

Peer Review Plan for the Northern Pintail Integrated Population Model

About the document

Subject and Purpose: the U.S. Geological Survey (USGS) and the U.S. Fish and Wildlife Service (USFWS), in consultation with the Flyway Councils, have collaborated on the development of an integrated population model to support the revised decision framework for pintail adaptive harvest management. The Flyway Councils and USFWS undertook the revision process due to several concerns about the existing strategy.

Importance of Scientific Information: A full evaluation of pintail population and harvest dynamics was undertaken to serve as a basis for a revised pintail population model with updated data and modern estimation methods. Output from the new pintail population model will inform the revised pintail adaptive harvest management decision framework that serves our partners from all 4 Flyways. Once adopted by the Service this new strategy will be used setting annual harvest regulations for northern pintails.

About the Peer Review Process

Type of Review: Independent Peer Review – Our USGS colleagues will solicit peer review of the model from independent scientific reviewers through the formal USGS peer review process. Reviewers will submit individual written comments and the Service will supply responses to comments.

Number of reviewers: The USGS Peer Review will include 2 independent reviewers who are knowledgeable of integrated population models.

Reviewer Expertise: Potential reviewers will have demonstrated expertise in wildlife population modeling. Reviewer selection will also be based on one or more of the following areas of expertise: developing integrated population models for wildlife populations, decision-support modeling, data collection and analysis to inform harvest management decisions, and waterfowl biology.

Selection of Peer Reviewer: Peer reviewers will be selected based on their subject matter expertise and USGS peer review guidelines.

Management of Peer Reviewer: The peer review will be managed through the USGS peer review process. Peer reviewers will be given 21 days to complete their reviews. The estimated start of the peer review is March 2024.

About Public Participation The public is invited to submit comments on this peer review plan by sending emails to scott_boomer@fws.gov (please state “pintail IPM review” in the subject line). The deadline for filing comments is March 15 2024.

Reviewers:

Thomas Riecke, PhD
Assistant Professor
James K. Ringelman Chair in Waterfowl Conservation
University of Montana

Nathan J. Hostetter, PhD
Assistant Unit Leader, USGS NC Cooperative Fish and Wildlife Research Unit
Assistant Professor, Department of Applied Ecology, North Carolina State University

Topic: Review of *An Integrated Population Model for Northern Pintail Adaptive Harvest Management*, 2024, Boomer, Runge, and Osnas.

I reviewed *An Integrated Population Model for Northern Pintail Adaptive Harvest Management*, including text, tables, figures, and appendices. The paper provides important updates on parameters needed for the adaptive harvest management framework of northern pintails.

The methods and analyses are robust and clearly explained, the conclusions are supported by the data and analyses, the appendices are appropriate and informative, and conclusions are based on sound scientific reasoning. The authors' approach integrates multiple sources of information, which results in defensible results with clear interpretations.

I found no technical issues or concerns. I provide some minor editorial suggestions below that may help improve clarity and reproducibility.

Minor comments:

(1) Section Population Model (paragraph 1): Be cautious with the phrasing “we developed ... an IPM... to evaluate *all* the available information from pintail monitoring programs...” (emphasis my own). While this paper summarizes an extraordinary effort, the phrase ‘*all* the available information’ may be an overstatement.

(2) Section Population Model (paragraph 2): Define WBPHS on its first use. Check the manuscript throughout to verify acronyms and abbreviations are defined. These terms are common to waterfowl research and harvest management, but non-waterfowl biologists would benefit from definitions.

(3) Figure 1. It is not clear why some Figure 1 parameters and events are indexed by tt while others are not. Additionally, a few of the parameters appear to be indexed differently in the figure compared to the text (e.g., Figure uses $NN_{aaaaaa,ssaass}$ while text defines $NN_{aaaaaa,ssaass,yyyy}$).

(4) Figure 1 and equations 1-4. Clarify the need for the doubling in “ $2 * R_t * SS_f$ ”. It is not clear how this relates to equations 1-4 and the associated definition of those parameters.

(5) Equation 5 is missing.

(6) Equations 11-12. Where possible, standardize indexing throughout the manuscript. For example, SS_{AAA} is first introduced as being indexed by age and sex (Population Model, first paragraph), then it is indexed with year as the first index in Fig 1 ($SS_{tt,AAA}$), then equation 11-12 use $SS_{aaaaaa,ssaass,yyyy}$.

