Author responses (AR) below in blue

Associate Editor

This paper has now received reviews from two referees—my sincere apologies for the length of time this has taken. While both referees agree this work would be of interest to readers of IJWF, they have each identified a number of issues that preclude acceptance for publication at this stage. Each referee has provided a detail assessment of the critical deficiencies and suggestions on how they could be addressed if you were to undertake the significant revisions required.

AR: We understand the delay and appreciate the careful consideration editorial staff and reviewers have given our manuscript. We agree with each of the concerns raised by the reviewers and have addressed each through revision of the manuscript as explained below. It is our belief that the detailed comments and suggestions of the reviewers and focus provided by the AE have enabled us to revise the manuscript in a manner that overcomes each of the critical deficiencies identified. With AE and reviewers' contributions, we believe this is a markedly better product, and we welcome the opportunity to continue improvement of the paper as necessary for publication in IJWF.

Referee 1 identified substantial gaps in the literature review and understanding of the context of fire behavior in grassland and provided a number of critical references that you should consider. This referee also identified major concerns with the method of assessing fuel moisture content that could have major ramifications for subsequent analysis and conclusions, particularly across field sites. A lack of detail on exactly what temperatures were being measured by your thermocouple array was identified by both referees. Referee 1 also raised doubts about the veracity of the rate of spread values, particularly in regard to low burning conditions (i.e. high fuel moisture and low wind speeds).

AR: We've addressed the issues with the rate of spread values and have substantially revised discussion of these data with respect to our conditions and those reported in the literature. We've clarified in the manuscript what our fuel moisture values represent and have responded below to the concerns about its assessment. We've updated our language about the measurements taken by thermocouples with respect to their positioning.

Referee 2 highlighted the residual variability associated with direct effects of the fire on below ground plant tissue and the lack of consideration of soil moisture limiting the robustness of the findings. Referee 2 further raised concerns about the scope of implications for wildland fire behaviour more generally arising from the observations of a small set of prescribed burns.

AR: The reviewer is correct in identifying soil moisture as an important modulator on belowground effects of soil heating. As the study was designed to address fire behavior, specifically, and neither heating below the soil surface nor any first- or second-order fire effect, plant tissue or otherwise, it should not seem surprising that discussion of such responses was minimal and should not be interpreted as a weakness of a paper clearly focused on fire behavior and the factors that drive it.

Furthermore, that 25 landscape-scale fires constitutes a “small set” suggests an unreasonable expectation with respect to acceptable sample sizes. Our sample size is larger than average for both factorial plot experiments and studies along gradients. While not exhaustive by any means, here’s a snapshot of sample sizes among grassland fire behavior/heating effects studies I’m currently citing in various papers now:

- 3 plot replicates x 3 treatments (Strong et al. 2013)
- 3 plot replicates x 8 treatments (Reinhart et al. 2016)
- 4, 10 x 10 m plots (Archibold et al. 2003)
- 4 plot replicates x 4 treatments (Russell et al. 2015)
- 4 fires x 1 location (Silvani & Morandini 2009)
- 4 plot replicates x 2 locations (Ohrtman et al. 2015)
- 12, 20 x 20 m plots (Augustine et al. 2014)
- 15 fires x 1 location (Williams et al. 2015)
- 8 plots x 2 years (Bidwell & Engle 1992)
- 20 wildfires between 1965 and 1990 (Cheney et al. 1998)
- 97 plots across 2 locations (Cruz et al. 2015)
- 315, 9 x 9 m plots in a 20-yr LTER experiment (Wragg et al. 2018)

We openly acknowledge and mitigate in the Discussion the shortcomings of the study; sample size was not one of them.

Given the scope of the referees’ concerns and potential work required to address them I am recommending rejection with encouragement to resubmit a revised manuscript.

AR: We trust that this revision in response to the reviewer’s pertinent concerns will be recognized as a substantial improvement in the manuscript, and again we appreciate the opportunity to resubmit after this constructive review process.

Reviewer 1

AR: Please note that, for whatever reason, at some point after the Abstract line numbers used by this reviewer are not consistent with the submission file we have available on ScholarOne. The second reviewer’s line number references do match up, and we’ve done our best to use these common references to adjust the line number references made by the first reviewer. We believe that the discrepancies generally did not create substantial misunderstandings but are aware there are a couple instances in which vague comments from the reviewer were difficult to pinpoint where a revision or reference insertion was being requested.

