Analysis of distruptive winds to overwintering monarch butterflies

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Table of contents

Introduction	2
Setup	2
Exploratory Data Analysis	3
Modeling Strategy	8
Model Building and Selection	9
Model Fitting	11
Model Comparison	11
Best Model Analysis	14
Effect Plots	15
Effect of Previous Butterfly Count	15
Effect of Temperature	16
Diurnal Pattern	17
Effect of Sun Exposure (Smooth)	17
Smooth Effects (ggplot2 style)	18
Model Diagnostics	21
Residuals vs Fitted Values	21
Q-Q Plot of Residuals	21
Distribution of Residuals	22
Second Best Model Analysis (Wind)	23
Effect Plots - Second Best Model	24
Model Diagnostics - Second Best Model	26

Threshold-Based Wind Models	28
Threshold Model Specifications	28
Threshold Model Fitting	30
Threshold Model Comparison	30
Best Threshold Model Analysis	33
Threshold Model Effect Plots	34
Effect of Previous Butterfly Count	34
Effect of Minutes Above Threshold	35
Comparison: Max Gust vs Minutes Above Threshold	35
Model Comparison: Gust vs Threshold Approaches	37
Results Summary	38

Introduction

This analysis investigates the first hypothesis of my master's thesis: that wind acts as a disruptive force to overwintering monarch butterflies. If true, we predict that monarch abundance at roosts will decrease when exposed to disruptive winds. I use labeled photos from my 2023-2024 dataset to test this hypothesis. I employed GAM (Generalized Additive Models) because they allow for non-linear relationships in fixed effects while maintaining the necessary random effect structure to account for temporal autocorrelation and nested sampling design.

Setup

Load libraries and data:

```
library(tidyverse)
library(mgcv)
library(lubridate)
library(plotly)
library(knitr)
library(DT)
library(here)
# Load the monarch analysis data
monarch_data <- read_csv(here("data", "monarch_analysis_lag30min.csv"))</pre>
```

Exploratory Data Analysis

The response variable is the difference in monarch counts between time t and t-1 at 30-minute intervals. I applied a cube root transformation to achieve a more normal distribution. Because the lagged comparisons create overlapping pairs of observations, I include an AR1 autocorrelation structure to account for temporal dependence.

knitr::include_graphics("images/clipboard-1435734413.png")

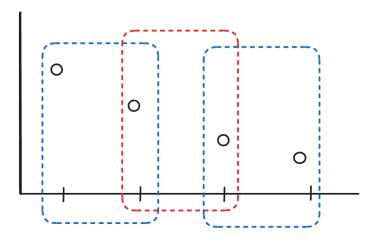


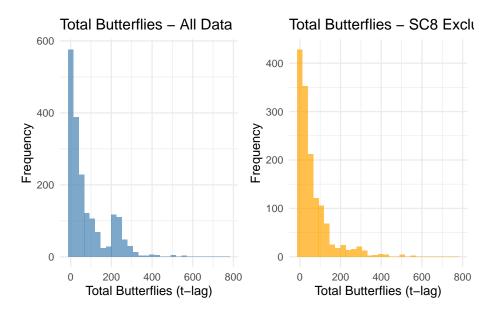
Figure 1: Illustration of temporal dependency in observation pairs. Points represent photos with labeled count data at 30-minute intervals. Blue boxes show non-overlapping pairs of observations. The red box shows an overlapping comparison where one observation is shared between adjacent pairs, creating temporal autocorrelation that is controlled by the AR1 structure.

```
library(gridExtra)

# Compare total butterfly counts with and without SC8
p_all <- ggplot(monarch_data, aes(x = total_butterflies_t_lag)) +
    geom_histogram(bins = 30, fill = "steelblue", alpha = 0.7) +
    labs(
        title = "Total Butterflies - All Data",
        x = "Total Butterflies (t-lag)", y = "Frequency"
    ) +
    theme_minimal()

p_no_sc8 <- ggplot(monarch_data %>% filter(deployment_id != "SC8"), aes(x = total_butterflies)
```

```
geom_histogram(bins = 30, fill = "orange", alpha = 0.7) +
labs(
    title = "Total Butterflies - SC8 Excluded",
    x = "Total Butterflies (t-lag)", y = "Frequency"
) +
    theme_minimal()
grid.arrange(p_all, p_no_sc8, ncol = 2)
```