(7) Text between equations 12 and 13 is awkwardly worded. Consider clarifying.

(8) Sentence after Equation 18. Clarify “with a *mean equal to 0* and an estimated variance ($\sigma\sigma^2$)” given equation 18 defines Normal- $(\mu\mu^{RR}, \sigma\sigma^2)$.
RR

(9) After equation 19. Define PCS on first occurrence.

(10) After equation 21. Clarify the adjustment equation for crippling loss. “We estimated the probability of being killed during the hunting season ($KK_{aa,ss,tt}$) by adjusting harvest probabilities by $1-CC \dots$ ” does not fully clarify the adjustment.

(11) Equations 14-16. The notation follows standards for adaptive harvest models of waterfowl; however, redefining notation can be confusing. For example, mm_{tt} is first defined as the age ratio in year tt (equations 1-4), then redefined as the number of recoveries ($mm_{aa,tt}$; equations 14-16). The authors are experts on these topics, and I will defer to them on what provides the greatest clarity.

(12) Equations 14-15 and 22-24. Equation 14-15 define $ff_{aa,tt}$ (“the direct recovery rate for birds aged aa in year tt ”), but the text immediately prior to equation 22 then redefines ff with new indexing $ff^{SS}_{aa,ss,tt}$ (different super- and subscripts).

(13) Equation 23 is missing.

Overall, this manuscript was informative, well written, and updates important information for adaptive harvest management framework.

Please feel free to contact me if there are additional questions.

An Integrated Population Model for Northern Pintail Adaptive Harvest Management

Boomer GS, Runge MC, Osnas EE

Summary

This manuscript supports the revision of an adaptive harvest management framework to inform pintail harvest regulations in the United States. The Authors use long-term banding, harvest, and aerial survey data to construct an integrated population model for northern pintail populations breeding in North America. This modeling framework (i.e., IPM) is currently the most advanced and appropriate approach to jointly analyze multiple types of abundance and demographic data (Schaub & Ke’ry, 2021). The Authors are clearly experts in this type of analysis, and they have used the most effective existing software to implement the model. Although I felt it was unnecessary, I’ve independently replicated their analyses using publicly available data and reached similar conclusions. In this review I’ve included some minor editorial comments meant to clarify the methods and results. Finally, I greatly appreciated the opportunity to review this manuscript draft.

Comments

Background and History: Just a note that this is exceptionally well framed. I think it might be helpful to explicitly revisit the relevant goals in the conclusion. In the summary section some text might be added clarifying that this analysis very clearly met the third motivating goal, and that this as well as other recent work (Osnas *et al.*, 2021) has led to improved predictive performance. Clearly, improved predictive ability will allow for improved ability to address the other clearly stated goals.

Section 2.2. introductory paragraph: Is there an opportunity to add a sentence here similar to: *These two hypotheses (i.e., additive and compensatory harvest) represent extremes on either end of a spectrum of harvest effects. To assess the observed effect of harvest rather than relative support for one of two extremes, we modeled annual survival.* Beyond the move to IPMs, I see this as a major change in the

most recent (MC mallards, E mallards, this study) versions of the models underlying these types of decisions. I feel it's a very beneficial change from a predictive perspective, and seems to be a fairly consistent result that has the potential to reduce conflict (i.e., it seems like the general answer across the three IPMs I've seen is that harvest is partially compensatory). I'm simply wondering if the Authors want to highlight this shift in thinking more directly.

Summer survival: Female summer survival has been modeled as a constant. Recent (Riecke *et al.*, 2022a,b) and previous (Dufour & Clark, 2002; Arnold & Howerter, 2012; Arnold *et al.*, 2012) research indicates that there can be substantial temporal variation in natural mortality in other species, which predominantly occurs during breeding (Richkus *et al.*, 2005). Although two-season banding data for pintail are quite limited, this might be an important topic to explore in the future. Summer survival of second-year (i.e., first-time breeders) females is also often higher than adult females in ducks, potentially as a result of reduced reproductive investment (Dufour & Clark, 2002; Riecke *et al.*, 2022b). I acknowledge that existing datasets may not support this level of complexity.

Equations 14-15,19: The number of trials ($M_{age,t}$) should come before the probabilities, e.g.,

$$m_{juv,t} \sim \text{binomial}(M_{juv,t}, f_{juv,t}).$$

Equations 19: Just a note to clarify that $w_{juv,t}$ is the number of juvenile female wings.

