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Dr. Prange,

First, please accept my apologies for the significant delay in returning revisions on this manuscript. A number of life and work priorities interfered with a more timely response schedule and I sincerely appreciate the flexibility PeerJ extends to authors. We are committed to a quick turnaround on any future revisions or tasks associated with this manuscript and we look forward to a final publication in PeerJ.

While many of the comments and suggestions from reviewers were minor, we feel they deserved appropriate time, consideration, and exploration. We have made several changes to the manuscript. We hope our responses here reflect that consideration and communicate our edits. We are grateful to the reviewers for their thoughtful comments. Lastly, we also used this opportunity to improve the quality of the underlying telemetry data set and expand the reproducibility of the analysis to meet or exceed expectations for open science, data availability, and code availability.

Below, please find detailed responses to each of the reviewer comments. In addition to this letter, the full suite of updates are all contained and documented within two pull requests (see https://github.com/noaa-afsc/berchukseals-haulout/pull/51 (initial resubmission) and https://github.com/noaa-afsc/berchukseals-haulout/pull/52 (additional suggestions from PeerJ staff). We have also provided a pdf document ([Compare Report] London_HauloutBehavior.pdf]) that indicates all changes between the compendium supporting this revised manuscript and the compendium supporting the originally submitted manuscript.

Thank you, again, for your time and consideration. And, additionally, thank you to the reviewers for their time. It is much appreciated and we feel the manuscript is a better product as a result.

Regards

Josh M London, PhD

Response to Reviewers

Here, we respond directly to each of the suggested edits and comments. These responses are organized by reviewer. All responses are prefaced with [author response] and line numbers in the original submission are used as reference.

Reviewer 1 (A. Fischbach)

The authors have put substantial efforts into setting the context for their analysis, citing relevant studies. I would like to see a more direct approach in the framing of their problem: the improvements of abundance estimates required by the Marine Mammal Protection Act and Endangered Species Act. I would like to see a specific example of how the modeled availability would have affect population abundance estimates by apply the availability model to aerial survey data and providing an adjusted abundance estimate.

[author response] We address this in the manuscript by introducing the importance of the statutory requirements of the MMPA and ESA early in the second paragraph of the introduction. We hope this frames the important link in the mind of the reader between the work described here and the need for improved abundance estimates.

Regarding the desire for specific examples of how the modeled availability would have impacted population abundance estimates from aerial survey data, we don't have the ability to provide a full example because the aerial survey data are not yet published and available. However, we note that Conn and Trukhanova (2023, Marine Mammal Science 39:648-661) used some of our preliminary estimates to assess potential aerial survey bias in using telemetered samples that are biased towards younger age-sex classes. Their analysis is based on bias(N) = bias(1/a) where a is availability (i.e., proportion hauled out).

The findings are appear robust and intuitive. The authors need to improve the presentation of the findings to improve clarity and help the reader understand how they addressed the knowledge gap.

[author response] The reviewer provided numerous comments and suggestions annotated throughout the PDF that address the concern of presentation and clarity. In the next section we provide responses to those annotations

Reviewer 1 (A. Fischbach) - PDF Annotated Comments & Suggested Edits

Title: The reviewer suggests removing and aerial survey detectability from the title of the manuscript and suggests adding the seasonal time period our study focused on.

[author response] We have changed the title to: Spring haul-out behavior of seals in the Bering and Chukchi seas

Abstract: Can you make a statement in your abstract that use of modeled haulout behavior using covariates available from regional reananalysis data improved the confidence intervals on availability estimates and that this would improve aerial survey abundance estimation efforts?

[author response] Unfortunately, we can't make this statement because inclusion of additional covariates (such as weather products) in haul-out models only serves to increase standard errors in predictions. The benefit of including weather covariates is to more accurately explain variation in survey counts; it is thus more relevant to reducing bias in aerial survey estimates than it is to increasing precision.

Please use direct language. You are not making findings on how seals rely on sea ice, rather you are improving methods to estimate their availability for improved aerial survey population estimation efforts. Here you are focused on modeling ice sea availability to aerial survey so that aerial survey counts may be appropriately interpreted. Please be clear that you are considering ice seal behaviors that may be telemtered as "dry out of water behaviors" that may be interpreted as behaviors that place the seal on top of the ice and available for observation by an aerial survey.

[author response] The opening sentence of the abstract is a statement regarding the reliance of ice-associated seals on sea-ice for a range of important life history behaviors. We think this statement is an important introduction for readers who are not familiar with ice-associated seals. We do agree with the reviewer's suggestion for more direct language and have made edits to the beginning of the abstract with this in mind.

Abstract: Did you use previously published data, or did you collect it? Be specific using an active voice so that readers may understand your effort.

For better flow, please indicate the behavioral data logging time scale here when you describe the data collection, not later when you speak to the analytical construct.

[author response] We have edited this to simply state data from satellite-linked bio-loggers ... we have also altered this sentence to specifically mention the hourly timescale for the bio-logger data

The term "basking" implies a subset of activities that ice seals may engage in when hauled out on sea ice and not an activity that can be directly telemetered using your data logger. Yet, what you are describing is "haul-out behavior". Please use this term here.