The topic of the manuscript is an essential subject concerning implementing prescribed fires in great plains grasslands. The authors provided an overview in the introduction sections, but more work on the literature review on grassland fire experiments would improve this section. Several failings in the manuscript need to be addressed before being accepted for scientific journal publication. The Methods and Results section needs substantial improvements with suggested amendments listed below.

AR: We appreciate the identification of the manuscript's failings and have followed the suggestions, which produced substantial improvements to the manuscript. The reviewer will find that the discussion of rate of spread has undergone particular attention.

The manuscripts require substantial amendments, clarification and editing, therefore recommend another review of the revised manuscript for publication.

AR: We trust that the substantial amendments, clarifications, and edits made here will be received well in a subsequent review, and we are happy to add further clarification where necessary.

Detail comments:
Line 15: replace Canopy temperature with "Above ground flame temperature"

AR: Correction made.

Line 19: lower fuel moisture- should this read "dead fuel moisture"

AR: Fuel moisture measurements were made on the entire herbaceous fuelbed, including standing dead, live, and litter fuel components. We explain this in greater detail in response to another comment below; please note that as part of that explanation and our efforts to clarify the scope of our data, we've added "overall fuelbed moisture' here.

Line 43: add reference:
Cheney, Gould, Catchpole (1993) and Cheney and Sullivan (2008) Grassfires: fuel, weather and fire behaviour, CSIRO Publishing, Collingwood, VIC, Australia 3006, pp150

AR: It is unclear how a reference to secondary literature adds value beyond the three primary references already cited.

Line 48-49: Incorrect, fire spread does not increase as more fuel available see:
Cheney et al., 1993, Cruz et al., 2018 (International Journal of Wildland Fire 27(11) 727-741 https://doi.org/10.1071/WF18082

AR: The statement has been corrected.

Line 56: see additional references:
Cruz et al., 2015 (International Journal of Wildland Fire 24(6) 838-848

https://doi.org/10.1071/WF14146),
Kidnie et al., (2015),
Sneeuwjagt, R.J. and Frandsen, W.H. (1977) Behaviour of experimental grass fires vs. Predictions based on Rothermel's fire model. Canadian Journal of Forest Research 7:357-367

AR: Additional references to Cruz and Kidnie papers added.

Line 65: Check references:
Wotton BM, Martin TL (1998) Temperature variation in vertical flames from a surface fire. In 'Proceedings 3rd International Conference on Forest Fire Research and 14th Conference on Fire and Forest Meteorology' 16-20 November 1998, Luso, Portugal. pp. 533-545 (ADAI: Coimbra, Portugal)
Wotton, BM, Martin, TL, Engel K (1998) A vertical flame intensity profile from a surface fire. In 'Proceedings 13th International Conference of Forest Fire and Meteorology', 27-31 October 1996. Lorne, VIC. pp. 175-182. (International Association of Wildland Fire: Missoula, MT)

AR: While the titles of these references look interesting and relevant, we were unable to find text for these 14+ year old conference papers and trust that the seven references on vertical profiles currently cited are sufficient.

Line 83: Check reference:
Walker JD, Stocks BJ (1968) Thermocouple errors in forest fire research. Fire Technology 4, 59-62. doi:10.1007/BF02588607

AR: We've added the reference where we believe it is the most effective given the context of this part of the Introduction.

Line 102: misuse of the term "canopy temperature". The canopy is usually referred to as tree or shrubland vegetation cover, not grasslands. Also, I do not think you measure the temperature of grass fuel, but the flame temperature above ground (15 cm). So delete canopy temperature and replace it with "flame temperature."

AR: The reviewer makes a good suggestion to improve the clarity of the paper, and "flame temperature" has been adopted throughout the manuscript.

Line 111: The supplemental Information document includes two figures plus a data analysis script. Recommend including supplementary Figures 1 and 2 in the manuscript.

AR: The reviewer is correct in identifying the components of the supplemental information document. We specifically placed these figures in the supplementary information because we believe they serve a supporting role for the study in general, but do not provide information necessary for readers to interpret the paper. As such, we doubt the efficiency of committing page space for them in the manuscript, but we are happy to move them upon the recommendation of the editorial staff.

