RESPONSES TO PEER REVIEW COMMENTS ON "EVALUATING KEY UNCERTAINTIES REGARDING ROAD GROOMING AND BISON MOVEMENTS"

Robert A. Garrott and P. J. White

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The responses of Drs. Garrott and White to the peer-review comments are inserted in CAPITAL letters in the text that follows:

Comments by Dr. Joshua J. Millspaugh, University of Missouri

Below are specific comments on the proposal by theme. The proposal represents a mix of very well-thought out hypotheses, experiments, data mining, and several studies described at levels ranging from very detailed to very general. I believe there is a very high probability that these studies will reduce the uncertainties associated with key aspects of bison management at Yellowstone National Park. Garrott and White have extensive experience in this system and have an excellent track record of producing high quality papers.

Theme 1: Influence of snow and terrain on bison movements

The authors do a great job of laying out detailed predictions based on the hypothesis that snow depth, a critical threshold for foraging, drives winter movements. Specific comments are below.

1. I wondered whether this was the only plausible hypothesis? This research might be more powerful if a plausible contrasting (or partially contrasting – an interaction of snow and some other factors) hypothesis/hypotheses were established as viable candidates.

WE REVISED THE TEXT AS FOLLOWS TO MAKE OUR ALTERNATIVE HYPOTHESIS CLEAR: "THUS, AN ALTERNATIVE HYPOTHESIS IS THAT A SNOW THRESHOLD MAY NOT EXIST OR BE BIOLOGICALLY MEANINGFUL FOR TRAVEL CORRIDORS BETWEEN FEEDING AREAS BECAUSE REPEATED USE OF TRAILS MAINTAINS THEM IN A COMPACTED, SELF-GROOMED STATE."

2. There is a general concern about the use vs. random analysis given comments by Keating and Cherry (2004). Have you considered alternatives such as case control designs (see comments below)?

TO ASSESS THE CONTRIBUTION OF SNOW WATER EQUIVALENT IN EXPLAINING VARIATION IN WINTER BISON DISTRIBUTION, WE PLAN TO USE MATCHED CASE-CONTROL LOGISTIC REGRESSION IN WHICH EACH BISON LOCATION (A CASE) IS MATCHED TEMPORALLY WITH 20 RANDOM LOCATIONS (CONTROLS).

3. I was curious about the average error of the snow model estimates. Error must be pretty low and unbiased for this application. How will error be accounted for when model output is used as a logistic-regression covariate?

WE RECOGNIZE THERE IS ERROR IN THE PREDICTED SNOW WATER EQUIVALENT (SWE) COVARIATE. THE EFFECT OF ERROR IN A PREDICTOR VARIABLE IS TO UNDERESTIMATE THE STRENGTH OF THE RELATIONSHIP BETWEEN THE PREDICTOR AND THE RESPONSE VARIABLE. WE WILL EXPLORE PROCEDURES TO ACCOUNT FOR ERRORS IN SWE PREDICTION. HOWEVER, WE HAVE SUCCESSFULLY APPLIED THIS ANALYTICAL PROTOCOL WITH ELK DATA AND SWE PREDICTIONS, AND FOUND STRONG RELATIONSHIPS BETWEEN MODEL-DERIVED SWE METRICS AND PROBABILITY OF ELK OCCUPANCY.

4. The thresholds might be estimated a bit coarsely. My general experience with logistic regression output indicates that confidence intervals around what should be ecologically tight relationships often are very big. This might have implications to your study. Also, although the approach will account for major bison trailing effects, it may not be sensitive to partial trailing in local patches, resulting in some homogenizing between used and random patches. Finally, bison for this component seem to be in areas with groomed travel routes. Less energy spent traveling = more energy available for foraging, and a higher threshold compared to if groomed travel routes were not available.

WE WILL NOT KNOW THE CONFIDENCE INTERVALS AROUND THE THRESHOLD ESTIMATE UNTIL AFTER WE HAVE COMPLETED THE ANALYSES. HOWEVER, THE KEY OBJECTIVE OF THIS EFFORT IS TO DISTINGUISH BETWEEN THE ALTERNATE HYPOTHESES (I.E., THRESHOLD OR NO THRESHOLD) AND NOT TO PRECISELY ESTIMATE A THRESHOLD. OUR ANALYSIS IS NOT AT THE PATCH LEVEL. THEREFORE, WE ARE NOT CONCERNED ABOUT PARTIAL TRAILING IN LOCAL PATCHES BECAUSE THIS WOULD BE INCORPORATED IN THE ANALYSIS OF NON-TRAVEL LOCATIONS.