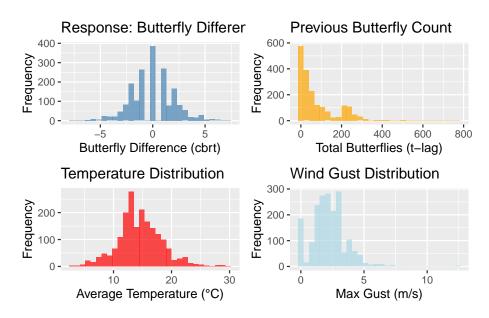


```
library(corrplot)
library(gridExtra)

# Select variables used in the models
model_vars <- monarch_data %>%
    select(
        butterfly_difference_cbrt, total_butterflies_t_lag, max_gust,
        temperature_avg, butterflies_direct_sun_t_lag, time_within_day_t
    )

# Histograms of key variables
p1 <- ggplot(monarch_data, aes(x = butterfly_difference_cbrt)) +
    geom_histogram(bins = 30, fill = "steelblue", alpha = 0.7) +
    labs(
        title = "Response: Butterfly Difference (Cube Root)",
        x = "Butterfly Difference (cbrt)", y = "Frequency"</pre>
```

```
)
p2 <- ggplot(monarch_data, aes(x = total_butterflies_t_lag)) +</pre>
    geom_histogram(bins = 30, fill = "orange", alpha = 0.7) +
    labs(
        title = "Previous Butterfly Count",
        x = "Total Butterflies (t-lag)", y = "Frequency"
    )
p3 <- ggplot(monarch_data, aes(x = temperature_avg)) +
    geom_histogram(bins = 30, fill = "red", alpha = 0.7) +
    labs(
        title = "Temperature Distribution",
        x = "Average Temperature (°C)", y = "Frequency"
    )
p4 <- ggplot(monarch_data, aes(x = max_gust)) +
    geom_histogram(bins = 30, fill = "lightblue", alpha = 0.7) +
    labs(
        title = "Wind Gust Distribution",
        x = \text{"Max Gust (m/s)", } y = \text{"Frequency"}
    )
grid.arrange(p1, p2, p3, p4, ncol = 2)
```



```
# Correlation matrix for model variables
cor_matrix <- cor(model_vars, use = "complete.obs")

# Create correlation plot
corrplot(cor_matrix,
    method = "color",
    type = "upper",
    order = "hclust",
    tl.cex = 0.8,
    tl.col = "black",
    tl.srt = 45,
    addCoef.col = "black",
    number.cex = 0.7,
    title = "Correlation Matrix: Model Variables"
)</pre>
```

Correlation Watrix. Wiouelovariables

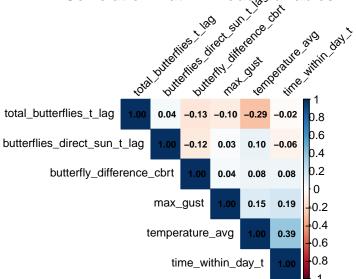
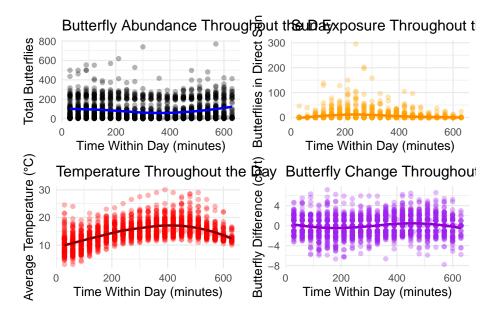