Line141: Include supplementary Figure 2 in the manuscript

AR: The reviewer makes an interesting suggestion on which we would appreciate input from the editorial staff. At present, because we have not leveraged the fractal design for geospatial analysis, we doubt that committing page space in the main manuscript to a full illustration of the fractal design is warranted. But if the editorial staff believes this is a worthwhile inclusion, we are happy to move the figure.

Line 146: no reference to fuel height, which would be helpful since the fire spread thermocouples were place 15 cm above ground

AR: Vegetation heights spanned the range of variability typical of mixed-grass prairie swards and were not measured in this study. We can add reference to height data derived from vegetation structure transects conducted in the field season prior to burns if reviewers and editors determine this information is necessary.

Line 150: See:
Matthews (2010) International Journal of Wildland Fire, 19, 800–802 "Effect of drying temperature on fuel moisture content measurements".
This study concluded that the differences between oven-dry masses of fuels dried at 60 and 105oC of up to 3.5% were measured. Thus, fuel moisture content value could be significant wetter (higher values) than presented in the paper.

AR: We're quite familiar with the Matthews paper. While it is technically correct we believe its application and impact are often over-extended, as is the case here.

- Firstly, Matthews was dealing with fully-cured fuels, and grasses showed 8% moisture at 60C and 10% at 105C. This is a minor difference when applied to overall fuelbed moisture that includes uncured material.
- Secondly, Matthews specifically referred to the impact on fire behavior predictions, which are indeed sensitive to a couple percentage points in cured fuel moisture. But we are using the fuel moisture to explain fire behavior that already occurred in a regression model. Even if we had major error in our measurements, as long as it was consistent, the data would have the same effect on response variables in the statistical models.
- Finally, subsequent work (e.g. Jolly & Hadlow (2012), Int J Wildland Fire 21, 180-185) concluded that drying temperature was less critical than Matthews suggested.

Line 152: delete dot (tonne (t) . ha-1

AR: Dot deleted.

Lines 153-163: Lazy writing, for all the details on the thermocouples and logging interval,

are in the references. More information on thermocouples needs to be presented. For example, depending on the application, the gauge (diameter) selected will affect their performance. Larger diameter thermocouples have a slower response time owing to their higher thermal mass. These thermocouples have greater stability and operating life but will be more influenced by radiation. Conversely, smaller thermocouples will have a shorter response time and improve the accuracy of flame arrival time but may not deliver the stability or operating life (see:
Walker JD, Stocks BJ (1968)
Butler BW, Cohen J, Latham DJ, Schuette RD, Sopko P, Shannon KS, Jimenez D, Bradshaw LS (2004) Measurements of radiant emissive power and temperatures in crown fires. Canadian Journal of Forest Research 34, 1577–1587. doi:10.1139/X04-060)

AR: We've added the gauge of the thermocouples. Logging interval was given in the next paragraph, and we've moved it up to here. It isn't clear what additional information the reviewer might have in mind. The reviewer is entirely correct about these trade-offs in wire size, but it isn't clear what purpose incorporating this discussion into the Methods section would achieve when only one wire size was used.

Line 173: lower case "M"

AR: We've corrected the case of variable names. (Fortunately the other reviewer noted this as well, using the line number consistent with the .pdf file of the submission we can access from ScholarOne (L 165). We've used this differential to try and better focus line references given by Reviewer 1; please accept our apologies if we've misunderstood requested revisions.)

Line 175: delete dot (m s-1) global change

AR: Dot deleted.

Line195-205: Authors need to explain the missing data of 17% and 27% of the fuel load and soil temperature, respectively. It was difficult to see why there were 17% of the fuel load data missing. Missing soil temperature resulted from the fires not burning over the thermocouples or faults in the instruments. Imputation of the missing fuel and soil temperature data will bias the analysis. The three missing samples of spread rate is low; thus no need for data Imputation.

AR: We share the reviewer's concern about bias in our analysis. We also agree with the reviewer's general sentiment that the ideal situation would be to not have any missing data. The question then is to decide how to proceed when missingness persists, as is the unfortunate but realistic outcome of research projects that attempt to collect a lot of data as close to complex events like multiple landscape-scale prescribed burns being conducted on a given day, over several days, with crews whose priority is operational safety. It is our belief that the risk of bias from imputing missing data using tested and accepted algorithms developed specifically for this purpose is substantially less than the bias created by discarding entire rows of multivariate data when a few points are missing, thus altering the distribution of the data and upsetting the balanced design, which would skew marginal sums of squared error in the multiple regression analysis.