5. What is the justification for a 99% kernel and an 1850 m bandwidth? It was unclear why random data from a 99% probability contour would be used to look at fine-scale relationships. You might consider a discrete-choice approach, with random locations within some radius of each observed location. This seems necessary in addition to or in place of this coarse approach. I am concerned that the 99% contour is poorly defined with kernel estimators, and you are measuring random points at locations far from what are realistically available to the individual. Will each individual be analyzed as a sample unit, or will observations be pooled? Would random points be limited to similar terrain as that of used locations, to avoid confounding snow depth with other factors?

The bandwidth selection of 1850 m seems arbitrary and this *a priori* selection should be explained. You might look at the paper by Gitzen et al. (2006) for some recent thoughts about bandwidth selection in kernel analysis.

Gitzen, R. A., J. J. Millspaugh, and B. J. Kernohan. 2006. Bandwidth selection for fixed kernel analysis of animal range use. Journal of Wildlife Management 70:1334-1344.

IT IS ALWAYS DIFFICULT TO DEFINE AVAILABILITY. WE AGREE THE 99% KERNAL AND 1850 METER BANDWIDTH ARE SOMEWHAT ARBITRARY AND HAVE

BEEN EXPLORING ALTERNATIVES FOR A FINER-SCALE APPROACH. HOWEVER, DEFINING A RADIUS AROUND EACH OBSERVED LOCATION WILL STILL REQUIRE AN ARBITRARY DECISION. FOR EXAMPLE, THE MAXIMUM DISTANCE A BISON COULD LIKELY TRAVEL WITHIN ONE DAY MAY APPROACH THE BREADTH OF THE ENTIRE CENTRAL RANGE.

6. I am not fully convinced of the proposed approach (p. 18) of fitting only linear covariate forms in the initial AIC-based model ranking, and then in this initially high-ranked model set, incrementally testing each non-linear form of the covariate. Particularly since existing analyses (Bruggeman et al. 2006) could be used to guide this analysis. So much of the analysis up to this point is based on careful *a priori* thought, which is great. I would suggest you stick with that approach. I suggest doing the same with the functional-covariate relationships: chose which (maybe all) of these forms make the most sense biologically and include *a priori* models that differ in this functional form. Explore other relationships post hoc but keep them out of the model set. The power of information-theoretic approaches comes from pre-specifying all meaningful models. I do not see the merit of putting the functional exploration in a gray area between *a priori* and post hoc.

THERE IS CONSIDERABLE DEBATE ABOUT THE NUMBER OF MODELS THAT SHOULD BE INCORPORATED IN THE *A PRIORI* MODEL SUITE. WE CHOSE A CONSERVATIVE APPROACH, BUT WILL CONSIDER A BROADER SUITE OF FUNCTIONAL FORMS FOR COVARIATES BASED ON THE FINDINGS OF BRUGGEMAN ET AL. (2006).

7. My general opinion is that the logistic-regression aspects of this proposal are interesting, and will produce useful results. However, I am curious about whether snow-movement relationships will be estimated well enough to provide precise answers to the underlying questions (p. 8-9). With such a large number of GPS-observations for some components of this theme, the authors might consider going beyond standard logistic-regression resource selection analyses, and make use of the time series of observations. For example, time spent in some patches/locations, and travel vectors between locations (I did not have access to Bruggeman's Ecological Applications paper which is "in press" to determine whether they took such an approach). It might be appropriate to make full use of the sequence of observations, preferably via mechanistic models of the movement process.

MECHANISTIC BEHAVIORAL MODELS ARE BEYOND OUR AREA OF EXPERTISE, BUT COULD BE CONSIDERED DURING FUTURE WORK.