Section 2.4: The sentence prior to equation 13 has a typo, perhaps 'from one year to the next with this information as,'

Section 2.4: That Vehtari *et al.* (2021) paper is fantastic. Just a note to indicate that I appreciate the

efforts the Authors have taken to ensure reliable inference.

Figure 3 and sex ratios: If we use the same equation used to estimate age ratios to instead estimate adult sex ratios, we reach fairly different conclusions (m is much greater and increasing, although it's measured in the fall using this approach and the spring using the IPM, the difference is too great to be explained by seasonal shifts in sex ratio). I understand there may be some underlying bias in the harvest data, and there are a number of potential explanations for this. I appreciate that the Authors' included some text regarding potential uncertainty here. As a final note, if m increases, then the γ_R parameter will be closer (much closer?) to 1.

Section 3.3, hunting mortality: There appears to be a very strong relationship between hunter numbers (indicated by duck stamps sold or USFWS estimates of active hunters) and pintail harvest probabilities. This is consistent for a number of other well-marked species, and generally expected. I don't think it's necessary to formally include this in the model, but some concern about potential changes in bag limits may be alleviated by a clearer recognition that there are simply fewer 'bags.' Perhaps something like this could be added at the end of the first sentence, e.g.; 'when more restrictive regulations were enacted (citations) and as the number of active hunters has declined.'

Section 3.3, adult female survival and harvest dynamics: I think it may be prudent to be more cautious when suggesting that harvest for adult females is 'more compensatory.' This is certainly what the data indicate if harvest is the sole covariate on survival. In fact, if you parameterize the model to estimate the correlation between survival and harvest, you can even recover a positive correlation (i.e., increasing harvest increases survival, Figure 2 in this review). I think it's possible that:

1. Harvest is a small component of overall mortality for adult females (Figure 1 in this review, Richkus *et al.* 2005).
2. Changes in habitat conditions have led to declines in pintail female survival, and also pintail populations.
3. Managers have restricted harvest in response to declines in N.

Put simply, even if harvest has a direct 'additive effect' on survival, if other mortality sources increase as harvest declines, this may lead to little change in survival. The theory underlying compensatory harvest is that this increase in other mortality sources is due to a decline in harvest, but it may be due to external unrelated factors (e.g., if we increased harvest back up to 0.07 for adult females there is no guarantee that other sources of natural mortality related to breeding would decline, these may be related entirely to habitat quality). This argument has been made in the past in the opposite direction (Sedinger & Herzog, 2012), here I'm suggesting that it applies more generally. The final observed relationship is thus not purely a 'causal' relationship where only harvest is affecting survival. Rather, it's an outcome with multiple contributing factors. For pintails, hunting mortality makes up 1/20th and 1/5th of adult

female and male mortality risk respectively (Figure 1 in this review). To be clear, I am not suggesting that it is necessary to incorporate this into the current manuscript, but it may be beneficial to allow survival to also vary as a function of other covariates such as reproductive investment or environmental conditions in the future (e.g., Osnas *et al.* 2021).

Page 15, interpreting β 's: The Authors state that '*posterior median estimates were between 0 and 1, suggesting a partially compensatory response to harvest mortality.*' In the model, beta(1,1) priors were assigned to these parameters, thus an outcome between 0 and 1 is the only possible outcome, regardless of the true underlying process. I fully agree with this conclusion, just a note that there may be a different way to explain it that isn't pre-determined.

Page 15, bottom paragraph: I believe there are alternative conclusions that could be drawn here. Specifically, one might also conclude that estimates from the BPOP are biased low to some degree. The Authors have already demonstrated some degree of bias both here (Figure 2 in the manuscript) and elsewhere (Runge & Boomer, 2005) as a function of population response to wetland conditions. Although alternative methods of abundance estimation (e.g., Lincoln estimates) rely on estimates of harvest that may be less reliable than estimates of abundance from aerial surveys, there is still certainly a possibility that part of this discrepancy may be due to additional unmodeled issues with abundance estimation. These are not mutually exclusive explanations, i.e., the harvest estimates may be high and the WBPHS may be low. It may be helpful to rewrite this section in a slightly more ambiguous way. I think it's also important that assuming that the BPOP is unbiased (once latitude is corrected for) and this is all an upward bias in the harvest data is the most conservative possible approach, i.e., if we just assumed the harvest data is accurate then we'd basically be saying the BPOP represents 50% of the 'true' population. That would lead to more liberal regulations, while the current approach would lead to more conservative potential harvest regs, if I understand it correctly.