[author response] edited to remove use of 'basking'

Can you help your naive reader understand why you consider these covariates to be of interest and why others were not considered.

[author response] The main body of the paper includes this discussion. Given the limited space and purpose of the abstract we feel it best to simply list the covariates of interest

Line 41: Please use specific terms and not metaphors so that second-language English readers may better understand your writing.

[author response] We have edited 'ripple effects' to 'tangible effects'

Line 41: What about human communities that don't live in the region, but that send large LNG tankers and other vessel through the region? The loss of sea ice has effects on those communities and activities too.

[author response] Clearly there are a large number impacts of loss of sea ice to human communities (and ecosystems) beyond the Arctic region to the rest of the world. However, for this sentence, we wanted to keep the reader focused on the Arctic region.

Line 44: Please use direct language you mean biologically important functions?

[author response] The term 'life history function' is a commonly used, direct term.

Here is a definition from Oxford:

"The life history of an organism is its pattern of survival and reproduction, along with the traits that directly affect survival and the timing or amount of reproduction. Rates of survival and reproduction can be estimated across age classes, or across different stages in organisms with complex life cycles. Life history traits include growth rate; age and size at sexual maturity; the temporal pattern or schedule of reproduction; the number, size, and sex ratio of offspring; the distribution of intrinsic or extrinsic mortality rates (e.g., patterns of senescence); and patterns of dormancy and dispersal."

To ensure the reader is clearly aware of which life-history behaviors/functions we are referring to we provide specific examples within the sentence.

Line 50: What does "readiness" mean in the context of a marine mammal?

[author response] This is a good catch and we have edited the sentence to, now, read:

"Knowledge about evolutionary constraints on the timing of reproductive and molting behavior is generally lacking, so it is difficult to predict how or if ice-associated seal species will adjust to future changes (e.g., by adjusting pupping or molting schedules to earlier dates or different locales)"

Line 56: Perhaps you mean to offer a topic sentence, stating "How ice-assoicated seals use sea ice as a haulout platform varies between species".

[author response] We have adopted this suggestion

Line 66-68: There is so much to state about ice-associated seals in the Pacific Arctic that this reference to Antarctic work seems out of place here.

[author response] We have moved this reference to later in the paragraph so the first references are about Arctic work. While the example is from the Antarctic, it is an important, early example of analysis using bio-logger data to estimate haul-out behavior in seals.

Line 77: suggested edit

[author response] We have adopted the suggested edit

Line 84: Do you mean age-class? The term life-history implies knowledge of previous behavioral efforts or occupancy of regions of interest. Here you are specifically interested in age-class.

[author response] We have edited to use the term 'demographic'

Line 92: Please help your reader understand why are you doing your analysis and not offer a wide and jargon rich inventory of concepts that may be considered.

Line 93-94: Please keep your introduction focused on establishing the knowledge gap that you are seeking to fill. Please do not lead your reader to the numerous other knowledge gaps that are not being addressed by your current study.

[author response] We have removed the sentence in question

Line 99: Please use the term "hauled-out". Neither the biologger nor the aerial survey is able to distinguish among the various seal behaviors that result in them being hauled out and available for view by an aerial survey.

[author response] noted, and the terms "hauled out", "to haul out", etc is used consistently throughout the manuscript

Line 114: You have indicate that you would consider sea ice extent. Here you introduce the concept of icescape. Please introduce this concept earlier and indicate how you will incorporate this into your analysis.

[author response] changed "icescape" to "sea-ice extent"

Line 117: Please use an active voice for clarity.

[author response] This sentence has been changed to:

"For this study we used haul-out behavior data and location estimates from bio-loggers deployed on bearded, ribbon, and spotted seals in the Bering, Chukchi, and western Beaufort seas by multiple organizations as part of collaborative investigations from 2005 through 2021."

Line 120: You summarize the years during which land-based studies applied biologgers.

Please do the same for the offshore deployments.

[author response] This sentence now reads:

"Ship-based capture events occurred during spring near the southern ice edge in the Bering Sea between 2005 and 2018."

Line 124: Please provide the geographic context of your tag deployments and data collection using a plot similar to that used by Jay et al. (2012: 10.3354/meps10057 figure 2). Please consider using a tabulation that enables readers to understand the geographic context of the deployments similar to that used by Jay et al. 2012, table 1.

[author response] We feel the spatial distribution of the actual transmitted data – compared to the deployment location – is most informative and relevant for the audience's understanding of how our data are distributed spatially and how well data represents the range of each species. We provide this visually in Figure 3 and adding an additional layer to that figure to show deployments would be an additional complication. To ensure the audience has a clear understanding of our study area, we have added an additional figure (now, Figure 1) with a map of the Bering and Chukchi sea region that indicates generally where deployments were initiated. In response to other reviewer comments this figure also indicates the spatial range of aerial survey effort to date.

Line 126: Please use active voice for all actions that you took in your data collection, preparation and analysis.