Theme 2: Determining drivers of migration, re-distribution, and demographic characteristics

This section describes additional analyses that will be performed for several existing, partially overlapping data sets. I had some difficulty determining which planned analyses are completely new, which are significant re-analyses, and which are relatively minor updates (with some new data) of strong completed analyses. For example, the authors propose a study of bison migration dynamics at a large scale, then describe conclusive results from a finer-scale study, but do not

identify how they will integrate this past fine-scale study with proposed large-scale analysis. As a result, it was unclear how the proposed demographic analyses (pp. 27-29) would provide more precise insight towards solving the management problem at hand, than any of the many demographic publications cited (including many by the proposal authors). A few sentences might help clarify these issues.

The management question justifying this study (Themes 1 and 2) seems clear: In the absence of road grooming, would bison still migrate to the Northern Range, and would over-winter survival, density, and out-of-park movements change?

WE MODIFIED THE TEXT TO MORE CLEARLY DIFFERENTIATE BETWEEN COMPLETED, ONGOING, AND PROPOSED STUDIES. WE DO NOT INTEND TO INTEGRATE PATCH SCALE FORAGING DYNAMICS AND RANGE SCALE MIGRATION DYNAMICS IN A MECHANISTIC MODEL. WE CONDUCTED THESE TWO STUDIES AT DIFFERENT SPATIAL SCALES TO BETTER UNDERSTAND THE BASIC LANDSCAPE AND ENVIRONMENTAL COVARIATES THAT INFLUENCE MOVEMENTS.

Theme 3: Effects of road grooming on bison use of travel corridors

I realize that experimental road closures are highly contentious at YNP. It seems clear that such adaptive-management experiments are the only way the most critical management-related question (how bison would respond to no grooming) can be answered definitively, at least in terms of the short-term behavioral responses. This theme (at least the experimental aspects) is by far the most relevant and necessary part of the proposal.

1. Certainly, with GPS collars on 50-60 bison, a wealth of data will be collected, and many interesting analyses could be performed. There was a lack of detail regarding analysis here compared with other sections of the proposal. Some more detail in this regard would be helpful.

THE DEPLOYMENT OF THESE COLLARS IS NOT AN INDEPENDENT RESEARCH EFFORT, BUT IS THE BASIC METHODOLOGY NECESSARY TO OBTAIN INFORMATION FOR THE DETAILED STUDIES DESCRIBED UNDER EACH THEME. AVAILABLE GPS DATA IS LIMITED IN SPATIAL SCALE BECAUSE MOST ANIMALS WERE INSTRUMENTED ON THE CENTRAL RANGE. ALSO, THESE DATA DO NOT YET SPAN THE RANGE OF ENVIRONMENTAL EXTREMES EXPERIENCED IN YELLOWSTONE. PREVIOUS EXPERIENCE INDICATES THAT ENVIRONMENTAL EXTREMES COMBINED WITH HIGH DENSITIES DRIVE BISON MOVEMENTS OUTSIDE THE PARK.

2. Regarding deployment of camera systems. The authors state that previous systems have had problems with power supply in extreme cold, as well as other factors. They might bolster the case for the likelihood that their new system will overcome these problems – it reads a bit exploratory. Also, I am not able to tell how data-rich the images will be – whether there is much chance of capturing data sufficient for interpreting behavior and number of bison traveling

together. In Bjornlie and Garrott (2001), only the number of bison photo-events and the direction of travel were discussed.

WE INTEND TO CONDUCT A PILOT PROJECT TO TEST AND REFINE THE PROPOSED CAMERA SYSTEM. IN CONTRAST TO THE CAMERA SYSTEMS USED BY BJORNLIE AND GARROTT (2001), THE NEW SYSTEMS WILL CAPTURE VIDEO THAT PROVIDES IMAGE STREAMS OF BISON BEHAVIOR.

3. Firehole Canyon Manipulation (and the two subsequent manipulations). This seems like a clever experiment, and the authors are very realistic about potential issues with the experiment. As they state, this experiment may take several winters to implement successfully (i.e., kinks worked out, sufficient snowfall).

4. I do not have a good feel for whether conclusions from this experiment will apply widely throughout the park – whether snowfall amounts, landscape pattern, etc., are similar enough here to the rest of the groomed roads in question so that this single experiment will give strong insights into effects of grooming in other areas.