Figure 7: These estimates, as well as the estimates from Osnas *et al.* (2021), represent a substantial change from the previous model. There may be a way to briefly mention this in the text as an advantage of the IPM framework to help justify future management decisions. It's raised as an important third motivation for updating the strategy in Section 1, and this (as well as Figure 6) clearly resolves some of this concern.

Broken links in references: It seems like the recent move to ServCat has led to a number of broken links. I've included a list below, I believe it's complete but could be good to double-check.

Conroy & Kremenetz 1990 (there's no version at the link)

Runge et al. 2002 (broken)

USDoI 2013 (broken)

USFWS 2010 (broken)

USFWS 2019 (broken)

Conclusions

The Authors have used the most effective existing modeling approach (Schaub & Ke'ry, 2021) to develop a population model for Northern Pintails. The new model recovers more biologically plausible parameter estimates than a previous model, resulting in enhanced predictive ability. This is tremendously valuable, as more effective predictions may allow for improved management decisions in the face of uncertainty. I hope that the Authors find this review to be constructively critical. I tremendously appreciate the opportunity to review the manuscript, as well as the substantial work that went into developing the new model.

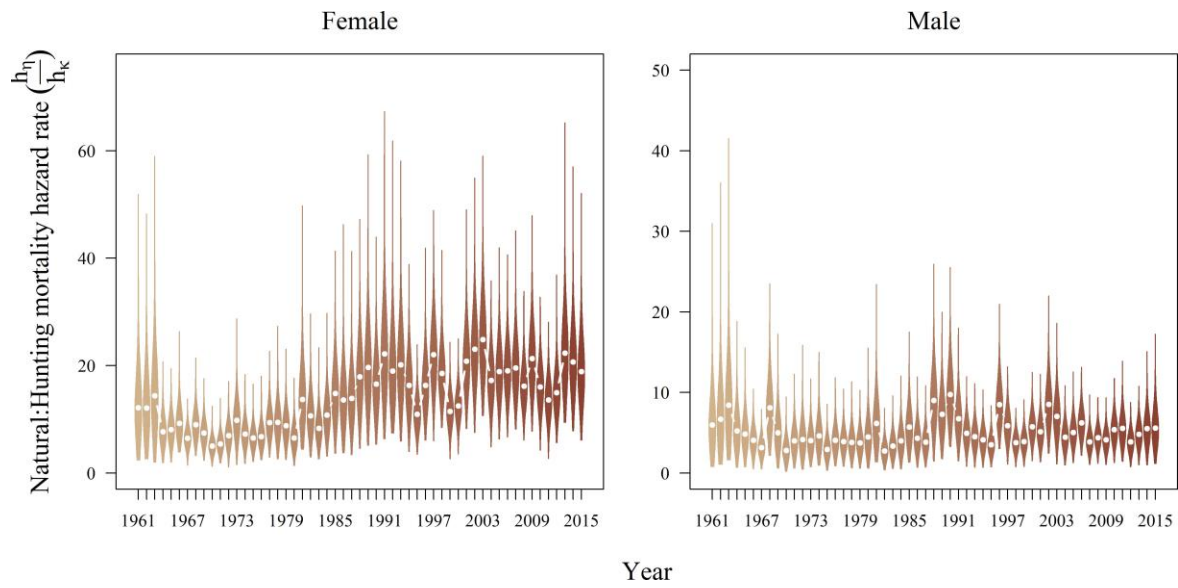


Figure 1. Violin plots of the ratio of natural to hunting mortality hazard rates, i.e., the relative risk of natural to hunting mortality, for adult female Northern Pintail.