[author response] Noted and addressed

Line 129-135: Please move this to the discussion. This is a summary of your data findings, not a description of your methods.

[author response] We can see the reviewer's point. However, we do not feel this topic is a summary of our data findings in this paper. Instead, our view is that this information provides the context and rationale for our methodological choice regarding bio-logger type and attachment methods. It is also important regarding the analytic methods – preference for flipper tag haul-out data over those from a tag adhered to the dorsal/head. If we were to move these important points to the discussion, we worry those points would be left disconnected.

Line 136: This is a discussion of your methods. This is not your methods. Please state how the data was collected in your Methods section and discuss how data collection have been uncertain or biased in your discussion section.

Line 141-143: Please move to your discussion.

[author response] We appreciate this suggestion from the reviewer and we have moved large portions of this paragraph to the discussion. However, some information regarding age/sex class determination is left here so the reader has context for Table 1.

Line 144: Please indicate how this was determined during data collection.

[author response] We have edited this sentence some to clearly communicate that field determination of reproductive status (and, thus ideal delineation of sub-adult and adult age class) was not possible.

Line 147-148: Please allow your readers the opportunity to understand the geographic context of these deployments through use of symbols that maybe used to cross-reference the deployment locations in a map that indicates deployment locations along with filtered movement tracks.

[author response] As previously addressed, there are now two figures available that provide geographic context of the deployments. Figure 3 shows the geographic distribution of the data from the deployments. The paper is not presenting or discussing movement ecology and, therefore, we do not present filtered movement tracks. We keep the focus on haul-out behavior data.

Figure 1: Please consider bar plot similar to that used by Jay et al. (2012: 10.3354/meps10057 figure 3), replacing the region with the seal species.

[author response] This figure has been updated with this suggestion in mind

Line 151: Please state clearly how you determined the end of a deployment. Here you indicate various elements of the haulout chronology, movement and dive chronology that may have been used, however not reader could replicate your methods base don this text.

[author response] We've added the following text to the paragraph:

"For example, a data record that ends with several consecutive days (~10+ days) of 100% dry observations and with locations indicating the tag was on land would be truncated to the final stretch of 100% dry observations. The vast majority of deployments end with the device detaching in the water and the deployment end date is obvious. There is no perfect algorithm for identifying deployment end dates and each deployment in question must be considered separately. While not perfect, we are confident our reliance on expert judgement and examination of multiple data streams provides the best option."

Line 152: Deployment activity is known to disrupt normal pinniped behavior. Did you censure some period of data collection during and after the deployment to ensure that that disruptions from the deployment activity did not bias your analysis?

[author response] For these phocid species, we have no empirical data (or even anecdotal observational data) on how captures may or may not disrupt 'normal' behavior. This is likely to be influenced by the capture method, how long the animal was restrained, whether the animal was with a dependent pup, whether the animal was molting, environmental variables such as wind and temperature, etc etc. Given all these unknowns, we have not applied a censure to the beginning of our deployment data. We can't 100% ensure this choice doesn't result in some level of bias. However, given the large sample size and duration of deployments we expect any bias imposed is negligible.

Line 154: This is a result. Please indicate the method that you used to distinguish "plausible" from "implausible" telemetered seal behavior. In your Results section, you may indicate how method was able to identify occasions of implausible seal behavior and any patterns that arose relative to tag model or attachment.

[author response] This sentence has been moved to the results section. Additionally, we've provided a brief explanation of implausible along with a reference for more details. For these devices, the percent-dry timeline reported 100% dry for several weeks followed by an additional period of time that was more typical of expected bearded seal behavior. During the extended dry time the locations indicated movement of the tag that would not be simply drifting ice. We also observed increasing transmission rates. The working hypothesis (i.e. unconfirmed guess) is that the wet/dry sensor surface became obscured by some corrosive element such that when in the water conductivity was prevented and, thus, recorded as dry.

Line 156-164: Please move to the Results section. Please move the discussion of how molt timing affects termination of tag deployments to the discussion section.

[author response] This figure has been moved to the results section along with additional descriptive text. We have left the discussion regarding molt timing and termination of the data record here to better communicate the point to the reader and prevent an isolated mention in the discussion that has no anchor.

Line 169-170: Thus, the a successful transmission of data was required at no greater than 48 h intervals.

[author response] We're not sure how to interpret this comment. The main point of the sentence is to explain the rationale/benefits of transmitting the limited selection of percent dry values. We have expanded the text to provide more details regarding the caching of messages and data transmission.

Line 174: Do you mean "atmospheric" magnetic interference.

Presumably "extra-terrestrial atmospheric" events (such as events on Venus or Mars) played no role in the transmission of the data signal to the Argos receivers in orbit around Earth.

[author response] We've edited to 'atmospheric interference'

Line 174-175: This note belongs in the Discussion, not the Results.

[author response] We feel this note is important to acknowledge in the methods because it speaks to the rationale for our methodological choices (bio-logger type, programming choices, analytic choices).

Figure 3: Do you mean that each cell "encompasses" and area of 50 km^2?

