assumptions. As pointed out in the common aphorism “all models are wrong, but some are useful” (Cox 1978), mathematical models generally cannot capture all of the complexities of reality but can nonetheless help us understand the natural world and make predictions. Thus, one question to ask is whether the models developed can be useful in a particular decision context. Based on my review, I found the analyses conducted by the USFWS useful, and the USFWS staff has clearly invested a significant effort in the development and implementation of their analyses. As noted throughout this review, there are several limitations to the models, which in my view could be clarified, and more details could be provided about the structure of some of the models used. For example, as I explained in *Section 3*, I suggest additional steps to make the process more transparent and reproducible, particularly given that at times it is difficult to understand what was done. With that said, there is obviously a cost – in the form of staff time investment - associated with perfecting models. There is a tradeoff between “model perfection” and timeliness when it comes to informing management decisions.

Overall, despite some evidence to support the hypothesis of population growth (historic growth, but with very large uncertainty), the information from the BO and the ecological literature points to some serious risks faced by the Florida panther. Some of the most important threats are summarized as follows:

- The evidence published in the BO and the literature indicate that the population of Florida panther is small (McBride 2008; McClintock et al. 2015). In small populations, a number of potentially interacting processes increase risks of destabilization and extinction, such as demographic stochasticity, genetic stochasticity (e.g., inbreeding depression, the Florida panther is a notorious example of inbreeding depression in the conservation literature), Allee effects, and environmental stochasticity (Lacy 2000).

- The range of the Florida panther has contracted substantially over time (Fig. 6) and faces additional threats to its habitat (e.g., expansion of urban developments, fragmentation, invasive species, potential impact of sea level rise and storms).

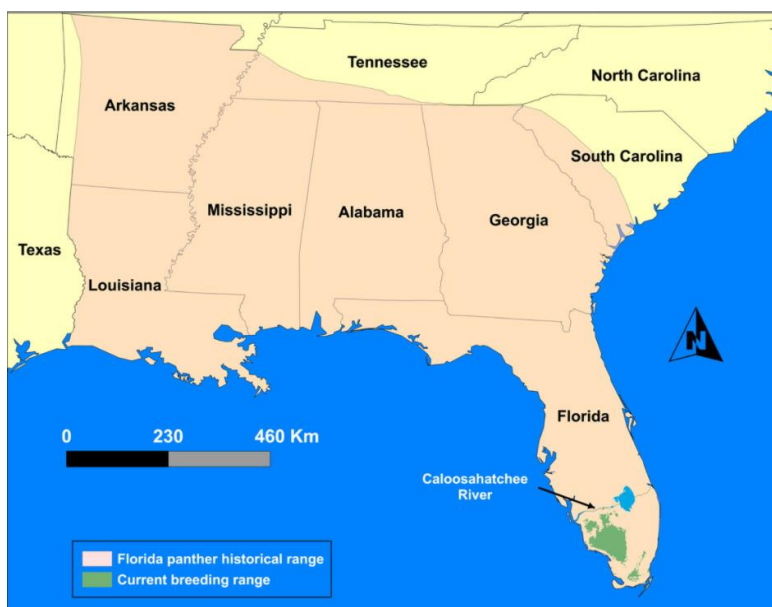


Figure 6. Range contraction of the Florida panther, from van de Kerk et al. (2019)..

- In addition to habitat loss, other notable environmental threats include the risk of diseases wiping out the population, potential impacts of invasive species, and road traffic.
- Scientific studies point to vehicle mortality as the most prominent and immediate threat faced by this population (Fig. 2-3). Thus, measures to mitigate that threat (e.g., wildlife corridors, (Downs et al. 2014)) are reasonable (and are discussed in the BO).
- The increase in MVM mortality (2014 to 2018) may deserve additional attention (section 3.2).

