Title: Critical reproductive behaviors in Scaled Quail and Northern Bobwhite are affected by thermal variability and mean temperature

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Keywords: climate change, environmental temperature, thermal variation, behavior, incubation, quail, *Colinus virginianus, Callipepla squamata*

Abstract

Environmental conditions can influence parental care behaviors, which in turn can greatly affect the microhabitat conditions experienced by developing offspring. It is critical to uncover relationships between ambient weather, parental behaviors, and offspring thermal environments to understand the ability of organisms to mitigate environmental conditions and predict outcomes under climate change. In warm conditions, avian parents may spend longer periods away from the nest, but we know little of how increased thermal variation drives these changes or what temporal scale influences the changes. We examined how parents mediate environmental conditions for developing offspring in two quail species, Scaled Quail (*Callipepla squamata*) and Northern Bobwhite (*Colinus virginiatus*), by examining changes in the duration and timing of incubation off-bouts (recesses away from the nest) in relation to mean temperature and temperature variability experienced over either a 24-hour period (low resolution) or in the two hours immediately preceding an off-bout (high resolution). We found species-specific differences in off-bout duration, with Scaled Quail spending a significantly shorter time off the nest daily. In both species, we detected a positive relationship between average thermal conditions and the start time of afternoon off-bouts. Alternatively, morning off-bouts occur earlier in response to increased thermal variation from the previous day. Warm conditions immediately preceding off-bouts led to increased off-bout duration with the opposite trend in response to increased variation. Our findings suggest that the thermal environment, in contrasting ways over varying thermal and temporal scales, can have a significant impact on parental care behaviors. These alterations can lead to altered thermal environments for offspring across multiple scales. Therefore, determining how the thermal environment induces behavioral changes requires high-resolution environmental data.

Introduction

Moderate projections of anthropogenic climate warming estimate an average global temperature increase of 1.1 – 2.6°C by 2100 (1) with projected losses of 7.9% of all species due to climate change (2). However, mean increases in temperature alone will not reflect the shifts in thermal conditions that organisms will experience. The fallacy of the average, known as Jensen's Inequality, highlights the importance of exploring thermal variability in natural systems, as relationships between external conditions and biological responses are often nonlinear and can change drastically under unusual or extreme conditions (ex. the relationship between metabolic rates and average thermal conditions described in Denny 2017; 3–5). Increases in thermal variability are increasing alongside warming average temperatures (6,7), and organisms can have differing responses to increasing thermal averages or variability (8,9).

Anthropogenic climate change is projected to cause phenotypic changes (10) which can be driven or mitigated by plastic behaviors (11). For wildlife, plastic behaviors are necessary to avoid reductions in fitness in response to extreme or novel thermal conditions (12). Thus, behavioral plasticity is an important driver of organismal responses to climate warming. Behaviors employed by parents to care for their offspring (i.e., parental care behaviors) are known to be plastic (13), play an important role in shaping the thermal environment of developing offspring, and are often directly linked to offspring phenotypic expression (14). Ambient thermal conditions can alter parental care behaviors and subsequently modify the thermal environment of the developing offspring to directly influence offspring phenotypes (15,16). Examining shifts in parental care behaviors of wild organisms in response to the natural thermal environment can reveal the ability of parents to modify their behaviors to meet the competing demands of their offspring's thermal needs and self-maintenance, which becomes critical in suboptimal thermal conditions (17,18). Multiple species have expressed these trade-offs (19,20), including large bodied homeotherms like Eastern Wild Turkeys (*Meleagris gallopavo silvestris*; 21).

Environmental temperature may be an important instigator of behavioral and phenotypic change (22,23) over distinct temporal scales that convey different information about how animals respond to the thermal environment. Understanding how short-term thermal fluctuations influence parental behavior in real time is critical for understanding drivers of the developmental environment (24). Low-resolution, temporally averaged thermal data is useful in many contexts, especially when exploring seasonal trends in behavioral patterns (25). For instance, greater than average temperature over the course of a reproductive season in birds (i.e., low-resolution thermal and behavioral data) is associated with shorter incubation periods (26,27), possibly indicating a reduced cost of reproduction for parents. However, assessing only average temperature over the entire incubation stage obscures the thermal variability occurring during this period. During an acute period of hot temperatures, parents may increase nest attendance to shield eggs or seek refuge, leaving eggs exposed to a suboptimal thermal environment. Thermal biologists have explored the relationship between phenological outcomes and their variation alongside long-term thermal trends (28), but less is known about how real-time or recently experienced temperatures shape isolated behavioral responses. Exploring the effects of both low-

and high-resolution thermal data on specific behavioral changes can inform the mechanisms behind large scale changes in species' ranges, phenotypic changes, and fitness (29).

Birds present a unique opportunity to investigate the relationship between high-frequency thermal measurements and behavioral decisions due to the role parents play in shaping the thermal environment for their developing offspring (30). Birds in hot environments require self-maintenance behaviors such as gular fluttering or retreating to cooler microclimates to avoid physiological stress (31,32). However, coping behaviors that cause the parent to leave the nest can come at the cost of offspring care, as the nest is left exposed to external thermal conditions (14,15,30). The timing of off-bouts (the time a parent spends off the nest) and their duration play important roles in the development of avian offspring (27). Lengthening and, in some cases, delaying off-bouts can lead to higher rates of predation (28) or thermal stress, reducing adult and offspring fitness (33).We know little of the scale at which these tradeoff decisions are being made and their relationship to natural thermal variation (34,35), but the importance of parental care on offspring development suggests that reproductive success would benefit from the ability of parents to delay off-bouts until temperatures are outside lethal levels for embryos (27). Acclimation to thermal variation and short-term thermal conditions has been evidenced in ectotherms (36–38), though evidence in endotherms is limited to animals living in the tropics due to their narrow ranges of thermal tolerance (39). Largely, studies focusing on temperate avian responses to thermal change focus on phenological adjustments and seasonal shifts in the thermal environment (40,41). There is little work focusing on avian responses to rapid changes in temperature, with the majority limited to individual thermoregulatory responses (20,21,42). The ability of parents to alter their behavior will depend on their ability to withstand physiologically demanding temperatures and to respond to thermal conditions as they are occurring, thus studies examining high resolution thermal and behavioral data are necessary.