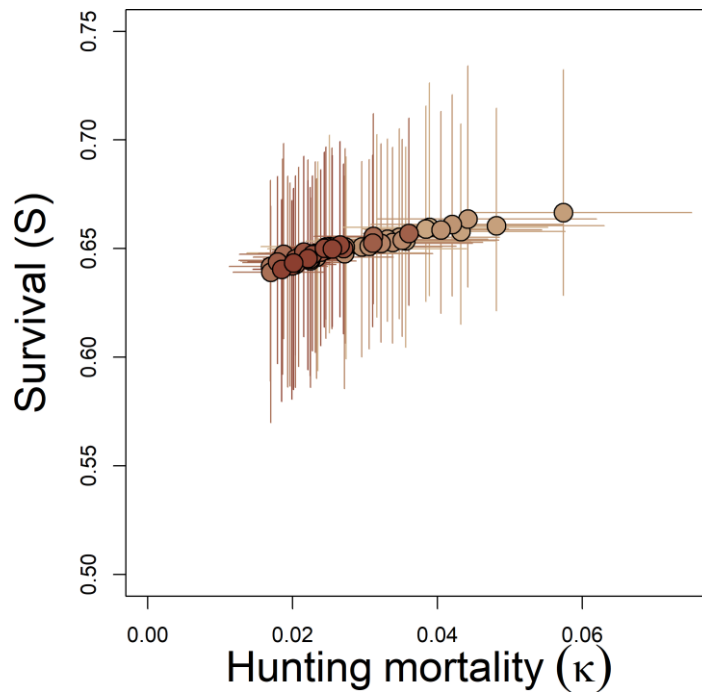


Figure 2. Medians and 95% credible intervals for survival and hunting mortality probabilities of adult female Northern Pintail.

References

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- Schaub, M. & Ke'ry, M. (2021) *Integrated population models: Theory and ecological applications with R and JAGS*. Academic Press.
- Sedinger, J.S. & Herzog, M.P. (2012) Harvest and dynamics of duck populations. *The Journal of Wildlife Management*, **76**, 1108–1116.
- Vehtari, A., Gelman, A., Simpson, D., Carpenter, B. & Bürkner, P.C. (2021) Rank-normalization, folding, and localization: an improved \hat{R} for assessing convergence of MCMC (with discussion). *Bayesian Analysis*, **16**, 667–718.

USGS Fundamental Science Practices

Response to Reviews

Boomer et al., “An Integrated Population Model for Northern Pintail Adaptive Harvest Management”

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I found no technical issues or concerns. I provide some minor editorial suggestions below that may help improve clarity and reproducibility.

Author response: Thank you for the editorial suggestions, most of which we have accepted.

Minor Comments:

- 1) Section Population Model (paragraph 1): Be cautious with the phrasing “we developed ... an IPM... to evaluate all the available information from pintail monitoring programs...” (emphasis my own). While this paper summarizes an extraordinary effort, the phrase ‘all the available information’ may be an overstatement.

Author response: We agree and have modified the sentence accordingly.

- 2) Section Population Model (paragraph 2): Define WBPHS on its first use. Check the manuscript throughout to verify acronyms and abbreviations are defined. These terms are common to waterfowl research and harvest management, but non-waterfowl biologists would benefit from definitions.

Author response: We have checked the document for acronyms and added necessary definitions upon first use.

- 3) Figure 1. It is not clear why some Figure 1 parameters and events are indexed by tt while others are not. Additionally, a few of the parameters appear to be indexed differently in the figure compared to the text (e.g., Figure uses $NNaaaaaa,sss ss$ while text defines $NNaaaaaa,sss ss,yyyy$).
- 4) *Author response: We agree and have modified the figure to include a consistent notation for the components of the population and the key demographic parameters.*
- 5) Figure 1 and equations 1-4. Clarify the need for the doubling in “ $2*R_t*SSf$ ”. It is not clear how this relates to equations 1-4 and the associated definition of those parameters.
- 6) *Author response: We have modified the figure and the text in sections 2 and 2.1 to fully describe how we use female age ratios to model pintail recruitment of each sex.*
- 7) Equation 5 is missing.

Author response: We checked each equation and re-numbered accordingly.

- 8) Equations 11-12. Where possible, standardize indexing throughout the manuscript. For example, $SSAAAA$ is first introduced as being indexed by age and sex (Population Model, first paragraph), then it is indexed with year as the first index in Fig 1 ($SStt,AAAA$), then equation 11-12 use $SSaaaaaa,sss ss,yyyy$.

Author response: We agree this notation is confusing. We checked each equation and made changes to include a consistent notation for each sex and age class designations.

- 9) Text between equations 12 and 13 is awkwardly worded. Consider clarifying.