One challenge for the USFWS is to quantify the magnitude of the effects that they have examined, such as the relationship between traffic and mortality. Although the analyses presented in the BO provide useful assessments about the potential impact of activities and changes in

abundance (assuming that the analyses were correctly implemented), there is so much uncertainty with the processes involved that I would be cautious when it comes to the interpretation of any specific values (e.g., Table 5.9 to 5.11 in the BO) such as measures of central tendencies (e.g., mean estimates) or any other point estimate. Indeed, these specific values may give a false sense of precision, when the uncertainty is actually large. This is especially true given that important sources of uncertainty were not fully accounted for. Whenever possible, it would be useful for a better interpretability of the results to systematically provide estimates of uncertainty (e.g., standard error, and confidence intervals) associated with each point estimate that are provided in the report. Analysts working on future model developments may want to put more emphasis on accounting for uncertainty and sources of errors (e.g., parametric uncertainty, model uncertainty, imperfect detection, sampling variation). There is support for the hypothesis that vehicle mortality represents a major threat to this population; the challenge is to assess more accurately the magnitude of this threat. As explained in my comments, one possible solution, until further model developments become available, may be to better recognize the limitations of the analyses, better acknowledge uncertainty and provide more details about the methodology in order to improve transparency and reproducibility.

6. ADDITIONAL MINOR COMMENTS:

- 1. 3342. Did you mean to include demographic stochasticity in this sentence? It seems like it is out of context. Demographic stochasticity is a source of variation and describes the random fluctuations in abundance that occur because the birth and death of individuals is a discrete probabilistic event.
- 1.3469. USFWS staff wrote: “In all, the most recent analysis of population viability performed by van de Kerk et al. (2019) indicates maintenance of genetic variability in the population will remain a challenge, but that as long as it is addressed with genetic augmentation at recommended intervals a projected population size of 187 adults and subadults should remain viable for the next 50 years if the current conditions (habitat availability, access, genetic health, and prey abundance) remain unchanged.”

- My comment: I do not think that providing such a specific value (i.e., 187) without estimates of uncertainty is helpful. Also, given the large uncertainty associated with the results, I would suggest avoiding statements that seem to imply more certainty than is supported by the analyses “should remain viable for the next 50 years.”
- In the literature cited you may want to provide full citation for: *van de Kerk, M., Onorato, D.P., Hostetler, J.A., Bolker, B.M. and Oli, M.K. (2019), Dynamics, Persistence, and Genetic Management of the Endangered Florida Panther Population. Wild. Mon., 203: 3-35. <https://doi.org/10.1002/wmon.1041>.*
- 1. 3591. USFWS staff wrote: “3.9/100km² and 4.03/100km² (Onorato et al. 2020). Based on the availability of habitat in the Action Area a density-estimated population size estimate ranges between 16.2 and 16.6 panthers utilizing the Plan Area (Table 5-3).”
 - My comment: These estimates appear unreasonably precise. You may want to mention the limitations of his extrapolation approach and the lack of consideration for important sources of uncertainty.
- 1.3597: “Uncollared panthers are regularly found among road mortalities in the Plan Area To estimate a more precise number of panthers”
 - My comment: You may want to replace “precise” with “accurate.” Precision generally refers to the reciprocal of the variance (i.e., more precise implies smaller variance). Accuracy is generally defined as the overall distance between estimated (or observed) values and the true value (it can combine both bias and precision). For example, “between 16.2 and 16.6 panthers” is overly precise, so I don’t think that the correction that you were seeking was related to precision.
 - Also in this section, USFWS staff present estimates obtained with the Chapman estimator (a bias-adjusted estimator of the Lincoln-Petersen estimator), which assumes geographic/demographic closure and equal capture probabilities (within each sample) among other assumptions. Acknowledging these assumptions and potential bias of the estimator would be helpful.