Line 212-214: lower case "M" and "R"

AR: All variable names have been converted to lowercase.

Results: The results shown in Figure 1 is inconsistent with other experimental grassland fires.
• Fuel moisture: (expressed on a dry-weight (Line 151)) exceeds fuel moisture of extinction (i.e., the moisture content at which the fuel will not burn (See Cheney and Sullivan 2008, pp 39). Grassfire experiments conducted in Australia (Cheney et al. (1993) fuel moisture values ranged from 2.7 to 12.1% (oven-dried weight - ODW), Cruz et al. (2018) fuel moisture values 3.5 to 12.6% (OWD). The authors need to check the fuel moisture values for both sites; the median and mean values are >30%, and in the Hettinger site, all fuel moisture above moisture of extinction, i.e., fuel will not burn. It appears there is a fault in the sampling and drying procedures to estimate fuel moisture.

AR: The reviewer is correct in identifying that our fuel moisture values are above those reported for fine dead fuel moisture in the literature, and indeed above the fine dead fuel moisture of extinction in fire spread models. The discrepancy is due to the fact that we report the moisture content of the entire fuelbed–standing live and dead fine fuels as well as litter–instead of collecting and measuring each component separately, which would have been prohibitively time-consuming within the operational context of these management burns. Thus, we present no a priori hypotheses about the relative contributions of various fuel component moistures, but refer instead to the overall moisture of the entire fuelbed. This approach is not without precedent in grassland fire behavior research, especially when moisture is but one predictor variable among many used to characterize the fire environment in multiple regression models (e.g., Trollope 1978, Trollope & Potgieter 1985, Bidwell & Engle 1992, Trollope et al. 2002, McGranahan et al. 2016, and Cruz et al. 2015, although they measured the components to calculate a weighted average). Note that several of those examples report overall fuelbed moisture values well above the moisture of extinction and consistent with our data, e.g. Trollope & Potgieter 1985 reported a mean of 22% and a maximum of 67%, Bidwell & Engle 1992 reported a mean of 31% and a max of 60%, and Trollope et al. 2002 reported an average of 32% and a high of 69%. In our revisions, we have made it more clear what our fuel moisture measurement refers to, especially in the Abstract, Methods, and Results (the original submission already committed a paragraph to this topic, which we've bolstered to clarify the reviewer's concerns).

• Rates of spread (m/s): unit appear to be incorrect, should it be m/min, which would give more realistic values for spread rates for observed burning conditions. Compared to the Central Grasslands fires, the Hettinger site spread rates seem high for the current fuel (low fuel loads, high fuel moisture) and weather conditions (low relative humidity and wind speed). These findings are inconsistent with other grassland fire Studies.

AR: The reviewer is correct, the units used throughout the manuscript were incorrect–m/min were in fact reported, not m/s. The comparison between these data and other grassland fire studies has been updated.

• Soil temperature: Line 247 interprets that the maximum measure soil temperature reached was 325oC; compared in Fig1, there were observations over 325oC; this needs clarification.

AR: We've replaced "reached" with "reached or exceeded" to clarify that 325 doesn't represent a maximum temperature.

• Replace "Canopy temp" with "Flame temp"

AR: Usage of "canopy temperature" has been replaced with "flame temperature" (or sometimes, "aboveground temperature" when appropriate) throughout the text.

• Change to IS units: Wind (m s-1), Fuel load (kg m-2), Rate of spread (m min-1)

AR: These changes have been made in both text and figures.

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Line 226: Fig. 1: Figure 1 appears to be a violin plot visualising the numerical distribution of the two sites. Recommend replacing these plots with box-and-whisker plots, which will show a more detailed statistical summary of the data (i.e., median/mean values, 25th and 75th quartiles and outliers). Finder y-axis scale will improve the interpretation of the data presented in the graphs. Recommend adding a table listing the range of data for the two sites, which would complement Figure 1. More text describing the result would be helpful. Example: Fifteen fires were sampled from spring burns in the North Dakota central grassland, with fire spread between xx(min value) and yy (max value). Compared to the Hettinger site, the fire spread ranges from xx to yy. (text supported by a table giving the range of weather, fuel, and fire behaviour data)

AR: The reviewer is correct, Fig. 1 presents violin plots, which are much more effective at visualizing data distribution that boxplots summarize. In response to the reviewer's suggestions, additional statistical summaries (quantiles) have been added to the plots and a table of summary statistics added to the supplemental information.