[author response] We have edited to the reviewer's suggested word 'encompasses'

Line 197: Please use the active voice.

[author response] Thank you for catching this. We have edited this sentence to active voice

Line 198-199: For most tags, your daily locations are from the Argos system, not from your data loggers. However, you included some FastLoc tag deployments. Please re-write for clarity of what these location are.

[author response] The previous paragraph describes how we determined daily locations. We see the reviewers point re: the data not technically coming from our data loggers. We have edited the sentence for additional clarity.

Line 199: What is a "key" weather variable? Please write for clarity.

[author response] We've edited this sentence and removed the word 'key'

Line 203: This is a procedural detail. Other readers may replicate your method without needing to do this. Please omit this detail.

Line 207-208: Readers can replicate your methods without the details on converting the NARR wind vectors into wind speed.

[author response] We're not sure why the reviewer would recommend omitting a 'procedural detail' as part of our methods. We feel it is important to clearly communicate our procedure for processing the large NARR data set and that we used the original grid size of 32km. Regarding the calculation of wind vectors, we include this detail because many readers, like us initially, may not be well versed in how wind vectors components are converted to wind speed.

Line 210: Please use an active voice: "For all seal species we considered the following variables when modeling the hourly haulout behavior..."

[author response] We have adopted the reviewer's suggestion

Line 224: Using the term "major focus" implies that there may be numerous minor foci. Can you not state that this is the goal of the study? Ancillary natural history insights can be discussed incidental to this, but are not driving the research. The statutory requirements of the MMPA and ESA are driving your study. These Federal laws require robust methods to monitor population status. Your study seeks to build this method. Discussion of natural history belong in your Discussion section and not in the framing of your study. Please help the reader focus on why the Federal government is doing this study.

Understanding pinniped haulout behavior is essential to designing and interpreting population estimation aerial surveys. Understanding how they use sea ice during a time when sea ice availability is rapidly changing is also important, but is ancillary to the paper's focus.

[author response] We have removed the term 'major focus' and, as the reviewer suggests, simply state that this is the goal of the study. We have also added mention of the statutory requirements to paragraph 2 of the Introduction section and expanded the text to acknowledge the importance of understanding how seals use sea ice during this period of change but, ultimately, it's ancillary to the focus of this paper.

As for providing the reader focus on why the Federal government is doing this study: this is a collaborative study across multiple organizations and the analysis/purpose is not limited to the Federal government. We've incorporated the reviewers suggestions to expand discussion of the statutory requirements of the MMPA and ESA but don't feel we need to single out the motivations for the Federal government.

We have also added additional general representation of recent aerial survey effort to the new Figure 1. This should better communicate to the reader how the spatial distribution of our haul-out behavior overlaps with the species range and survey effort.

Line 227: Seals can just as happily be on foraging trips within the pack and marginal sea ice as in the open water, depending on the species. Suggesting that foraging trips are associated with ice-free conditions is misleading.

[author response] We have removed 'e.g., foraging trips' from this sentence so as not to mislead the reader.

Line 229-230: This is your primary reason for not including sea ice geography in your analysis: you simply lacked geolocation of much of your haulout behavior data.

Please help the reader understand how coarse your tracking data was for the flipper tagged animals and what proportion of each species was tracked with these flipper tags. Please also help the reader understand how the tracking data relates geographically to regions that may be subject to aerial survey efforts (i.e. are your tracking

data collected from across the regions that may be surveyed during range-wide spring aerial surveys?).

[author response] We have re-organized this paragraph to, hopefully, better communicate our choice not to explore sea-ice related covariates. As the reviewer suggests, we have limited geo-location data for in-water periods of our haul-out behavior data – we know the seal was in the water but don't have any estimates of location when only a flipper tag is attached. By leading with this statement, we hope that communicates our primary rationale. But, the other rationales are also important and we still include them. We have also moved this section to the 'Discussion' in response to other reviewer comments.

We have also added a figure 1 depicting a spatial representation of recent aerial survey effort (which reflects estimated species range for bearded, ribbon, and spotted seals in US waters). This should better communicate to the reader how the spatial distribution of our haul-out behavior overlaps with the species range and survey effort.

Line 229-230: Please help the reader understand why you have not included a basic metric of sea ice geography, such as distance from marginal ice edge (from the NIC's daily Marginal Ice Zone charts), which is a metric that would be available for all data collected during an aerial survey.

[author response] We have revised the text in this section to try to provide a clearer understanding of our reasoning. Also, note this has been moved to the Discussion section.