Table 1: Correlation Matrix for Model Variables

butterfly_differ	teanl <u>ceb</u> ucton	etrflies <u>x</u>	t grekstg perat	bbretterfeies_di	r ein tn <u>esu</u> wwi <u>t</u> la	inla g lay_
butterfly_difference 1.000	-0.131	0.040	0.079	-0.116	0.077	
total_butterflies_t_0alg31	1.000	-	-0.291	0.041	-0.023	
		0.105				
max_gust 0.040	-0.105	1.000	0.145	0.027	0.185	
temperature_avg 0.079	-0.291	0.145	1.000	0.099	0.386	
butterflies_direct_s0nl16_lag	0.041	0.027	0.099	1.000	-0.064	
time within day t0.077	-0.023	0.185	0.386	-0.064	1.000	

```
# Butterfly activity by time of day
p1 <- ggplot(monarch_data, aes(x = time_within_day_t, y = total_butterflies_t_lag)) +
   geom_point(alpha = 0.3) +
   geom_smooth(method = "loess", se = TRUE, color = "blue") +
   labs(
       title = "Butterfly Abundance Throughout the Day",
       x = "Time Within Day (minutes)", y = "Total Butterflies"
    ) +
    theme_minimal()
# Sun exposure patterns by time
p2 <- ggplot(monarch_data, aes(x = time_within_day_t, y = butterflies_direct_sun_t_lag)) +
    geom_point(alpha = 0.3, color = "orange") +
    geom_smooth(method = "loess", se = TRUE, color = "darkorange") +
   labs(
       title = "Sun Exposure Throughout the Day",
       x = "Time Within Day (minutes)", y = "Butterflies in Direct Sun"
    theme_minimal()
# Temperature patterns by time
p3 <- ggplot(monarch_data, aes(x = time_within_day_t, y = temperature_avg)) +
   geom_point(alpha = 0.3, color = "red") +
   geom_smooth(method = "loess", se = TRUE, color = "darkred") +
    labs(
       title = "Temperature Throughout the Day",
       x = "Time Within Day (minutes)", y = "Average Temperature (°C)"
    ) +
    theme_minimal()
# Response variable by time
p4 <- ggplot(monarch_data, aes(x = time_within_day_t, y = butterfly_difference_cbrt)) +
    geom_point(alpha = 0.3, color = "purple") +
```

```
geom_smooth(method = "loess", se = TRUE, color = "darkviolet") +
labs(
    title = "Butterfly Change Throughout the Day",
    x = "Time Within Day (minutes)", y = "Butterfly Difference (cbrt)"
) +
    theme_minimal()
grid.arrange(p1, p2, p3, p4, ncol = 2)
```



Modeling Strategy

Our modeling approach used a comprehensive AIC-based comparison to evaluate all possible combinations of three key environmental predictors: wind speed (max_gust), temperature (temperature_avg), and solar exposure (butterflies_direct_sun_t_lag). We tested two fundamental modeling frameworks: models that include total_butterflies_t_lag as a control variable (testing effects on relative/proportional change) and models that exclude it (testing effects on absolute change). Within each framework, we systematically evaluated linear main effects, two-way and three-way interactions, and non-linear relationships using smooth terms. We also incorporated time-of-day effects to capture diurnal patterns. This resulted in 47 candidate models that comprehensively explore the parameter space while maintaining proper mixed-effects structure with random effects for deployment, observer, and day, plus AR1 correlation for within-day autocorrelation.