The primary goal of this study is to determine the influence of average environmental temperature and thermal variability on incubation behaviors and resulting offspring microhabitat in Scaled Quail (*Callipepla squamata*) and Northern Bobwhite (*Colinus virginianus*) across two temporal scales: immediately or over a full day prior to parents leaving the nest. Using data collected in 2015 and 2016 and described in Carroll *et al*. (30), we compare differences in behavioral modifications of these species as it relates to temperature variability, average temperature, and the resolution of thermal data. Scaled and Northern Bobwhite overlap in the Southwestern US; Northern Bobwhite typically occupy a temperate climate across their range while Scaled Quail largely occupy arid, desert-like environments like the study locale. Nest construction is similar in both species, though Scaled Quail select nesting locations with more favorable vegetation for thermal buffering (30). We hypothesize that: 1) Thermal variability is an important driver of total daily off-bouts, with greater thermal variation delaying off-bout start time and shortening individual off-bout duration to avoid inhospitable nest conditions. 2) The temporal scale of thermal measurements will influence the resulting relationships between behavior and temperature, with short term thermal trends and behavior exhibiting a stronger relationship than extended, temporally averaged thermal trends.

Methods

Monitoring Temperature and Incubation Patterns

All nests were monitored in the Beaver River Wildlife Management Area in Oklahoma, USA (36°50′21″N, 100°42′15″W). Environmental temperature data was collected every 30 seconds within and outside the nest using modified Onset Computer HOBOware (Onset Corporation, Borne, MA) thermal sensors. External temperatures were taken with HOBO U23 Pro v2 External Temperature Loggers (30). The internal temperature was taken using egg shaped clay models inserted into the nest that matched the dimensions of quail eggs. Each model egg was inserted into the center of the nest and external sensor was placed within 2m of the nest for standardization of thermal measurements. More details of thermal probes and data collection can be found in Carroll *et al.* (30).

The machine learning software NestIQ was used to determine off-bout length and timing from the raw nest temperature data (43). To assess the impact the rate of thermal change has on off-bout duration, we calculated the average and standard deviation of environmental temperature measurements during the two hours before each off-bout. To assess the impact the daily thermal environment has on total daily off-bout, we calculated average and standard deviation of temperatures from the morning (sunrise to noon), afternoon (noon to sunset), and night (previous day sunset to sunrise) as well as the temperatures from the previous day and previous afternoon. All sunrise and sunset times were recorded for each day of the summers of 2015 and 2016 at the field site.

Statistical Methodology

All statistical analyses were conducted with R version 4.1.2 (44). To test the effect of the mean and standard deviation of temperature during the two-hour period before each off-bout (i.e., high-resolution environmental data) on off-bout duration, we developed a linear mixed model (45). The universal model included mean and standard deviation of the two-hour period preceding the off-bout as predictors and off-bout length (in minutes) as the response variable. We included a two-level categorical predictor for whether the off-bout took place in the morning or afternoon, as each species takes a maximum of two off-bouts per day, in the early morning or late afternoon (referred to as AMPM in models). We also included species (Scaled Quail or Northern Bobwhite). To control for non-independence of the measurements at a single nest and year, we included individual nest ID and year as random intercepts. All possible interactions between predictors were included in the universal model. To test for relationships between temperature and off-bout start time, we conducted a separate linear mixed model with the same predictors, interactions, and random intercepts described above but with off-bout timing as the response variable (Table 1).

To address the effect of temperatures experienced over a longer time period (i.e., low-resolution environmental data) on total daily off-bout, we developed a linear mixed effects model which included the sum of all off-bouts in 24 hours as the response variable. We selected total daily off-bouts as our response variable because the predictors are date-specific thermal measurements instead of off-bout specific thermal measurements. The predictive variables

included the mean and standard deviation of external temperature from the following timeframes relative to the date: 24hr (temperatures from 12AM-11:59PM of the current day), Morning (sunrise to 12PM), Afternoon (12PM to sunset), Previous Night (sunset to sunrise of previous night), Previous Day (12AM to 11:59PM of the previous day), and Previous Afternoon (12PM to sunset of the previous day). We chose these time periods to allow for comparison of longer-term trends in temperature. While they are likely highly correlated with one another, our model selection strategy (see below – *Model Selection*) corrected for this issue. We included a two-level categorical predictor for species (Scaled or Northern Bobwhite). To control for non-independence of the nest location and year, we included individual Nest ID and year as random intercepts. To test for relationships between mean and standard deviation of temperature on the average daily time of each off-bout, we conducted two separate linear mixed models with the same predictors, interactions, and random intercepts described above, but the response variables were the timing of the morning or afternoon off-bout respectively, given that each species takes at most, two off-bouts during the day in the morning, evening, or both.

Model Selection

For each universal mixed-effects model (high and low-resolution), we used the dredge function from the MuMIn package for model selection (46). We chose the best fit model by finding the model with the lowest relative AICc score (47). All values represented in our figures are partial residual plots generated using the predict function in R.