The text now reads:

Notably missing from our list of haul-out model explanatory variables is any spatial-temporal representation of sea ice concentration, area, or extent. This may seem counterintuitive when modeling the haul-out behavior of seal species with such a close association to sea ice; seals haul out in the presence of sea ice, and we could assess the local concentration of sea ice during these events (see Olnes et al., 2020). This, however, expands the scope of our analysis into the realm of habitat selection and many of our deployments consisted of a single device attached to the rear flipper of the seal which meant we only received locations when seals were hauled out on sea-ice, limiting our ability to fully evaluate fine-scale habitat preferences related to sea-ice. Insight into how seals use and interact with sea-ice during an extended period when the availability and characteristics of sea-ice is rapidly changing is important (Breed et al., 2018; Cameron et al., 2018) but ancillary to the focus of this analysis – and, in the end, not possible given key limitations of our data. Additionally, our study was limited to the spring season when seal haul-out behaviors are strongly influenced by pupping, nursing, breeding behavior, and molt. These drivers are likely more influential on haul-out behavior than seaice concentration. Crawford et al. (2019) compared haul-out probability models for ringed seals and found those that only included season (and not sea-ice concentration) were the most parsimonious. For all of these reasons, we have elected not to use sea ice concentration as a predictor for haul-out probability in the present study.

Table 2: It is a bit misleading to indicate that the NARR variables were sourced from NARR alone. Their values were interpolated onto a geographic location that was widely variable in precision and that precision relates to the both the tag attachment (glued on or flipper attached) and the seal behavior (in water, hauled out).

Indicating that your "Northing" variable was from the "Bio-logger" is also misleading because your locations was determined by either the Doppler inflection point time, satellite orbitography and a model of the Earth (the Argos relocation method) or by reprocessing of GNSS signals that were logged and then transmitted via the Argos system as a data message. Really, neither of these were determined by the "Bio-logger", rather they were determined by a very complex system of geolocation.

Your readers may be better served by not including this "Source" field, given that you describe how you obtained or estimated these variable values in your methods text. Offering an over-simplified "Source" in the table obscures your actual methods.

[author response] We appreciate the reviewer's thoughts on this and agree with that removing the 'Source' column better serves the readers.

Line 244: Neither your telemetry data nor aerial surveys can distinguish "basking" as a behavioral state. You are measuring "hauled out" behavior and aerial surveys observe "hauled out" seals. I encourage you to use these terms and not mix in ideas of "basking", "nursing", "breeding", "taking refuge from marine predators" etc.

[author response] As previously mentioned, we've addressed this and consistently use "hauled out" and not "basking"

Line 254: It is nice that you have sufficient data to do this. However, the reason for having separate models for each species is because you expect different behaviors from each specifies and because you expect that aerial efforts will be able to distinguish sea species and be able to apply an availability correction factor for each species. Please correct me if I am wrong, else, please keep your reader focused on the value that you are bringing to the analysis here in the Methods section and the good fortune that you have in the sample size, which should be noted in the Results and Discussion section.

[author response] We have rephrased this sentence to emphasize that we fit each species separately because a) we expected differing behaviors across species and b) fitting a single model was not possible with such a large data set (even with the advantages provided by the glmmLDTS package).

Line 263: Please clarify what is intended by the notation "only -99% or our observations".

[author response] This is an error in the code that has been fixed.

Line 263: Also, please consider using consistent terms for "behavior records". Perhaps it could be fair to term your telemetered haulout status as an "observation", however, it seems more intuitive to reference this a "record"

[author response] We have made edits throughout the manuscript to use consistent terms for 'behavior records'

Line 263: Please help your reader understand why you have not adopted use of a classified variable for each telemetered behavior interval whereby it could be either "wet" or "dry" based on a threshold proportion of readings reported as "dry". This has two advantages: (1) were this enabled through processing on-board the tags, it would greatly increase your data compression and collection; (2) it may enable greater analytical power in your modeling effort.

[author response] We provide fairly clear and detailed information on the haul-out behavior records, how they are recorded and transmitted in the methods section. We have further edited this to make sure it is clear that these are standard settings within the Wildlife Computers tag platform — we do not have direct control over the details for on-board processing or transmission. As stated in the text, for this analysis, the linear predictor was modeled on the logit scale as a Bernoulli response where tags are either 'wet' or 'dry' for a given hour based on whether the tag was greater than 50% dry. This is a classified variable as suggested. The difference is that we conducted this classification post-transmission instead of on-board the tag. We feel the transmission of various percent-dry values for a given hour provide more flexibility in the types of analyses and insights that can be gained from deployments.

Line 265-272: Please seek input from a competent biometrician. I am not able to offer any guidance on this other than to muse why you are pushing to estimate six parameters for a time of day covariate when your seals are not known to keep track of time.

It would be reasonable to assume that seals respond to insolation or the angular height of the sun in its daily arc. Please help your reader understand why you have sought to model a complex representation of hourly time when you could have pulled insolation from NARR or calculated sun angular altitude (perhaps as a linear proportion of the day's maximum sun angular altitude) from standard astronomical functions.

Perhaps your motivation is to provide plots that appear intuitive with hours on the y-axis, day of year on the x-axis and haulout proportion as a "heat map". However beautiful these plot are, I wonder if your goal for improving precision and reducing bias when estimating availability during an aerial survey would not be better served by the alternative and simpler variables.