Model Building and Selection

Please expand the code block to see the full list of models tested.

```
library(nlme)
# Define the random effects structure and correlation
random_structure <- list(deployment_id = ~1, Observer = ~1, deployment_day = ~1)</pre>
correlation_structure <- corAR1(form = ~ observation_order_within_day_t | deployment_day)</pre>
 # Model specifications for AIC comparison
model_specs <- list(</pre>
               # Null model
                "MO_null" = "butterfly_difference_cbrt ~ total_butterflies_t_lag",
                # Single variable models
               "M1_gust" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + max_gust",
                "M2_temp" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + temperature_avg",
                "M3_sun" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + butterflies_direct_su
                # Two-variable combinations
                "M4_gust_temp" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + max_gust + temperature total_butterflies_t_lag + temperatur
                "M5_gust_sun" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + max_gust + butter
                "M6_temp_sun" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + temperature_avg ·
                # Three-variable model (main effects only)
                "M7_all_main" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + max_gust + temper
                # Two-way interactions
                "M8_gust_temp_int" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + max_gust * 1
                "M9_gust_sun_int" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + max_gust * butterfly_difference_cbrt ~ total_butterflies_t_lag + max_gust * butterflies_t_lag + max_gu
                "M10_temp_sun_int" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + temperature
                # Two-way interactions with third variable as main effect
                "M12_gust_sun_int_plus_temp" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + magnetic temp" = "butterflies_t_lag + magn
                "M13_temp_sun_int_plus_gust" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + to
                # All two-way interactions
                "M14_all_two_way" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + max_gust * to
                # Three-way interaction
                "M15_three_way" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + max_gust * temp
                # Smooth terms models (with lag term)
                "M16_smooth_temp" = "butterfly_difference_cbrt ~ s(total_butterflies_t_lag) + s(temperate
```

```
"M17_smooth_sun" = "butterfly_difference_cbrt ~ s(total_butterflies_t_lag) + temperature
          "M18_smooth_gust" = "butterfly_difference_cbrt ~ s(total_butterflies_t_lag) + s(max_gust
         "M19_smooth_temp_sun" = "butterfly_difference_cbrt ~ s(total_butterflies_t_lag) + s(temp_sun" = "butterflies_t_lag) + s(temp_sun" = "butte
         "M20_smooth_all_main" = "butterfly_difference_cbrt ~ s(total_butterflies_t_lag) + s(max
          "M21_time_of_day" = "butterfly_difference_cbrt ~ s(total_butterflies_t_lag) + temperatus
          "M22_temp_time" = "butterfly_difference_cbrt ~ s(total_butterflies_t_lag) + s(temperatus
          "M23_all_smooth_time" = "butterfly_difference_cbrt ~ s(total_butterflies_t_lag) + s(max_
         # Models WITHOUT lag term - testing environmental effects on absolute change
         "M24_no_lag_null" = "butterfly_difference_cbrt ~ 1",
         "M25_no_lag_gust" = "butterfly_difference_cbrt ~ max_gust",
          "M26_no_lag_temp" = "butterfly_difference_cbrt ~ temperature_avg",
          "M27_no_lag_sun" = "butterfly_difference_cbrt ~ butterflies_direct_sun_t_lag",
          "M28_no_lag_gust_temp" = "butterfly_difference_cbrt ~ max_gust + temperature_avg",
          "M29_no_lag_gust_sun" = "butterfly_difference_cbrt ~ max_gust + butterflies_direct_sun_i
          "M30_no_lag_temp_sun" = "butterfly_difference_cbrt ~ temperature_avg + butterflies_direction."
          "M31_no_lag_all_main" = "butterfly_difference_cbrt ~ max_gust + temperature_avg + butter
          "M32_no_lag_gust_temp_int" = "butterfly_difference_cbrt ~ max_gust * temperature_avg",
         "M33_no_lag_gust_sun_int" = "butterfly_difference_cbrt ~ max_gust * butterflies_direct_:
          "M34_no_lag_temp_sun_int" = "butterfly_difference_cbrt ~ temperature_avg * butterflies_
          "M35_no_lag_gust_temp_int_plus_sun" = "butterfly_difference_cbrt ~ max_gust * temperatus
          "M36_no_lag_gust_sun_int_plus_temp" = "butterfly_difference_cbrt ~ max_gust * butterflic
          "M37_no_lag_temp_sun_int_plus_gust" = "butterfly_difference_cbrt ~ temperature_avg * but
          "M38_no_lag_all_two_way" = "butterfly_difference_cbrt ~ max_gust * temperature_avg + max
          "M39_no_lag_three_way" = "butterfly_difference_cbrt ~ max_gust * temperature_avg * butter
         # Smooth terms models WITHOUT lag term
         "M40_no_lag_smooth_temp" = "butterfly_difference_cbrt ~ s(temperature_avg) + s(butterfl:
          "M41_no_lag_smooth_sun" = "butterfly_difference_cbrt ~ temperature_avg + s(butterflies_c
         "M42_no_lag_smooth_gust" = "butterfly_difference_cbrt ~ s(max_gust) + temperature_avg +
          "M43_no_lag_smooth_temp_sun" = "butterfly_difference_cbrt ~ s(temperature_avg) + s(butterfly_difference_cbrt ~ s(temperature_avg)) + s(bu
          "M44_no_lag_smooth_all_main" = "butterfly_difference_cbrt ~ s(max_gust) + s(temperature_
          "M45_no_lag_time_of_day" = "butterfly_difference_cbrt ~ temperature_avg + s(butterflies
          "M46 no lag temp time" = "butterfly difference cbrt ~ s(temperature avg) + s(butterflies
          "M47_no_lag_all_smooth_time" = "butterfly_difference_cbrt ~ s(max_gust) + s(temperature
cat("Total models to fit:", length(model_specs), "\n")
```