Author response: We agree and have modified the sentence accordingly:

“We can also update the estimate of the male fraction of the population for the next year with...”

- 10) Sentence after Equation 18. Clarify “with a mean equal to 0 and an estimated variance ($\sigma\sigma RR2$)” given equation 18 defines $\text{Normal}(\mu\mu ttRR, \sigma\sigma RR2)$.

Author response: We have modified the sentence to more accurately define the log-linear model and the corresponding variance term.

- 11) After equation 19. Define PCS on first occurrence.

Author response: We have added the necessary definition in the first sentence of section 2.1.

12) After equation 21. Clarify the adjustment equation for crippling loss. “We estimated the probability of being killed during the hunting season ($KK_{aa,ss,tt}$) by adjusting harvest probabilities by $1-CC$...” does not fully clarify the adjustment.

Author response: We have clarified the equation with the following:

“We estimated the probability of being killed during the hunting season ($K_{a,s,t}$) by dividing harvest probabilities by $(1 - C)$ where C is the crippling loss rate and equal to 0.2 (Anderson and Burnham 1976).

13) Equations 14-16. The notation follows standards for adaptive harvest models of waterfowl; however, redefining notation can be confusing. For example, $mmtt$ is first defined as the age ratio in year tt (equations 1-4), then redefined as the number of recoveries ($mmaa,tt$; equations 14-16). The authors are experts on these topics, and I will defer to them on what provides the greatest clarity.

Author response: We agree this notation is confusing. We checked each equation and made changes to eliminate redefinitions in our notation.

14) Equations 14-15 and 22-24. Equation 14-15 define $ffaa,tt$ (“the direct recovery rate for birds aged aa in year tt ”), but the text immediately prior to equation 22 then redefines ff with new indexing $ffaa,ss,ttSS$ (different super- and subscripts).

Author response: This comment is a good catch. We have removed the parameter in parentheses and define the conditional recovery probabilities with equations 21 and 22.

15) Equation 23 is missing.

Author response: We checked each equation and re-numbered accordingly.

Summary

This manuscript supports the revision of an adaptive harvest management framework to inform pintail harvest regulations in the United States. The Authors use long-term banding, harvest, and aerial survey data to construct an integrated population model for northern pintail populations breeding in North America. This modeling framework (i.e., IPM) is currently the most advanced and appropriate approach to jointly analyze multiple types of abundance and demographic data (Schaub & Ke’ry, 2021). The Authors are clearly experts in this type of analysis, and they have used the most effective existing software to implement the model.

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Author response: Thank you for the editorial suggestions, most of which we have accepted.

Comments:

- 1) Background and History: Just a note that this is exceptionally well framed. I think it might be helpful to explicitly revisit the relevant goals in the conclusion. In the summary section some text might be added clarifying that this analysis very clearly met the third motivating goal, and that this as well as other recent work (Osnas *et al.*, 2021) has led to improved predictive performance. Clearly, improved predictive ability will allow for improved ability to address the other clearly stated goals.

Author response: We agree. We have re-structured the summary section to highlight the structural changes resulting from this IPM and the implications for pintail AHM strategy development.

- 2) Section 2.2. introductory paragraph: Is there an opportunity to add a sentence here similar to: *These two hypotheses (i.e., additive and compensatory harvest) represent extremes on either end of a spectrum of harvest effects. To assess the observed effect of harvest rather than relative support for one of two extremes, we modeled annual survival.* Beyond the move to IPMs, I see this as a major change in the most recent (MC mallards, E mallards, this study) versions of the models underlying these types of decisions. I feel it's a very beneficial change from a predictive perspective, and seems to be a fairly consistent result that has the potential to reduce conflict (i.e., it seems like the general answer across the three IPMs I've seen is that harvest is partially compensatory). I'm simply wondering if the Authors want to highlight this shift in thinking more directly.

Author response: This is a great comment that highlights an important point about how we arrived at the decision to model annual survival as a function of harvest mortality. We have re-structured the opening paragraph of section 2.2 to explain our rationale for the survival submodel.