The best fit model for the high-resolution approach to analyze individual off-bout duration (referred to in Results as High Duration) included 2-hour mean temperature, 2-hour standard deviation of temperature, morning or afternoon (AMPM), and species as main effects with three interactive effects: 2-hour mean*species, 2-hour standard deviation of temperature*species, and AMPM*species (Table 1).

Two models were used to predict individual off-bout start time, one that included all morning off-bouts (referred to in Results as High AM Start Time) and one that included all afternoon off-bouts (referred to in Results as High PM Start Time). Both models included 2-hour mean temperature and 2-hour standard deviation of temperature as main effects, but only High AM Start Time included species (Table 1).

The best fit model for predicting total daily off-bout (referred to in Results as Low Duration) included 24hr standard deviation of temperature, morning standard deviation of temperature, and previous night standard deviation of temperature; Species and two interactive effects were included: species*morning standard deviation of temperature and species*previous night standard deviation of temperature (Table 1).

Two models were used to predict daily off-bout start time, one that included morning off-bouts (referred to in Results as Low AM Start Time) and one that included afternoon off-bouts (referred to in Results as Low PM Start Time) since each species take a maximum of two off-bouts per day in either the morning or evening. The best fit model for the morning off-bouts (Low AM Start Time) included standard deviation of temperature in the previous day and species as main effects with no interactive effects (Table 1). The best fit model for the afternoon off-

bouts (Low PM Start Time) included mean temperature during the afternoon and species with no interactive effects (Table 1).

High-Resolution Best Fit Models						
Model Name	**Response Variable**	**Main Effect(s)**	**Interactive Effects**	**AIC_c**	**df**	**AIC_c w_i**
High Duration	Off-bout Duration	2hr Mean, 2 hr SD, AMPM, Species	2hr Mean:Species, 2hr SD:Species, AMPM:Species	8952.7	11	0.742
Null	Off-bout Duration	~	~	9154.8	4	< 0.0001
High AM Start Time	Off-bout Timing - AM	2hr Mean, 2hr SD, Species	~	1375.2	7	0.429
Null	Off-bout Timing - AM	~	~	1417.8	4	< 0.001
High PM Start Time	Off-bout Timing - PM	2hr Mean, 2hr SD	~	1580.9	6	0.425
Null	Off-bout Timing - PM	~	~	1654.8	4	< 0.001
Low-Resolution Best Fit Models						
Model Name	**Response Variable**	**Main Effect(s)**	**Interactive Effects**	**AIC_c**	**df**	**AIC_c w_i**
Low Duration	Daily Off-bout Duration	24hr SD, Morning SD, Previous Night SD, Species	24hr SD:Species, Previous Night SD:Species	5666.7	10	0.02
Null	Daily Off-bout Duration	~	~	5706	4	< 0.001
Low AM Start Time	Off-bout Timing - AM	Previous Day SD, Species	~	1378.9	6	0.075
Null	Off-bout Timing - AM	~	~	1395.6	4	< 0.0001
Low PM Start Time	Off-bout Timing - PM	Afternoon Mean, Species	~	1349.7	6	0.22
Null	Off-bout Timing - PM	~	~	1374.4	4	< 0.0001

Table 1. The best fit models for each suite of thermal predictors as selected by AICc using the package MuMIn. High-resolution: The universal model included mean and standard deviation of the two-hour period preceding the off-bout as predictors and off-bout length (in minutes) as the response variable. We included a two-level categorical predictor for whether the off-bout took place in the morning or afternoon (referred to as AMPM) and species (Scaled Quail or Northern Bobwhite). The universal model for morning and afternoon start time included all above (except for AMPM) with individual off-bout start time as the response. Low-resolution: All models were structured as above except with averaged thermal data over 6 deterministic timeframes as predictors (24hr (temperatures from 12AM-11:59PM of the current day), Morning (sunrise to 12PM), Afternoon (12PM to sunset), Previous Night (sunset to sunrise of previous night), Previous Day (12AM to 11:59PM of the previous day), and Previous Afternoon (12PM to sunset of the previous day)). We included individual nest ID and year as random intercepts in all models. All possible interactions between predictors were included in each universal model.

Results

High-Resolution Thermal Data – Duration

As described by model High Duration, off-bout duration increased by ~4.4 ± 0.48 minutes per degree increase of 2-hour mean temperature ($\beta = 4.37 \pm 0.48$, $t = 9.1$, $p < 0.001$; Figure 1A). Off-bout duration decreased by ~ 4.2 ± 2.2 minutes per unit increase of 2-hour standard deviation of temperature, though the association was only moderate ($\beta = -4.16 \pm 2.16$, $t = -1.9$, $p = 0.055$; Figure 1B).

Northern Bobwhite averaged 140 ± 68 minutes per off-bout while Scaled Quail averaged 110 ± 57 minutes ($\beta = 62 \pm 14.7$, $t = 4.2$, $p < 0.001$). Northern Bobwhite exhibited longer afternoon off-bouts (159 ± 61 minutes) than Scaled Quail (Afternoon =108 ± 48 minutes; $\beta = -43.1 \pm 10.5$, $t = -4.1$, $p > 0.001$; Supplementary Figure 1A) even when mean temperatures 2 hours preceding the off-bout were high ($\beta = -1.8 \pm 0.7$, $t = -2.7$, $p = 0.007$, Supplementary Figure 1B). For both species morning off-bouts were not significantly longer than afternoon off-bouts,

though they were different ($\beta = 1.5 \pm 7.4$, $t = 0.2$, $p = 0.8$; Morning = 110 ± 66 minutes; Afternoon = 138 ± 61 minutes).