Total models to fit: 48

Model Fitting

```
# Function to safely fit models
fit_model_safely <- function(formula_str, data) {</pre>
    tryCatch(
        {
            formula_obj <- as.formula(formula_str)</pre>
            gamm(formula_obj,
                data = data,
                random = random_structure,
                 correlation = correlation_structure,
                method = "REML"
            )
        },
        error = function(e) {
            message("Failed to fit model: ", formula_str)
            message("Error: ", e$message)
            return(NULL)
        }
    )
}
# Fit all models
cat("Fitting models...\n")
Fitting models...
```

```
fitted_models <- map(model_specs, ~ fit_model_safely(.x, model_data))</pre>
# Remove failed models
successful_models <- fitted_models[!map_lgl(fitted_models, is.null)]</pre>
cat("Successfully fitted", length(successful_models), "out of", length(model_specs), "models
```

Successfully fitted 48 out of 48 models

Model Comparison

```
# Extract AIC values
aic_results <- map_dfr(names(successful_models), function(model_name) {</pre>
    model <- successful_models[[model_name]]</pre>
    data.frame(
```

```
Model = model_name,
        Formula = model_specs[[model_name]],
        AIC = AIC(model$lme),
       LogLik = logLik(model$lme)[1],
        df = attr(logLik(model$lme), "df")
    )
}) %>%
   arrange(AIC) %>%
   mutate(
        Delta_AIC = AIC - min(AIC),
        AIC_weight = \exp(-0.5 * Delta_AIC) / \sup(\exp(-0.5 * Delta_AIC))
    )
# Display results
aic_results %>%
    select(Model, AIC, Delta_AIC, AIC_weight, df) %>%
   kable(digits = 3, caption = "Model comparison by AIC")
```