LITERATURE CITED

- Caswell H (2001) Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Sunderland, MA
- Crum, N., Gowan, T.A., Krzystan, A.M., Martin, J. (2019) Quantifying risk of whale–vessel collisions across space, time, and management policies. *Ecosphere*, 10, e02713.
- Downs, Joni, Mark Horner, Rebecca Loraamm, James Anderson, Hyun Kim, and Dave Onorato. (2014) Strategically locating wildlife crossing structures for Florida panthers using maximal covering approaches. *Transactions in GIS* 18, 1, 46-65.
- Gerritsen, J. & Strickler, J.R. (1977) Encounter probabilities and community structure in zooplankton: a mathematical model. *Journal of Fisheries Research Board Canada*, 34, 73–82.
- Gurarie, E. & Ovaskainen, O. (2013) Towards a general formalization of encounter rates in ecology. *Theoretical Ecology*, 6, 189–202.
- Hostetler, J. A., D. P. Onorato, D. Jansen, and M. K. Oli. 2013. A cat's tale: the impact of genetic restoration on Florida panther population dynamics and persistence. *Journal of Animal Ecology* 82:608-620. <<http://onlinelibrary.wiley.com/doi/10.1111/1365-2656.12033/abstract>>.
- Lacy, R. (2000) Considering Threats to the Viability of Small Populations Using Individual-Based Models. *Ecol. Bull.* 48:39-51.
- Koopman, B.O. (1956) The theory of search I. kinematic bases. *Operations Research*, 4, 324–346.
- Martin, J., Q. Sabatier, T. A. Gowan, C. Giraud, E. Gurarie, C. S. Calleson, J. Ortega-Ortiz, C. J. Deutsch, A. Rycyk, and S. M. Koslovsky. 2016. A quantitative framework for investigating

- risk of deadly collisions between marine wildlife and boats. *Methods in Ecology and Evolution* 7:42–50.
- McClintock, B, Onorato, D, Martin, J. (2015). Endangered Florida panther population size determined from public reports of motor vehicle collision mortalities. *Journal of Applied Ecology*, 52, 893-901.
- Morris WF, Doak DF (2002) Quantitative conservation biology. Theory and practice of population viability analysis. Sinauer Associates, Sunderland, MA.
- R Core Team (2020). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org/
- Rockwood, R. W., J. Calambokidis, and J. Jahncke. 2017. High mortality of blue, humpback and fin whales from modeling of vessel collisions on the U.S. West Coast suggests population impacts and insufficient protections. *PLoS ONE* 12:e0183052.
- Runge, M.C., Sanders-Reed, C.A., Langtimm, C.A., Hostetler, J.A., Martin, J., Deutsch, C.J., Ward-Geiger, L.I., and Mahon, G.L. (2017). Status and threats analysis for the Florida manatee (*Trichechus manatus latirostris*), 2016: U.S. Geological Survey Scientific Investigation Report 2017–5030, 40 p
- Slade, N.A., Gomulkiewicz, R., Alexander, H.M., 1998. Alternatives to Robinson and Redford's method of assessing overharvest from incomplete demographic data. *Conserv. Biol.* 12, 148–155.
- Van Der Hoop, J.M., Vanderlaan, A.S.M. & Taggart, C.T. (2012) Absolute probability estimates of lethal vessel strikes to North Atlantic right whales in Roseway Basin, Scotian Shelf. *Ecological Applications*, 22, 2021–2033.

- van de Kerk, M., Onorato, D.P., Hostetler, J.A., Bolker, B.M. and Oli, M.K. (2019), Dynamics, Persistence, and Genetic Management of the Endangered Florida Panther Population. *Wild. Mon.*, 203: 3-35. <https://doi.org/10.1002/wmon.1041>.
- Williams, B.K., Nichols, J.D. & Conroy, M.J. (2002) *Analysis and Management of Animal Populations*. Academic Press, San Diego, CA.
- Wilson, B., Batty, R.S., Daunt, F. & Carter, C. (2007) *Collision Risks between Marine Renewable Energy Devices and Mammals, Fish and Diving Birds*. Report to the Scottish Executive. Scottish Association for Marine Science, Oban, Scotland. Oban, UK. PA37 1QA.