High-Resolution Thermal Data – Start Time

As described by model High AM Start Time, per degree increase of 2-hour mean temperature, morning off-bouts began 9 ± 3 minutes later ($\beta = 0.09 \pm 0.03$, $t = 3.2$, $p = 0.002$; Figure 1C. Similarly, off-bouts began 37 ± 10 minutes later per unit increase of 2-hour standard deviation ($\beta = 0.37 \pm 0.10$, $t = 3.7$, $p < 0.001$; Figure 1D). Scaled Quail began their off-bouts 55 ± 28 minutes earlier in the morning than Northern Bobwhite, though the association was only moderate ($\beta = -55 \pm 0.28$, $t = -1.9$, $p = 0.06$).

As described by model High PM Start Time, per degree increase of 2-hour mean temperature, afternoon off-bouts began 21 ± 3 minutes earlier ($\beta = -0.21 \pm 0.03$, $t = -8{,}1$, $p < 0.001$; Figure 1E. Alternatively, off-bouts began 33 ± 7 minutes later per unit increase of 2-hour standard deviation ($\beta = 0.33 \pm 0.07$, $t = 4.5$, $p < 0.001$; Figure 1F).

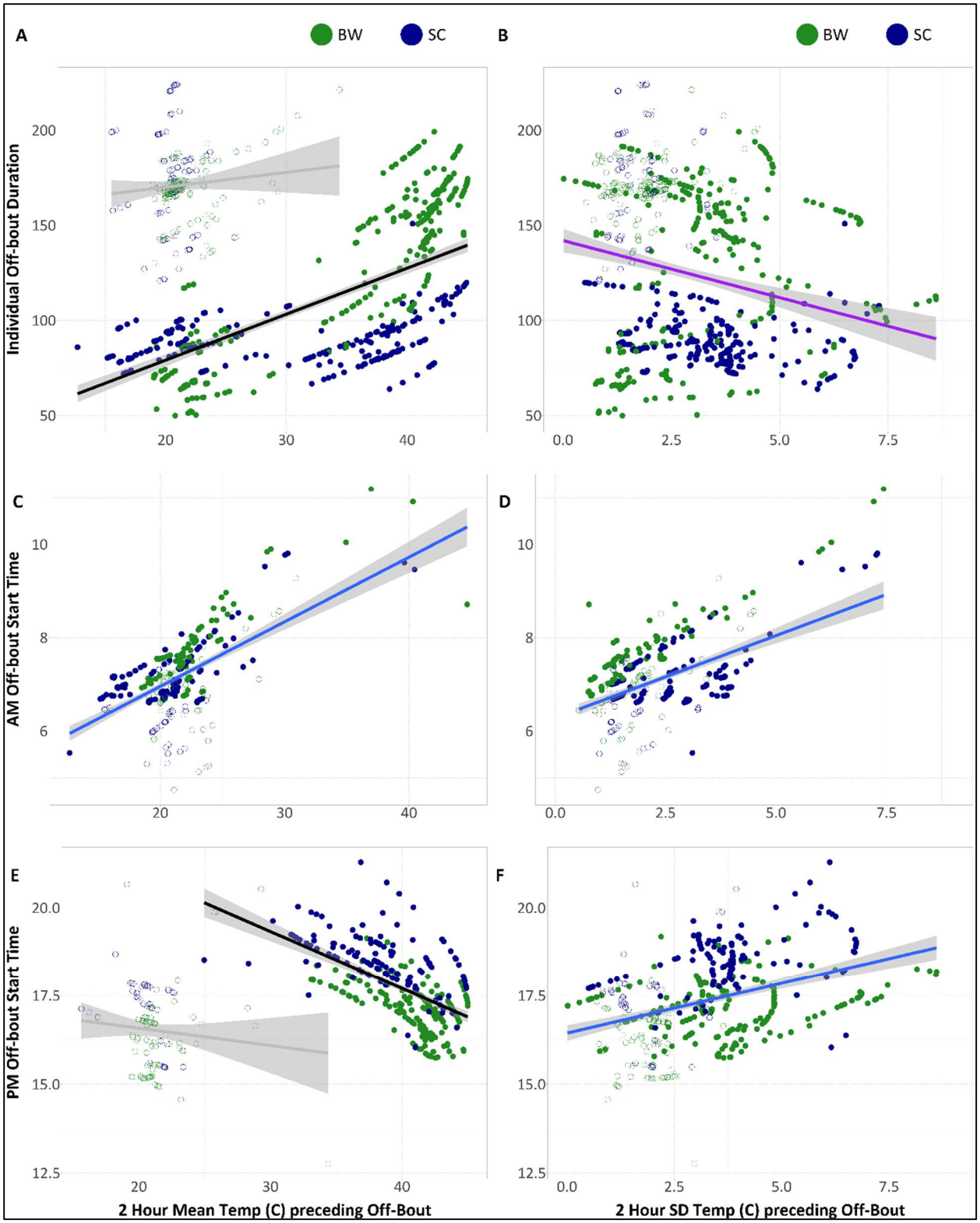

Figure 1. Partial residual plots showing the relationships between the thermal environment immediately preceding individual off-bouts and off-bout duration (A, B) as well as off-bout start time (C-F). Blue lines exhibit the association across both years while black and gray lines represent 2015 and 2016, respectively. Open circles represent quail nests in 2015, and closed

circles are 2016 nests. X-values represent thermal averages 2 hours prior to the off-bout for A, C, and E. Whereas x-values for B, D, and F represent standard deviation (thermal variation) two hours prior to the off-bout. A) As mean temperature in the 2 hours preceding each off-bout increased, Northern Bobwhite (green) and Scaled Quail (blue) off-bout duration increased. Nest sites in 2015 were cooler on average than 2016 (2015 = 21.5 C, 2016 = 31.2 C). B) As standard deviation of temperature increased, individual off-bout duration decreased. C) Both species delayed taking off-bouts until later in the morning as mean temperature two hours preceding the off-bout increased, and D) a similar relationship exists with standard deviation of temperature. E) Afternoon off-bout start time began earlier as average temperature 2 hours prior to the off-bout increased while F) start time was delayed as thermal variation increased. All points are predicted model values.