- 3) Summer survival: Female summer survival has been modeled as a constant. Recent (Riecke *et al.*, 2022a,b) and previous (Dufour & Clark, 2002; Arnold & Howerter, 2012; Arnold *et al.*, 2012) research indicates that there can be substantial temporal variation in natural mortality in other species, which predominantly occurs during breeding (Richkus *et al.*, 2005). Although two-season banding data for pintail are quite limited, this might be an important topic to explore in the future. Summer survival of second-year (i.e., first-time breeders) females is also often higher than adult females in ducks, potentially as a result of reduced reproductive investment (Dufour & Clark, 2002; Riecke *et al.*, 2022b). I acknowledge that existing datasets may not support this level of complexity.

*Author response: We agree that this is an important part of the pintail annual cycle. Given the difficulties we found in attempting to use post season banding data to estimate seasonal survival rates (Osnas *et al.* 2021), we were left to specify informative priors for male and female summer survival rates based on parameters taken from the literature.*

- 4) Equations 14-15,19: The number of trials ($M_{age,t}$) should come before the probabilities, e.g., $m_{juv,t} \sim \text{binomial}(M_{juv,t}, f_{juv,t})$.

Author response: We agree and edited each equation accordingly.

- 5) Equations 19: Just a note to clarify that $w_{juv,t}$ is the number of juvenile female wings.

Author response: We have modified the notation to clarify that we use female wings.

- 6) Section 2.4: The sentence prior to equation 13 has a typo, perhaps 'from one year to the next with this information as,'

Author response: We have edited the sentence to read: "We can also update the estimate of the male fraction of the population for the next year with..."

- 7) Section 2.4: That Vehtari *et al.* (2021) paper is fantastic. Just a note to indicate that I appreciate the efforts the Authors have taken to ensure reliable inference.

Author response: Thank you. We appreciate the acknowledgement and agree that this reference provides important diagnostics to include in assessment featuring MCMC methods.

- 8) Figure 3 and sex ratios: If we use the same equation used to estimate age ratios to instead estimate adult sex ratios, we reach fairly different conclusions (m is much greater and increasing, although it's measured in the fall using this approach and the spring using the IPM, the difference is too great to be explained by seasonal shifts in sex ratio). I understand there may be some underlying bias in the harvest data, and there are a number of potential explanations for this. I appreciate that the Authors' included some text regarding potential uncertainty here. As a final note, if m increases, then the γ_R parameter will be closer (much closer?) to 1.

Author response: This is an interesting comment and touches on an important aspect of the pintail population structure (sex ratio) which has major implications for harvest policy. We acknowledge that our model formulation is constrained by the harvest management decision context which historically has relied on BPOP estimates from the WBPHS. As a result, our frame of reference is based on these observations and we have attempted to develop a model that predicts changes in this state variable. We appreciate the observations in this comment that describe how sex ratios derived from and analysis of harvest data may offer a different pattern of changing pintail sex ratios. We agree that there are many explanations for the differences in these estimates and that our decision to structure our population model around BPOP observations may also explain how these values are different. The reconciliation of these multiple data sources describing pintail population dynamics was a major challenge in developing the pintail IPM.

- 9) Section 3.3, hunting mortality: There appears to be a very strong relationship between hunter numbers (indicated by duck stamps sold or USFWS estimates of active hunters) and pintail harvest probabilities. This is consistent for a number of other well-marked species, and generally expected. I don't think it's necessary to formally include this in the model, but some concern about potential changes in bag limits may be alleviated by a clearer recognition that there are simply fewer 'bags.' Perhaps something like this could be added at the end of the first sentence, e.g.; 'when more restrictive regulations were enacted (citations) and as the number of active hunters has **declined.**'

Author response: This is a useful suggestion and we have added the text describing declining hunter numbers.

- 10) Section 3.3, adult female survival and harvest dynamics: I think it may be prudent to be more cautious when suggesting that harvest for adult females is 'more compensatory.' This is certainly what the data indicate if harvest is the sole covariate on survival. In fact, if you parameterize the model to estimate the correlation between survival and harvest, you can even recover a positive correlation (i.e., increasing harvest increases survival, Figure 2 in this review). I think it's possible that:

1. Harvest is a small component of overall mortality for adult females (Figure 1 in this review, Richkus *et al.* 2005).
2. Changes in habitat conditions have led to declines in pintail female survival, and also pintail populations.
3. Managers have restricted harvest in response to declines in N.