[author response] We appreciate the suggestion and find the possibility of using insolation values from reanalysis products as a covariate intriguing. As the reviewer suggests, such an approach could provide a less complicated and more parsimonious model than the approach we have taken with the Fourier series as a cyclic representation of hour-of day. We have taken the time to do some additional analysis and methodological exploration and provide additional details in Supplement 2. Note, our initial exploration of this approach resulted in lower AIC values for the Fourier series approach presented in the analysis. While promising and worth even further exploration, we feel the approach taken in the analysis is the most appropriate because it distinguishes daily bi-modal (e.g. crepuscular) patterns that might be important but would not be detected by insolation alone (i.e. insolation at dawn or dusk would be similar values but occur at different times of day that might be ecologically important). Additionally, as the reviewer points out, results from the analysis and haul-out predictions are more intuitive and applicable to aerial survey methods when using hour-of-day.

Line 278: Please help your reader understand what is meant by your term "horizontal shift". It is clear that you have a graphical representation in your mind that has not been shared with your reader. Please rewrite to avoid "jargon".

Line 285: Please help your reader understand what could be "important" about these terms. Please write for clarity, avoiding jargon.

Figure 4: Please use standard conventions for plot titles. Your title deserves a statement in your Results or Discussion section. It does not follow the expectations for a publication figure title.

[author response] We have removed plot titles and edited the figure captions to include the title information to be consistent with the journal styling and requirements. We've also revised many of the figure legends to better communicate the information to the reader and ensure if any figures are presented out of context (e.g. without the figure caption) in other venues the information is clear.

Figure 4: Please scale your color ramp to enable better visualization of the subject: limit the color ramp to the modeled values (which appear to be from zero to ~ 0.5).

[author response] We have adjusted the color ramp such that the pattern for bearded seals is more visible. We've also noted this change/difference in the figure caption so the reader is aware.

Figure 4: Please switch to a color ramp that is suitable for readers with color perception disabilities such as the viridis color ramps.

[author response] The color ramp used has been updated to use palettes from the R package 'scico' have been tested and confirmed to be colorblind friendly and appropriately balanced for scientific interpretation. We initially used the viridis color palette for these plots but the 'scico' palette colors provided additional visual detail we feel is important.

Figure 4: This is unclear. Your plot indicates a y-axis of local solar hour which varies from 0 to 24. This is clearly not fixed at local noon.

[author response] This was an error and has been fixed. We thank the reviewer for recognizing this and highlighting the mistake.

Line 323: Please use standard English. "Ontongeny" is generally understood to describe the physical development of an individual organism. Here you are referencing the onset of of behaviors within the life of an organism. It may benefit your readers to use a term that is more direct, such as "development".

[author response] We have replaced 'ontongeny' with 'development' as suggested

Line 326-327: Given that Ribbon seals occupy a high latitude region during this time and given that there is scarcely any twilight during this season, please consider using a term other than "crepuscular".

[author response] Subsequent model runs (with improved QA/QC on telemetry data) have reduced the indication of any crepuscular or bi-modal haul-out behavior of ribbon seals and we no longer feel it is worth mentioning in the paper so it has been removed.

Line 331-332: This is a fair summary of your modeling efforts. However, it raises the questions as to what these seals are responding to. Do they sense air pressure and make a decision on their haulout behavior or are low pressure conditions associated with low insolation and they are responding to that? Given that you can readily extract insolation from the NARR, please consider use of insolation as a covariate that may more directly relate to seal behavior.

[author response] See previous responses regarding the potential use of 'insolation' from NARR or other reanalysis products.

Figure 5: Please use standard figure titling and not use a statement that should below in a PowerPoint slide or in your Results and Discussion section.

Figure 6: Please use standard conventions for plot titles. Your title deserves a statement in your Results or Discussion section. It does not follow the expectations for a publication figure title.

[author response] See previous response regarding our choice in plot titles and subsequent edits

Figure 8: Please label your plots using standard capitalization and words, instead of all capitalized abbreviations.

[author response] We have made edits based on this suggestion

Line 360-362: This belongs in the discussion, not results.

[author response] The suggestion to move the mention that there "were still some years where the pattern shown was informed by a small number of individuals that may not represent population-level patterns" to the discussion is noted and changes have been made.

Line 371-372: Please indicate the season (or months of the year) in this statement.

[author response] Noted and edited to include mention of the spring season

Line 375-376: Do you mean to state that "haulout behavior modeled from telemetered haulout behavior records may represent population-level behavior patterns."

[author response] Noted and edited accordingly

Line 377-378: Feltz and Fay (1966) offer (an amazingly cool) functional explanation of the thermal constraints on hair follicle growth. Whether seals during specific study times are optimizing hair follicle growth is unknown.

[author response] We have edited this statement for additional clarity

Line 418-419: Yes, and you have had access to direct estimates of insolation from the NARR. Can you incorporate that and find a tighter model of haulout behavior. This would be an improvement for design and interpretation of aerial survey efforts.

[author response] See previous comments regarding the potential use of insolation values from reanalysis products

Line 420-421: You may state this if you first offered an estimate of haulout behavior and confidence intervals on that behavior state, then compared that with your estimated haulout behavior modeled with the use of co-variates. Once you perform this, you may state that inclusion of weather co-variates improved haulout state estimates. However, you have not done this. If you wish to state this, please do this.