Low-Resolution Thermal Data – Total Daily Off-Bout

As described by model Low Duration, per unit increase of 24hr standard deviation of temperature, total daily off-bouts lengthened by 11.9 ± 3.7 minutes ($\beta = 11.9 \pm 3.7$, $t = 3.2$, $p = 0.001$; Figure 2A). Alternatively, per unit increase of morning standard deviation of temperature, total daily off-bout decreased by 4.2 ± 2.3 minutes, though the association is only moderate ($\beta = -4.2 \pm 2.3$, $t = -1.8$, $p = 0.07$; Figure 2B). Scaled Quail spent less total time off the nest daily (156 ± 74 minutes) than Northern Bobwhite (197.2 ± 81 minutes; $\beta = 71 \pm 34$, $t = 2.1$, $p = 0.03$). Scaled Quail had significantly shorter off-bouts than Northern Bobwhite in more variable environments ($\beta = -9.9 \pm 3.8$, $t = -2.5$, $p = 0.01$; Supplementary Figure 1C). There were no other significant effects.

Low-Resolution Thermal Data – Start Time

As described by model Low AM Start Time, per unit increase of previous day standard deviation, off-bout start time in the morning began 15 ± 3 minutes earlier ($\beta = -0.15 \pm 0.03$, $t = -4.4$, $p < 0.001$; Figure 2C).

As described by model Low PM Start Time, as afternoon average temperature increased, afternoon off-bouts started 7 ± 2 minutes later ($\beta = 0.07 \pm 0.02$, $t = 4.1$, $p < 0.001$; Figure 2D).

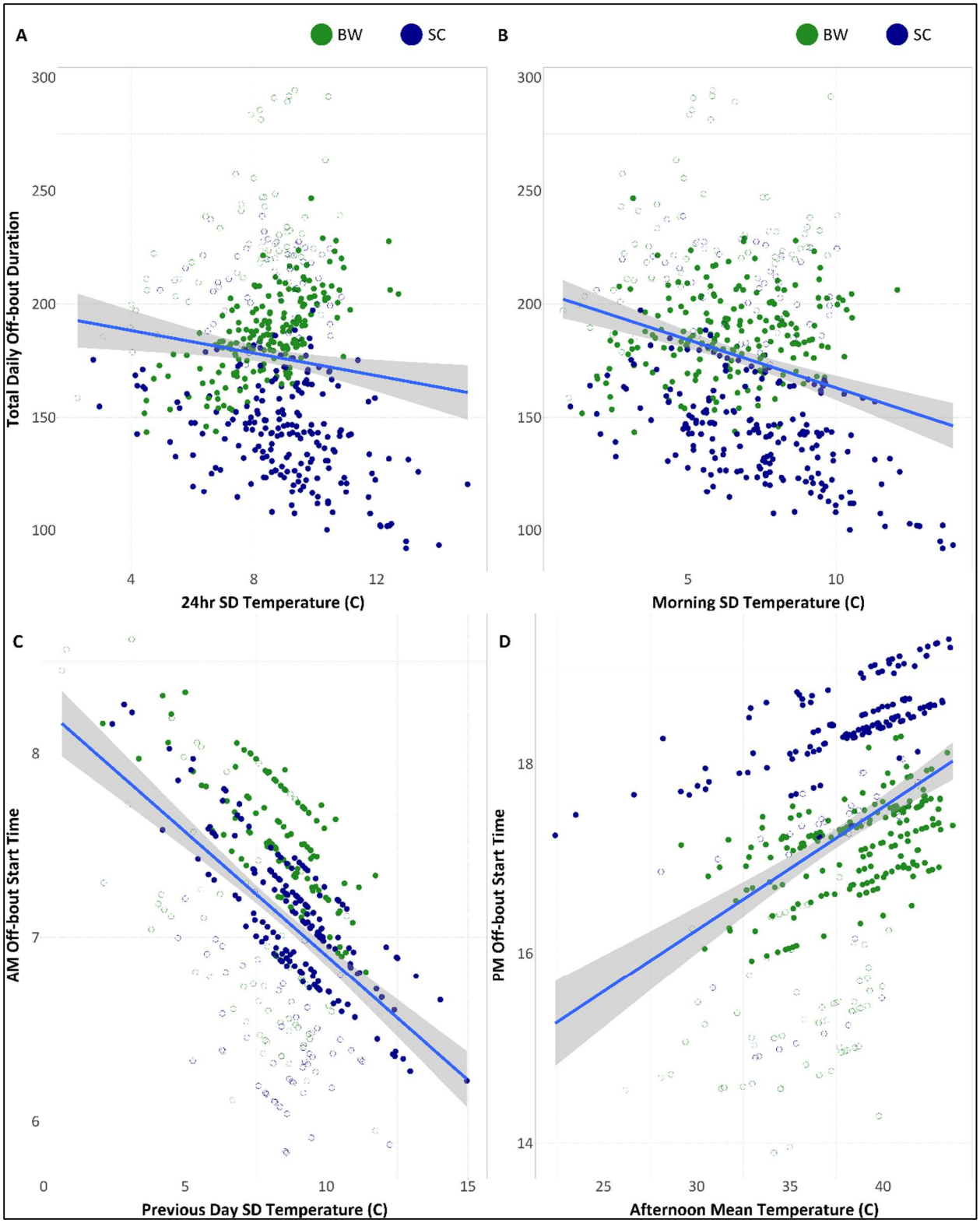

Figure 2. Partial residual plots showing the relationships between the thermal environment averaged over defined deterministic timeframes and off-bout duration (A, B), morning off-bout start time (C), and afternoon start time (D). A) X-values represent the standard deviation of

temperature over a 24 hour period. As thermal variation increased, both species reduced their total daily off-bout duration. B) X-values represent the standard deviation of temperature over the morning (sunrise-noon). As thermal variation in the morning increased, both species reduced their total daily off-bout. C) X-values represent the standard deviation of temperature of the previous day. Morning off-bouts began earlier as the standard deviation of the temperature of the previous day increased. D) X-values represent the average afternoon temperature. As afternoons became warmer on average, both species delayed their off-bouts until later in the evening. All points are predicted model values.