Table 2: Model comparison by AIC

Model	AIC	Delta_AIC AI	C_weight	df
M22_temp_time	8081.848	0.000	0.88	14
$M21_time_of_day$	8086.644	4.796	0.08	13
M23_all_smooth_time	8088.049	6.200	0.04	16
$M46_no_lag_temp_time$	8101.296	19.448	0.00	12
$M16_smooth_temp$	8105.876	24.028	0.00	12
M19_smooth_temp_sun	8105.876	24.028	0.00	12
M47_no_lag_all_smooth_time	8107.724	25.876	0.00	14
M45_no_lag_time_of_day	8108.295	26.447	0.00	11
$M20_smooth_all_main$	8109.249	27.401	0.00	14
$M17_smooth_sun$	8114.431	32.583	0.00	11
$M18_smooth_gust$	8119.075	37.227	0.00	13
$M40_no_lag_smooth_temp$	8126.061	44.212	0.00	10
$M43_no_lag_smooth_temp_sun$	8126.061	44.212	0.00	10
$M44_no_lag_smooth_all_main$	8127.871	46.023	0.00	12
$M6_temp_sun$	8130.775	48.927	0.00	9
M3_sun	8131.696	49.848	0.00	8
M15_three_way	8132.647	50.799	0.00	14
M5_gust_sun	8134.945	53.097	0.00	9
M11_gust_temp_int_plus_sun	8135.392	53.544	0.00	11
M7_all_main	8136.217	54.369	0.00	10
M39_no_lag_three_way	8137.407	55.559	0.00	13
M41_no_lag_smooth_sun	8139.237	57.389	0.00	9
M9_gust_sun_int	8139.410	57.562	0.00	10

Model	AIC	Delta_AIC	AIC_weight	df
M12_gust_sun_int_plus_temp	8140.795	58.946	0.00	11
M35_no_lag_gust_temp_int_plus	8 1141.931	60.082	0.00	10
M42_no_lag_smooth_gust	8142.038	60.190	0.00	11
M30_no_lag_temp_sun	8142.927	61.079	0.00	8
M10_temp_sun_int	8144.554	62.705	0.00	10
M31_no_lag_all_main	8146.374	64.526	0.00	9
M36_no_lag_gust_sun_int_plus_	te\$n1∎48.813	66.964	0.00	10
M13_temp_sun_int_plus_gust	8150.004	68.156	0.00	11
M0_null	8153.582	71.734	0.00	7
M29_no_lag_gust_sun	8154.129	72.281	0.00	8
M27_no_lag_sun	8155.073	73.225	0.00	7
M14_all_two_way	8155.075	73.227	0.00	13
M34_no_lag_temp_sun_int	8156.678	74.830	0.00	9
M33_no_lag_gust_sun_int	8156.943	75.095	0.00	9
$M2_temp$	8157.623	75.775	0.00	8
M1_gust	8157.885	76.037	0.00	8
M38_no_lag_all_two_way	8160.095	78.247	0.00	12
M37_no_lag_temp_sun_int_plus_	_g8ils60.174	78.326	0.00	10
$M8_gust_temp_int$	8162.939	81.091	0.00	10
$M4_gust_temp$	8163.059	81.210	0.00	9
M26_no_lag_temp	8170.575	88.727	0.00	7
M32_no_lag_gust_temp_int	8171.945	90.096	0.00	9
M28_no_lag_gust_temp	8175.113	93.264	0.00	8
M24_no_lag_null	8177.191	95.342	0.00	6
$M25_no_lag_gust$	8178.495	96.647	0.00	7

```
# Show top 5 models
cat("\nTop 5 models by AIC:\n")
```

Top 5 models by AIC:

```
head(aic_results, 5) %>%
  select(Model, Formula, AIC, Delta_AIC) %>%
  kable(digits = 3)
```

```
Model
                                                                      AIC Delta AIC
          Formula
M22 temp<u>buttitenelly</u> difference cbrt \sim s(total\_butterflies\_t\_lag)
                                                                      8081.848000
          + s(temperature\_avg) +
          s(butterflies\_direct\_sun\_t\_lag) +
          s(time_within_day_t)
M21\_timeboottedtay\_difference\_cbrt \sim s(total\_butterflies\_t\_lag)
                                                                      8086.644796
          + temperature avg +
          s(butterflies\_direct\_sun\_t\_lag) +
          s(time_within_day_t)
M23_all_sbutctdflytindiefference_cbrt ~ s(total_butterflies_t_lag)
                                                                      8088.04.2200
          + s(max\_gust) + s(temperature\_avg) +
          s(butterflies_direct_sun_t_lag) +
          s(time within day t)
M46\_no\_lagtttrflyp\_difference\_cbrt \sim s(temperature\_avg) \ +
                                                                      8101.299.448
          s(butterflies_direct_sun_t_lag) +
          s(time_within_day_t)
M16\_smodth\underline{tteeflyp}\_difference\_cbrt \sim s(total\_butterflies\_t\_lag)
                                                                      8105.876.028
          + s(temperature\_avg) +
          s(butterflies direct sun t lag)
```