Put simply, even if harvest has a direct ‘additive effect’ on survival, if other mortality sources increase as harvest declines, this may lead to little change in survival. The theory underlying compensatory harvest is that this increase in other mortality sources is due to a decline in harvest, but it may be due to external unrelated factors (e.g., if we increased harvest back up to 0.07 for adult females there is no guarantee that other sources of natural mortality related to breeding would decline, these may be related entirely to habitat quality). This argument has been made in the past in the opposite direction (Sedinger & Herzog, 2012), here I’m suggesting that it applies more generally. The final observed relationship is thus not purely a ‘causal’ relationship where only harvest is affecting survival. Rather, it’s an outcome with multiple contributing factors. For pintails, hunting mortality makes up 1/20th and 1/5th of adult female and male mortality risk respectively (Figure 1 in this review). To be clear, I am not suggesting that it is necessary to incorporate this into the current manuscript, but it may be beneficial to allow survival to also vary as a function of other covariates such as reproductive investment or environmental conditions in the future (e.g., Osnas *et al.* 2021).

Author response: We agree with this comment and have expanded this section of the discussion to acknowledge that caution is warranted in drawing strong conclusions regarding the true relationship between harvest mortality and annual survival. We have included the following: “However, caution is warranted in drawing strong conclusions about the causal relationships between changes in harvest rates and variation in annual survival for pintails. Recent work investigating alternative predictive relationships between harvest and natural mortality as a function of covariates (e.g., hunting effort) and density dependence demonstrate the limitations of these more simplified models and their ineffectiveness in uncovering the true underlying relationship between harvest mortality and annual survival (Riecke et al. 2022a,b).”

- 11) Page 15, interpreting β 's: The Authors state that ‘*posterior median estimates were between 0 and 1, suggesting a partially compensatory response to harvest mortality.*’ In the model, beta(1,1) priors were assigned to these parameters, thus an outcome between 0 and 1 is the only possible outcome, regardless of the true underlying process. I fully agree with this conclusion, just a note that there may be a different way to explain it that isn’t pre-determined.

Author response: We agree and edited our interpretation of the B1 estimates to remove this confusion.

12) Page 15, bottom paragraph: I believe there are alternative conclusions that could be drawn here. Specifically, one might also conclude that estimates from the BPOP are biased low to some degree. The Authors have already demonstrated some degree of bias both here (Figure 2 in the manuscript) and elsewhere (Runge & Boomer, 2005) as a function of population response to wetland conditions. Although alternative methods of abundance estimation (e.g., Lincoln estimates) rely on estimates of harvest that may be less reliable than estimates of abundance from aerial surveys, there is still certainly a possibility that part of this discrepancy may be due to additional unmodeled issues with abundance estimation. These are not mutually exclusive explanations, i.e., the harvest estimates may be high and the WBPHS may be low. It may be helpful to rewrite this section in a slightly more ambiguous way. I think it's also important that assuming that the BPOP is unbiased (once latitude is corrected for) and this is all an upward bias in the harvest data is the most conservative possible approach, i.e., if we just assumed the harvest data is accurate then we'd basically be saying the BPOP represents 50% of the 'true' population. That would lead to more liberal regulations, while the current approach would lead to more conservative potential harvest regs, if I understand it correctly.

Author response: We agree and have added text to the results paragraph describing this alternative explanation for the discrepancies between the harvest data measured through HIP and the predicted harvest from the IPM. We have also added additional context describing how the observed BPOP measured through the WBPHS forms the basis for our AHM decision making and therefore is the baseline we have chosen to use as a reference when reconciling the scaling differences associated with the major pintail monitoring data.

13) Figure 7: These estimates, as well as the estimates from Osnas *et al.* (2021), represent a substantial change from the previous model. There may be a way to briefly mention this in the text as an advantage of the IPM framework to help justify future management decisions. It's raised as an important third motivation for updating the strategy in Section 1, and this (as well as Figure 6) clearly resolves some of this concern.

Author response: We agree and have included language in the summary to highlight the benefits of updated harvest and survival rates for the survival sub-model development and ultimately the modeling framework for pintail AHM.

14) Broken links in references: It seems like the recent move to ServCat has led to a number of broken links. I've included a list below, I believe it's complete but could be good to double-check.

Conroy & Krementz 1990 (there's no version at the link)

Runge et al. 2002 (broken)

USDoI 2013 (broken)

USFWS 2010 (broken)

USFWS 2019 (broken)

Author response: Thanks for checking these links. Given the recent changes in USFWS webpages, we have re-formatted the Literature Cited section to remove all URLs.