Line 230-231: Comment on the lower relative humidity at Hettinger than the central grassland site.

AR: The reviewer is correct, relative humidity was lower at Hettinger. This relationship is reflected in the statement about drier air and hotter fires at Hettinger.

Line 235-238: Sentence requires rewording, appears to be repetitive

AR: Inconsistencies in line number references prevented us from pinpointing the exact sentence referred to here, but we have tried to reduce repetition throughout in our revision and have paid particular attention to the paragraphs around this point in the Results–the reviewer was likely referring to repeated references to “marginally related” and “marginally significant” in a grammatically-poor sentence that has been revised accordingly.

Line 240: replace plant canopy with flame temperature (a global reference to canopy or plant canopy temperature to flame temperature above ground. Reviewing the graph in Figure 1, the majority of the flame temperature (canopy temp) is below 3250C. Check the frequency to a temperature above and below 325oC,

AR: We’ve revised these sentences accordingly.

Figure 3: Replace Figure with a table listing regression coefficient, standard error, MBE (mean bias error, MAE (absolute error), and RMSE (root mean squared error) See: Willmott, C.J., 1982. Some comments on the evaluation of model performance. Bull. Am. Meteorol. Soc. 63, 1309–1312

AR: The reviewer does not make clear why the visual representation of regression coefficients and confidence intervals, a standard means to present regression results as relative effect sizes of terms in multiple regression models (e.g., Nakagawa & Cuthill (2007) Biological Reviews 82: 591-605), should be replaced with a table of error statistics. The given reference critiques the use of Pearson’s correlation coefficients, which we do not report here.

Line 281: Check other references related to grassland fire experiments and related analysis (Sneeuwjagt & Frandsen (1977), Cheney et al. (1993 & 1998), Kidnie & Wotton (2015), Cruz et al. (2018)

AR: The reviewer is correct to call out this section and has provided useful references. The entire discussion of rate of spread has been entirely revised to reflect the proper units of measurement.

Line 287: See Wotton & Martin reference above

AR: Again, we were unable to find full-text access to this conference paper.

Line 288-289: move this sentence to the result section

AR: Apologies, discrepancies in the line numbers prevented us from identifying the exact line being referenced here. But we’ve focused on keeping Results-oriented sentences out of the

Discussion. However, to provide context for the reader, we do feel it is appropriate to briefly re-state our own average values when discussing the ranges of values in the literature.

Line 310: Cheney et al. (1993) drier fuel moisture values (2.7 – 12.1%) compared to data shown in Figure 1.

AR: The reviewer is correct. We’ve revised our discussion to reflect the differences in our fuelbed moisture content and the cured fine fuels Cheney et al. report.

Reviewer 2

Comments to the Author
International Journal of Wildland Fire
WF21119

General Comments:
I enjoyed reading the manuscript and found it full of creativity and insightfulness studying the effects of fire weather on fire behavior from 25 prescribed fires at two locations in North Dakota. The greatest strength of this paper is the scrutiny of combined fire spread and temperature data from thermocouples. However, several weaknesses exist in the manuscript that may not support some of the final conclusions. While the authors acknowledge the variability, there is still much variability associated with direct effects on belowground plant tissue from aboveground heating and fire spread. Very little mention of soil moisture is discussed throughout the manuscript. Even though thermocouples were placed at the soil surface and 15 cm above the soil surface, the fuel type at the research sites is known for a microclimate due to the robust litter layer. Even without the litter layer from KBG, soil moisture greatly affects soil surface conditions which in turn affects fire behavior. Another disconcerting research site comparison is the fuel loading difference, the varying ignition sequences executed, and the size differences among research plots.

AR: While soil moisture is certainly an important modulator of sub-surface soil heating and post-fire effects in soil strata, we are unaware of literature that connects soil moisture to fire behavior at or above the soil surface, which are the response variables measured here. We did in fact measure soil moisture, but in an effort to provide an instantaneous estimate of fuel moisture prior to conducting a prescribed burn, not to explain variation in belowground effects of heating (the data were excluded because our sampling during prescribed fires, not surprisingly, created a bias towards specific precipitation patterns that would require much broader, season-long sampling, as well, to establish an informative gradient). We address the other points of variability below, and how they are either accounted for in our statistical models or tangential to the response variables targeted in this study.