[author response] Here we simply state that 'our results highlight the importance of incorporating weather covariates' and that importance is indicated with the reported 'type III' F statistics for the weather covariate terms in the results section. We are clear in our methods that the use of pseudo-likelihoods in the analysis prevent us from conducting typical model selection with AIC or similar as suggested. We have moved a separate discussion of comparison with previous analysis results here to provide additional comparative context.

Line 425: This term suggests some evaluation of a threshold above which haulout behavior shifts. Please write for clarity and for what you have presented in your results.

[author response] We have edited this sentence for improved clarity

Line 455: Please be clear as to why you anticipate greater unmodeled heterogeneity of availability for Arctic seals? Here you have considered Arctic seals, have you not? Or are you using a different definition of the Arctic other than the ice bearing waters occupied by ice-associated seals?

[author response] We have edited this statement to now read:

The most challenging element in developing availability correction factors is with annual variability. It can be difficult to get a sufficient sample size to estimate year-specific correction factors, particularly because research teams would likely need to deploy bio-loggers on seals and conduct aerial surveys concurrently, requiring considerably more personnel and money. One possible suggestion is to include year as a random effect within models for aerial survey counts such that, without specific knowledge of any particular year, the among-year variance is included in the modeled standard errors. Regardless of the specific approach, future estimates of Arctic seal abundance will require specific consideration of annual variability and changes in the timing of peak haul-out behavior when estimating trends, as one will not know if moderate differences in abundance estimates are attributable to changes in abundance or changes in haul-out behavior.

The interpreted emphasis on 'Arctic seals' was not intended. Instead, the key point is that there is likely unmodeled heterogeneity related to the seasonal distribution and annual timing of peak haul-out behavior. This is an acknowledgement that our model is not a complete picture or perfect representation of seal haul-out behavior. In an environment like the Arctic that is undergoing dramatic change and inter-annual variation in climate and sea-ice distribution, this is important to keep in mind.

Line 459-464: Here you provide the discussion required to make the statement that inclusion of weather and other covariates results in a different estimate of haulout proportion. Can you extend this to indicate an improvement in the confidence interval on this estimated proportion?

[author response] Noted and this section has been moved to that discussion

Line 465-466: Please be specific. Here you linked the telemetered haulout behavior to available covariate data then modeled haulout behavior.

[author response] Noted and additional specifics have been added to this statement

Line 467-473: This can be stated in the introduction so that you can clearly indicate the framing of your study. "We modeled availability from telemetered haulout behavior records of seals that haulout on ice where they may be viewed by aerial surveys (list the species considered).

[author response] This section has been moved to the introduction.

Reviewer 2

One suggestion I would share with the authors is the addition of a limitations section in the discussion. The limitations were outlined throughout the methods, but a succinct accounting of these limitations in the discussion would allow readers who do not want to carefully dissect all of the modeling in the methods to be able to better interpret the robustness of the results and conclusions.

[author response] We thank the reviewer for this question and, in response to this and other reviewer feedback, have moved much of the limitations outlined in the methods to the Discussion section and hope this provides a clearer picture to the reader regarding limits of our analysis.

I still had one remaining question on why the authors couldn't run the models with and without the sea ice concentration as a predictor. The comparative results might be interesting (I understand why the correction factor might be biased...but given that this is a baseline study, it would have been an interesting comparison to see whether it was or wasn't a decent predictor for the different seal species).

[author response] We think we've addressed this in edits and comments to reviewer #1. We think the inclusion of sea ice as a predictor is better suited for a habitat use/habitat preference study and we hope to pursue that in future analyses. We have also emphasized that our reliance on flipper-mounted bio-loggers for a portion of our data limited our understanding of movement and use away from sea-ice.

The authors need to explain more how they are attributing statistical significance. For example, in lines 344-345, they ascribe strong influence of temperature with a p-value of 0.064.

Not to be one who is fixated on a p-value of 0.05 denoting significance, I was a bit surprised to see the same authors, in lines 364-366, to state that there is 'no indication that the observed trend is meaningful' for spotted seal adult females having an R2 of 0.767, p=0.022. If the extent of sea ice explains nearly 80% of the variance in peak haul-out probability, how is it that the author's call this a 'trend'? This requires more explanation. As does the statement in line 427-428.

[author response] We appreciate the reviewer highlighting this confusion and apologize for it. These were typos or mis-coded values that snuck into the section. We have reviewed and revised all of them to ensure they are correct and that we are consistent in our attribution of significance. We have tried to be judicious in our use of the work 'significant'.

I found 463-464 confusing. This is an important part of the discussion (using your framework to assess previous results from another study), but it could be more clearly written. The sentence, 'Applying models that ignore age, sex, and year

effects...under the current analysis framework' is very confusing and doesn't seem to follow the argument of the paper easily. Could this be reworded so that the full intent of the paragraph is communicated?

[author response] Reviewer #1 also commented on this section and offered suggestions for editing. With both comments in mind, we have made edits to the text and hope this, now, more clearly communicates how our results compare with previous approaches.