WE HAVE FOCUSED THE PROPOSED MANIPULATIONS ON CONSTRICTION POINTS IDENTIFIED BY PREVIOUS ANALYSES OF THIS ISSUE.

5. Given that the proposed camera system seems so early in development, I wonder whether the authors should consider a more reliable primary way of detecting how bison respond to the closure – direct observation of the gate and/or daily snow-trail checks? I would want to ensure they collect relevant data if the camera system fails.

WE RECOMMENDED AN AUTOMATED PRIMARY DATA COLLECTION SYSTEM BECAUSE BISON COULD ENCOUNTER THE GATE AT ANY HOUR OF THE DAY. DEPLOYING PERSONNEL FOR DIRECT OBSERVATIONS IS NOT EFFICIENT OR PRACTICAL GIVEN YELLOWSTONE'S SEVERE WINTER CONDITIONS. HOWEVER, WE DO INTEND TO AUGMENT THIS AUTOMATED DATA COLLECTION WITH DAILY SNOW CHECKS AND OBSERVATIONS BY PARK STAFF.

6. Will you integrate results from the three planned manipulations into a single analysis?

AT THIS TIME, IT IS NOT CERTAIN WHICH MANIPULATIONS WILL BE CONDUCTED OR WHAT ADDITIONAL ANALYSES WILL BE SUPPORTED. HOWEVER, INTEGRATION OF THE RESULTS WOULD BE ANTICIPATED.

7. The logistic regression analysis (1= used ungroomed, 2 = turned back) assumes each group is independent. However, I'm not convinced that is the case. If one group uses the ungroomed road, subsequent groups are more likely to use the road (and its packed trail). If a group turns back once and the same individuals come to the gate again, they may be more likely to give up, or more desperate to find an alternate route. How will you account for this non-independence?

WE CONSIDER EACH BISON GROUP ENCOUNTERING THE GATE TO BE INDEPENDENT BECAUSE THE QUESTION WE POSED WITH THIS MANIPULATION IS WHETHER BISON WILL TRAVEL ALONG AN UNGROOMED ROAD IF THEY ARE DENIED ACCESS TO THE GROOMED ROAD. THE MANIPULATION WAS NOT DESIGNED TO ADDRESS WHETHER BISON PREFERENTIALLY TRAVEL THROUGH UNBROKEN SNOW ON THE ROAD. OUR EXPECTATION IS THAT, IN THE ABSENCE OF MECHANICAL GROOMING, BISON WILL MAINTAIN SELF-COMPACTED TRAILS ALONG THE UNGROOMED TRAVEL ROUTES.

Last comment

The work being proposed is solid. I have one last suggestion that the authors might consider. In my view, this suggestion would not need to be incorporated in a final proposal.

In the absence of strong, multi-year road-closure experiments – long-enough to assess consequences for demography and outside-of-park movements – you could combine the smaller-scale closure experiments (Theme 3) with a demographic/landscape-movement simulation-modeling approach to specifically examine the underlying questions. This model could be used to integrate all the relevant information discussed in Themes 1 and 2. Construct a demographic spatially explicit model that relates survival and outside-of-park movements to snow levels and the ability to migrate or move on groomed roads. You could follow the guidelines of Starfield – start simple, add in complexity as necessary, and identify which supplementary studies of Themes 1 and 2 really are essential for building/testing the model. This approach might result in a more problem-driven approach that might prove powerful.

THIS APPROACH WAS PROPOSED DURING THE 1990'S WHEN WORK WAS INITIATED ON THIS ISSUE. AT THAT TIME, WE DID NOT HAVE DETAILED BEHAVIORAL DATA TO PARAMETERIZE SUCH A MODEL. OVER THE PAST DECADE, WE HAVE BUILT A FOUNDATION OF DATA THAT CAN BE INTEGRATED INTO A MORE GLOBAL, MECHANISTIC MODEL AS A FINAL PRODUCT TO THIS EFFORT.

Comments by Keith Aune, Montana Department of Fish, Wildlife, and Parks

In general, this project proposal is very thorough and substantive. I would support further development of this project with a few comments considered below.

1) It has always baffled me that nobody considers the Northern bison as a control group considering that they are not influenced greatly by any snow grooming activity with the exception that central bison move into this area at times. How could the northern herd be considered in the design of this study?