Specific Comments:

Line 9: Since this study was conducted on prescribed fires, assumptions about connections to wildland fire behavior are over-reaching beyond the scope of the study. Only conclusions and implications regarding prescribed fire within these ignition sequences should be extrapolated out to implications.

AR: The reviewer is correct, our study was conducted on prescribed fires, and we agree that one should not over-reach in making conclusions. As for the specific terminology, the reviewer seems to be conflating here the definitions of wildland fire vs. wildfire. Several (most? all??) established definitions of wildland fire refer to it as open combustion that occurs outside of a compartment and beyond the scope of structural fire management. These definitions of wildland fire include both prescribed burning and wildfire. We have ensured that the revised draft emphasizes the prescribed fire context.

Line 109: How much do you attribute the variability in heat generated due to the variable ignition sequences utilized? Wouldn't a ring-fire ignition generate more intensity than strip head fires? How do you compare the thermocouple data that registered temperatures from fire fronts aimed directly at the sensors (line 335-339)?

AR: We attribute no variability in heat generated to variability in ignition sequences. While under particularly unstable atmospheric conditions conducive to rapid convection a ring fire might be expected to generate greater intensity (along a difficult-to-determine gradient towards the point of frontal convergence), the fact is that a ring fire pattern would not have spread through these fuelbeds under the described conditions. All flame fronts were predominately wind-driven, with little interaction between plumes and flame fronts. We've added text to contextualize the discussion of Williams et al. (2015) and the effects of ignition pattern on fire behavior. That study used smaller human ignitions to mitigate extreme fire behavior from broad ignitions and wildfire, while we used different patterns simply to get fire to spread.

Line 108: Fire sizes vary tremendously throughout the study. How do you account for these differences between sites?

AR: The reviewer is correct that there are two different sizes of burn units–about 25% were 8 ha and the other 75% were 16 ha–in which a 100m plot was placed in the center of each. The reviewer has an interesting take on what qualifies as "tremendous" variability, though: we have just the two areas, and those areas really aren't all that different. We attribute none of the variability in our data to these differences, and are not aware of any literature suggesting we might expect otherwise.

Lines 157-163: How was the data logger tip secured to the target area? Did this interfere with the temperature?

AR: We've added the following to the Methods: "Beads of the thermocouple probes extended at least 3 cm from the supporting apparatus, to which the insulated lead was attached with wire." To the reviewer's second question, no, this did not interfere with the temperature.

Line 162: Was plant litter fuel moisture assessed? If not, why? If a thermocouple was placed under the litter layer, wouldn't the fuel moisture of the litter layer buffer the temperature registered?

AR: Indeed, as the reviewer suggests, the temperature recorded by the thermocouple placed under the litter would be affected by litter moisture. Plant litter was included in the overall fuelbed moisture measurement (see response to Reviewer 1 above). Thus, greater moisture would be expected to produce a lower temperature reading on that thermocouple. This is why these measurements were made, and why we discuss in the Discussion the values of parsing various fuelbed components, which was not feasible in this study on management-scale burns. We've explicitly added litter to the live and dead categories discussed.

Line 165: Lower case m on maximum.

AR: Thanks, correction made.

Lines 281-282 & 317: At what point does the thatch/litter layer from KBG factor into the temperature?

AR: The role of thatch in grassland fire behavior remains much less well-known than other factors. The thatch layer introduced by *Poa pratensis* is likely a novel phenomenon for grassland fire ecologists, more like a forest duff layer or O horizon closely associated with the soil surface than a conventional litter component of fallen grass & forb material. Take, for example, the absence of such parameters from rangeland vegetation types vs. forest types in the First Order Fire Effects Model (FOFEM). These are all interesting questions and because they remain speculative, we believe we have considered them to an appropriate degree in the present Discussion.

Lines 325-335: How can you compare data from KBG dominated sites to sites that struggle with fuel continuity for adequate consumption?

AR: The reviewer has correctly identified the meaningful ecological gradients that we sampled across. We make these comparisons by testing our response variables against these gradients in mixed-effect regression models that account for the random effects of location-specific differences when determining whether each gradient has a meaningful effect on the response variables. These steps are described in the Data analysis subsection of the Methods, and we've added a phrase to make the handling of location-specific error in the random effect term more explicit.