I appreciate the acknowledgement that it is difficult to know whether differences in abundance estimates are attributable to changes in abundance or changes in haulout behavior and the potential proposed solution (lines 450-458) Has anyone done a smaller-scale study that would address this inherent problem?

[author response] To our knowledge a smaller-scale study addressing this issue has not been done

Reviewer 3 (M. Carter)

I have only a few minor comments, mostly where the text would benefit from extra clarity:

L43: Word missing? ...Bearing [and] Chukchi Seas...

[author response] noted and fixed

L63: It may be useful to highlight somewhere that matching seal haulout behaviour to environmental conditions with any degree of certainty requires location data as well as wet-dry data, and that modern bio-logging devices can collect both data streams simultaneously.

[author response] thank you for this suggestion and we have edited this paragraph to include mention regarding the ability of modern bio-logging devices to collect both behavioral and location data streams which allows inclusion of environmental covariates.

L82-83: All citations given here relate to ice-associated seals, but these techniques are also relevant to seals that haul-out on land. Lonergan et al. (2013) Aquatic Conservation: Marine and Freshwater Ecosystems 23: 135-144 is a key example from non-polar regions.

[author response] we have expanded the list of references to include Lonergan et al

L110: Clarify why meteorological factors affecting walruses may be relevant to the study species.

[author response] thank you for the suggestion. We've edited the sentence to, now, read:

"Previously estimated availability correction factors accounted for variables such as time-of-day and day-of-year but did not investigate the impact of meteorological variables. Such variables have been shown to influence walrus haul-out behavior and we expect weather conditions to also influence seal haul-out behavior and including them within the model framework will benefit our estimates of seal availability during aerial surveys."

L120-124: A map of the study area with deployment areas indicated would be useful for those readers not familiar with the local geography.

[author response] Reviewer 1 had a similar suggestion and we now include such a figure.

L126-128: More information is required on the location data type (e.g. GPS or ARGOS?) and data retrieval (e.g. archival loggers or ARGOS-relay?).

[author response] we have added the following sentence:

"All data were transmitted by the deployed instruments via the Argos satellite network and location data were either derived from Argos transmissions or transmitted FastLoc GPS data."

L133-135: Please clarify, were there any cases where only head/back-mounted tags were deployed? If so, how did you deal with the potential for false haul-out records due to prolonged surface activity?

[author response] we've clarified the language in this paragraph so it's clear that deployments consisted of head/back tag only, flipper tag only, and combined. Examination of the haul-out records hasn't indicated there's a propensity for these tags to record extended dry periods when surface resting at sea for the head/back tags.

L135: At this stage you have not yet explained what type of data each device collects, so we do not know what the hourly percent-dry observations from the flipper tag were preferred to.

[author response] thank you for noting this. we have moved the later paragraph (starting line 165) up so it is before this section.

L139: Which species?

[author response] we have removed the 'for some species' from this sentence

L136-144: This could be clearer. I assume the "some species" part refers only to pelage, but it appears at first read to refer to the whole list of metrics. I would suggest re-wording this section to improve clarity regarding which factors were used for which species and with what degree of certainty age class could be determined.

[author response] as noted in the previous response, we've removed the 'for some species' and think this improves the clarity of this section. Unfortunately, we don't have any way to quantify a degree of certainty for age class determination across the various field teams responsible for field identification.

L146: How many YOY were advanced to subadult?

[author response] there were 11 YOY advanced to subadult. We considered adding this into the results but struggled to find a place where the information fit and was relevant.

L188: On land as well as ice?

[author response] we have edited this sentence to state 'also haul out on land'

L194: It is not clear to me if all tags for a given species were deployed in the same region, or across multiple regions (a map of the study area with deployment regions per species would help here). Given regional differences in phenology mentioned in the Introduction (L52-53), did you consider whether region should be included as a covariate?

[author response] we have added a figure/map as suggested

Figs 4, 6, 8: How is that hour of the day is fixed at local solar noon if predictions are shown for all hours? Also, is it possible to show uncertainty (lower and upper CIs) for these figures, perhaps in Supplementary Materials?

[author response] Reviewer 1 also noted the incorrect statement that hour of day was fixed at local solar noon and this has been corrected. We have taken the reviewer's suggestion and added supplemental materials with plots (this time fixed at solar noon) that indicated the lower/upper CIs.

L316: Use of "additionally" negates the need for "also".

[author response] noted and removed 'also'

L341: Word missing? ...and [spent] more time out of the water...

[author response] noted and we've made the suggested correction

L387-390: It is not clear what species was studied by Thometz et al, and thus maybe a citation is needed for the information relating to ribbon and spotted seals.

[author response] we've added a clarification that the Thometz et al study and data presented was for bearded seals.

L393: Use "both species" instead of "all species" to avoid confusion.

[author response] we've edited to specifically state 'ribbon and spotted seals' to avoid any confusion

The paper could benefit from a brief concluding paragraph summarising the importance of the work in the context of climate change and population trends, as outlined in the Introduction.

[author response] thank you for this suggestion. we've added a concluding paragraph that addresses this comment.