Discussion

We investigated the relationship between thermal means, thermal variability, and incubation behaviors across multiple timescales in Scaled Quail and Northern Bobwhite. We provide evidence that both species are modifying behavior to avoid even short periods of higher thermal variability, a novel finding among studies of avian parental behavior. Further relationships between thermal endpoints (mean vs. variation) and behavior differed depending on the resolution of the data. These results provide evidence that thermal-behavioral relationships depend on the scale at which endpoints are measured, and scale is important to consider when contextualizing behavioral outcomes.

Short-term increases to the mean and variation of temperature delay the beginning of the morning off-bout by ~9 and ~37 minutes, respectively (Figure 1C, D). However, when we examine similar responses on a low-resolution timescale, thermal variation of the previous day advanced the start of morning off-bout by 15 minutes (Figure 2C). On the surface, this seems like the opposite of what was observed on the high-resolution scale, but the interpretation of these relationships requires contextualization beyond direct comparison, as the high-resolution measurements examine the relationship between the rate of environmental thermal change and a direct measurement of decision-making (i.e., individual timing of off-bouts). However, the low-resolution result examines the relationship between single measurement predictors averaged over time and their impacts on an averaged response, providing context for periods in the day that may be influential to general trends in behavior, but these measurements say little about moment-to-moment decision-making. Similarly, while afternoon average temperatures pushed each species to delay the start of an off-bout by 7 minutes (Figure 2D), the opposite was observed on the high-resolution scale (off-bouts began 21 minutes earlier, Figure 1E). These seemingly alternating relationships provide more evidence that sole characteristic predictors require careful contextualization. The low-resolution predictors (model name – Low Duration, 0.02 AIC_C w_i) may be significant, but the model weights suggest that the high-resolution predictors make for a better predictive model (Table 1), likely due to the loss of resolution that comes with averaging behavioral data.

Northern Bobwhite and Scaled Quail increased the duration of their individual off-bouts in response to the immediate thermal environment at a rate of 4.4 minutes/mean degree increase (Figure 1A) and decreased off-bouts in more variable environments at a rate of 4.2 minutes/unit increase of variation (Figure 1B). Both species are more comfortable leaving eggs in warm, stable conditions which are less likely to expose eggs to temperatures outside of critical ranges.

Yet, when we examined these relationships at a lower resolution, total daily off-bout was not influenced by average temperatures, only thermal variation (with significantly reduced model weights – Table 1; Figure 2A, B). These findings further suggest that the timescales we use to measure thermal change and behavioral modification alter how we view the plasticity of organismal behavior to the thermal environment. Multiple studies have shown that the relationship between temperature and the average lengths of off-bouts predicts avian reproductive success (48–51). Approaches considering averaged conditions can contextualize general trends in behavior (52,53), but as we show above, only examining behavior in this way risks missing the relationship between the rate of thermal change and organismal behavior. Our findings are supported by studies of other species nesting in hot conditions. Least Terns (*Sternula antillarum*; 52,53) and Piping Plovers (*Charadrius melodus*; 53) exhibit some thermoregulatory behaviors but only within only certain breadths of experienced temperature. Using low-resolution thermal data alone to predict behavior would limit our understanding of these responses, as the breadth of behavior may be washed out in a sole-characteristic thermal predictor (56).

Here, both species expressed similar trends in their behavioral modifications but differed in individual off-bout duration and environmental temperature of their nests (Supplemental Figure 1). Scaled Quail spent significantly less time off the nest on average (110 minutes) than Northern Bobwhite (140 minutes). The interactive effects of each model may be influenced by natural history differences of the two species (57,58). The typical breeding habitat of Northern Bobwhite is temperate, consisting of habitat exposed to a wide range of temperatures, but extreme temperatures rarely reach those experienced by Scaled Quail across their range (57). Scaled Quail are a grassland desert-dwelling species, adapted to the extreme highs and lows present in the Western Oklahoma field site (58), reflected in superior thermal buffering observed in nestbuilding compared to Northern Bobwhite (30). Behavioral adaptation to thermal extremes can be limited by range-specific adaptations (59). Range edges are dynamic, and while high turnover species adapt quickly to shifts in the environment on the edge of their range (60), Northern Bobwhite have a limited ability to adapt to novel climates due to high temporal investment in offspring, long generation time, and slow physical development (57). It should be noted that direct comparisons between each species based on results found here need to be made with caution, as thermal and behavioral measurements across each species' range would be required to make species level comparisons in behavioral plasticity.

Behavioral plasticity during breeding generally benefits both the parent and dependent offspring by keeping the thermal environment stable over time (61–63), but shifts in behavior alone cannot completely negate the impacts of poor or unexpected environmental conditions (64), as self-maintenance may take precedence over offspring care (35). Our results indicate that the rate of environmental temperature change can have a direct influence on parental behavior. We also demonstrate that thermal variability can be lost in averages, as evidenced by the lack of a significant relationship in daily off-bout duration and temperature (Figure 2A) but a significant relationship between acute thermal environment and off-bout duration (Figure 1A). Therefore, averaged conditions may provide inaccurate assessments of organismal vulnerability to thermal

change if characterized incorrectly (8,65). Models with averaged, lone sole-characteristic predictors should not be avoided but contextualized as we do here (56).