WE PROPOSED TO RADIO COLLAR BISON IN BOTH HERDS SPECIFICALLY TO ENABLE COMPARISONS.

2) Little is mentioned about the spring snow plowing that produces a mini-tourist season and creates a large tunnel effect for bison traveling the road network. Bison move out of the park more readily and commonly during the spring (April and May) after road grooming has been stopped and plowing begins. Is not plowing in the spring a consideration to ponder?

IT IS WELL ESTABLISHED THAT BISON MOVE TO LOWER ELEVATION AREAS WITH MORE HETEROGENEOUS SNOW COVER DURING THE SPRING MELT-OUT PERIOD. THE ISSUE UNDER CONSIDERATION IS WHETHER ROAD GROOMING CURRENTLY ENABLES OR FACILITATES BISON MOVEMENTS TO THE PARK BOUNDARY. THE NATIONAL PARK SERVICE WILL NEED TO PLOW ROADS IN THE SPRING REGARDLESS OF WHETHER GROOMING IS IMPLEMENTED OR NOT.

These are relatively well considered in the design but I have a comment to add here:

3) Timing and seasonal snow patterns as well as severe cold or mild weather are an uncertainty that will challenge this study design. Also I often wonder about the effects of summer drought. Unfortunately these are experimental conditions that cannot be controlled. The results of this study, of course, are likely to be confounded by dramatic weather events so results must be carefully framed in the context of the winter/spring weather and perhaps summer drought.

WE RECOGNIZE THAT THE ENVIRONMENTAL CONDITIONS UNDER WHICH THESE STUDIES WOULD BE CONDUCTED CANNOT BE CONTROLLED. THUS, THE PROPOSED STUDIES WILL NEED TO BE CONDUCTED FOR A NUMBER OF YEARS TO SPAN THE RANGE OF ENVIRONMENTAL CONDITIONS EXPERIENCED IN YELLOWSTONE.

4) There are some habitat dynamics at play here but I think the study design will capture that……the patchy distribution of resources and the thermal activity in portions of the Yellowstone dramatically influence bison distribution….hence foraging pressure on critical ranges. Although snow is found to be a big driver I wonder if we often miss some of the habitat effects that interplay with bison distribution over time and need tobe careful to include them as you have done in research theme 2.

5) One other factor is the management activity outside the Park at the time of the study could influence bison distribution and movements. Forced movements of bison along the boundaries or intensive hunting pressure could be a factor influencing the current road use patterns within the system. Careful monitoring of management activity along the borders will need to be considered as a covariate in this analysis.

MANAGEMENT ACTIVITIES AT THE BORDER WILL BE CLOSELY MONITORED.

6) The authors considered the foraging behaviors for bison….how about anti-predator behavior. It might be important to consider what affect wolf occurrence has on the distribution of bison as a new player in the mix. Especially considering that elk

numbers are going to continue to decline as a result of low calf recruitment and old age structure. Will wolves shift more heavily to bison and do they influence bison distribution?

LONG-TERM WOLF-UNGULATE STUDIES ASSESSING THE EFFECTS OF WOLVES ON THE DISTRIBUTION OF BISON AND ELK IN THIS SYSTEM WERE INITIATED FOLLOWING WOLF COLONIZATION AND WILL CONTINUE.

7) Is it possible to use some loop drives in this as experimental areas. Leave ungroomed and monitor then introduce grooming or alternate grooming on alternative trails?

THE MANIPULATIONS WE PROPOSED INVOLVE PROVIDING BISON WITH UNGROOMED ALTERNATE ROUTES (I.E., LOOPS) AT THE POINTS WHERE ACCESS TO GROOMED ROADS ARE DENIED.

8) One concern I have is that with multiple treatments on various segments what will be the effect of one on the other. What will treatment on the Firehole Canyon do to the experiment on the Firehole?

WE DO NOT INTEND TO CONDUCT BOTH EXPERIMENTS SIMULTANEOUSLY.

9) I did not see where the authors proposed any products from the study. One assumes they will produce something in writing but it might help if there was a clearer commitment to some product or outcome following the experiment.

WRITTEN REPORTS AND SCIENTIFIC ARTICLES WILL BE GENERATED AFTER STUDIES ARE COMPLETED.