Acknowledgements

We would like to thank Rachel Carroll, Craig Davis, and Sam Fuhlendorf for permission to use their thermal data from Scaled and Northern Bobwhite Quail nests. Thanks to Wayne Hawkins for assistance with NestIQ.

Funding

This work was supported by the Oklahoma Department of Wildlife Conservation through funding administered through the Oklahoma Cooperative Fish and Wildlife Research Unit (grant #F11AF00069), the Oklahoma Agricultural Experiment Station at Oklahoma State University, and the Bollenbach and Groendyke Endowments.

Ethics

Animal welfare approval was obtained from IACUC at Oklahoma State University.

Data, Code, and Materials

All supporting data and annotated R scripts are available in a Data Dryad repository.

Competing Interests

We declare we have no competing interests.

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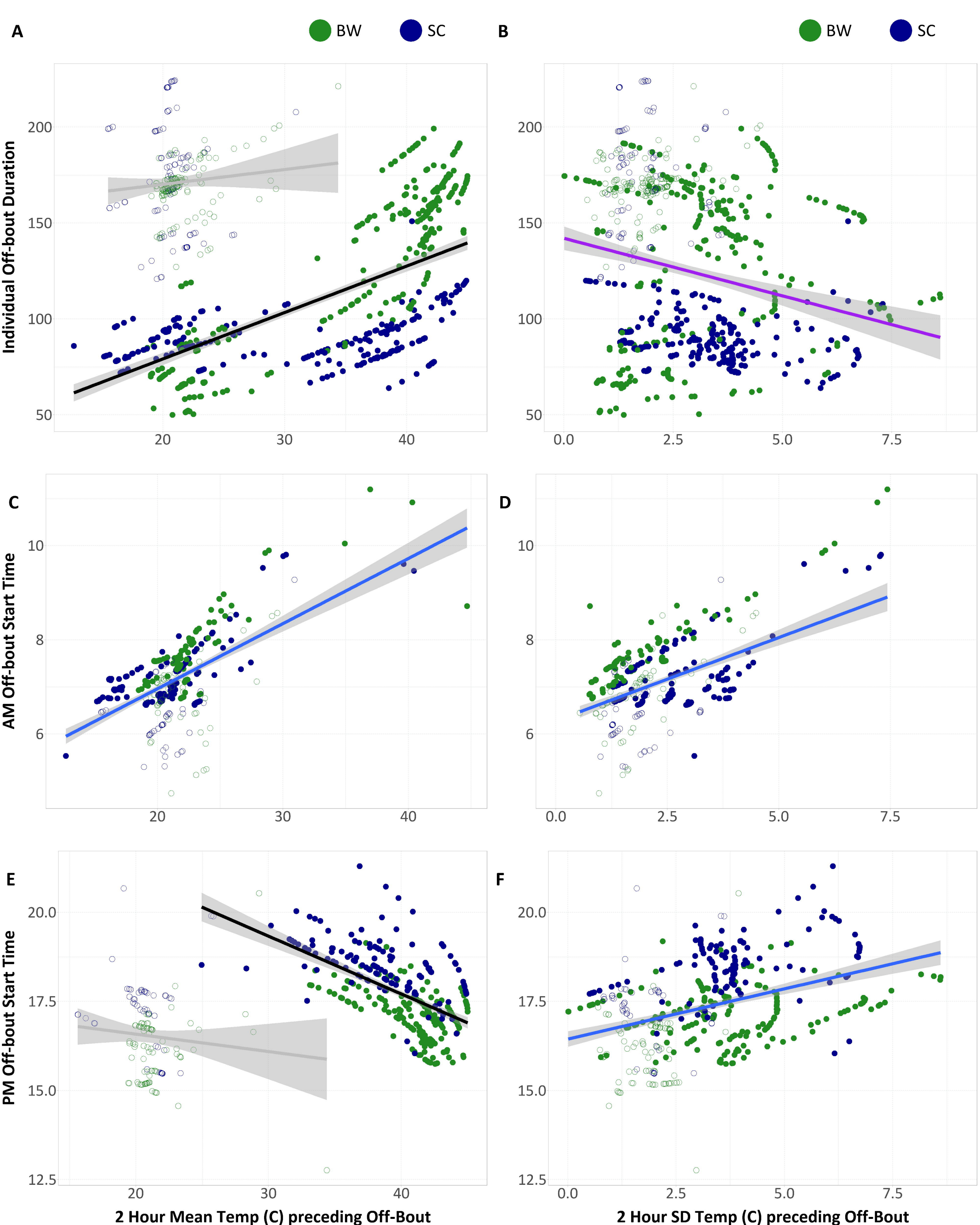
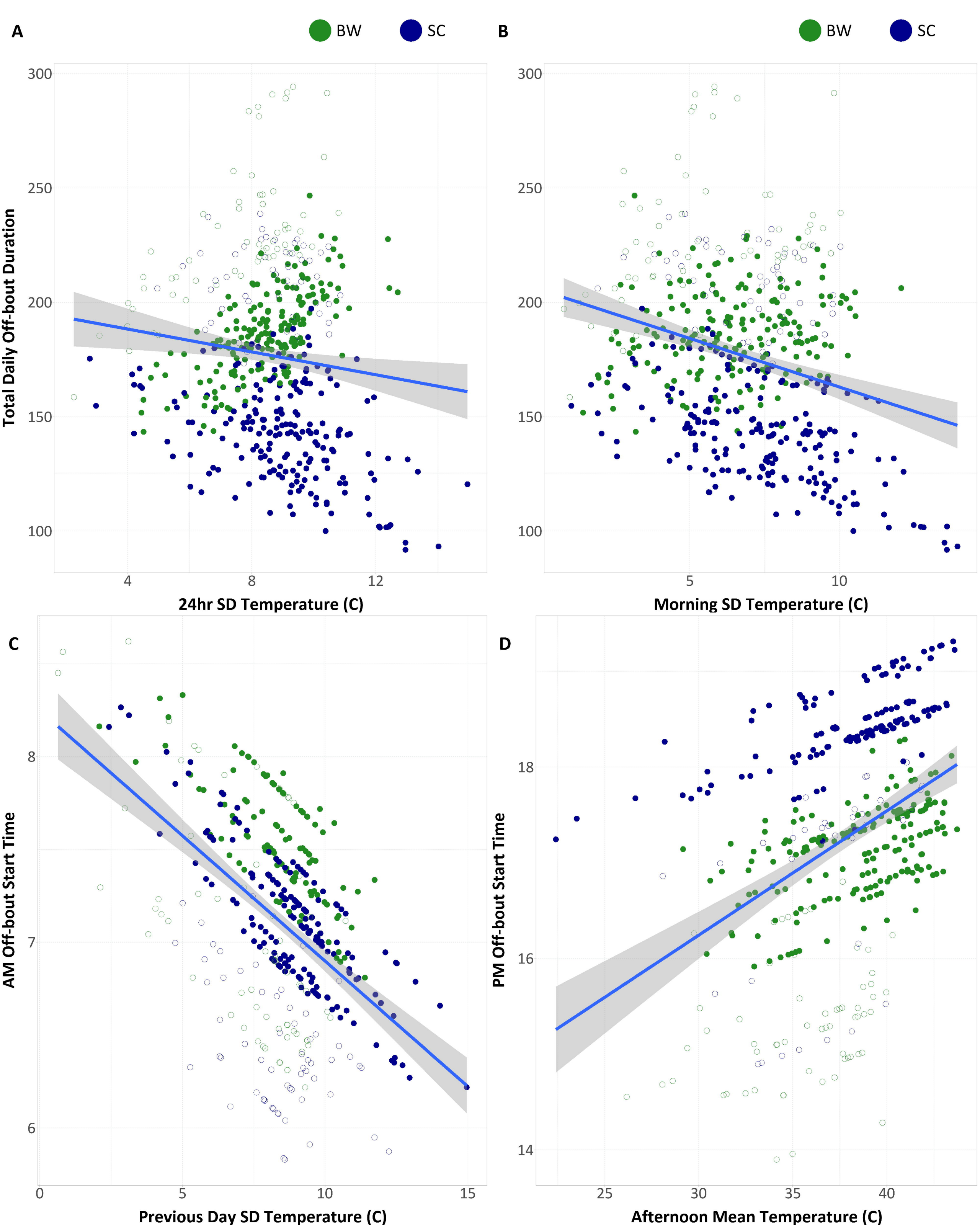

A
BW
SC
B
BW
SC
Individual Off-bout Duration
200
150
100
50
20
30
40
0.0
2.5
5.0
7.5
C
D
AM Off-bout Start Time
10
8
6
E
F
PM Off-bout Start Time
20.0
17.5
15.0
12.5
2 Hour Mean Temp (C) preceding Off-Bout
2 Hour SD Temp (C) preceding Off-Bout


A
BW
SC
Total Daily Off-bout Duration
300
250
200
150
100
4
8
12
24hr SD Temperature (C)
B
BW
SC
300
250
200
150
100
5
10
Morning SD Temperature (C)
C
AM Off-bout Start Time
8
7
6
0
5
10
15
Previous Day SD Temperature (C)
D
PM Off-bout Start Time
18
16
14
25
30
35
40
Afternoon Mean Temperature (C)

High-Resolution Best Fit Models						
Model Name	**Response Variable**	**Main Effect(s)**	**Interactive Effects**	**AIC_c**	**df**	**AIC_c w_i**
High Duration	Off-bout Duration	2hr Mean, 2 hr SD, AMPM, Species	2hr Mean:Species, 2hr SD:Species, AMPM:Species	8952.7	11	0.742
Null	Off-bout Duration	~	~	9154.8	4	< 0.0001
High AM Start Time	Off-bout Timing - AM	2hr Mean, 2hr SD, Species	~	1375.2	7	0.429
Null	Off-bout Timing - AM	~	~	1417.8	4	< 0.001
High PM Start Time	Off-bout Timing - PM	2hr Mean, 2hr SD	~	1580.9	6	0.425
Null	Off-bout Timing - PM	~	~	1654.8	4	< 0.001

Low-Resolution Best Fit Models						
Model Name	**Response Variable**	**Main Effect(s)**	**Interactive Effects**	**AIC_c**	**df**	**AIC_c w_i**
Low Duration	Daily Off-bout Duration	24hr SD, Morning SD, Previous Night SD, Species	24hr SD:Species, Previous Night SD:Species	5666.7	10	0.02
Null	Daily Off-bout Duration	~	~	5706	4	< 0.001
Low AM Start Time	Off-bout Timing - AM	Previous Day SD, Species	~	1378.9	6	0.075
Null	Off-bout Timing - AM	~	~	1395.6	4	< 0.0001
Low PM Start Time	Off-bout Timing - PM	Afternoon Mean, Species	~	1349.7	6	0.22
Null	Off-bout Timing - PM	~	~	1374.4	4	< 0.0001