Best Model Analysis

```
# Get the best model
best_model_name <- aic_results$Model[1]
best_model <- successful_models[[best_model_name]]
cat("Best model:", best_model_name, "\n")

Best model: M22_temp_time
cat("Formula:", aic_results$Formula[1], "\n\n")</pre>
```

Formula: butterfly_difference_cbrt ~ s(total_butterflies_t_lag) + s(temperature_avg) + s(but

```
# Model summary
summary(best_model$gam)
```

Family: gaussian

Link function: identity

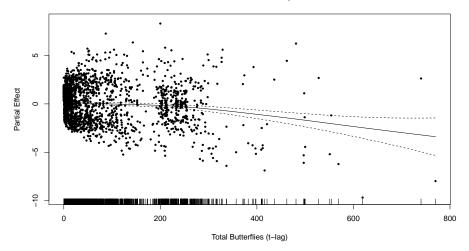
```
Formula:
butterfly_difference_cbrt ~ s(total_butterflies_t_lag) + s(temperature_avg) +
    s(butterflies_direct_sun_t_lag) + s(time_within_day_t)
Parametric coefficients:
           Estimate Std. Error t value Pr(>|t|)
(Intercept) 0.1765 0.4453 0.396
Approximate significance of smooth terms:
                                edf Ref.df
                                                F p-value
s(total_butterflies_t_lag)
                              2.621 2.621 12.020 8.26e-07 ***
                              3.930 3.930 3.230
s(temperature_avg)
                                                  0.0283 *
s(butterflies_direct_sun_t_lag) 1.534 1.534 19.356 1.22e-05 ***
                              4.898 4.898 8.901 < 2e-16 ***
s(time_within_day_t)
Signif. codes: 0 '*** 0.001 '** 0.01 '* 0.05 '.' 0.1 ' ' 1
R-sq.(adj) = 0.0568
 Scale est. = 4.0332
                       n = 1894
```

Effect Plots

Effect of Previous Butterfly Count

```
plot(best_model$gam,
    select = 1, main = "Effect of Previous Butterfly Count",
    xlab = "Total Butterflies (t-lag)", ylab = "Partial Effect",
    residuals = TRUE, pch = 19, cex = 0.5
)
```

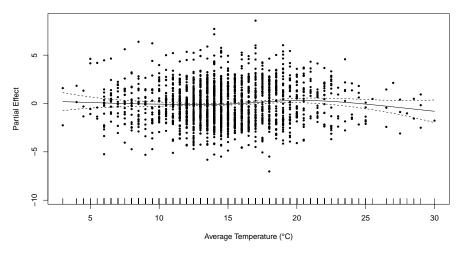
Effect of Previous Butterfly Count



Effect of Temperature

```
plot(best_model$gam,
    select = 2, main = "Effect of Temperature",
    xlab = "Average Temperature (°C)", ylab = "Partial Effect",
    residuals = TRUE, pch = 19, cex = 0.5
)
```

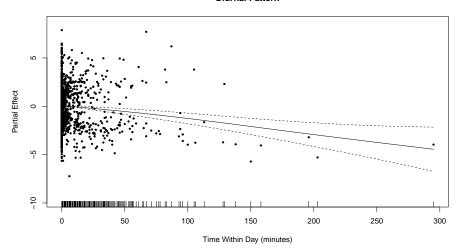
Effect of Temperature



Diurnal Pattern

```
plot(best_model$gam,
    select = 3, main = "Diurnal Pattern",
    xlab = "Time Within Day (minutes)", ylab = "Partial Effect",
    residuals = TRUE, pch = 19, cex = 0.5
)
```

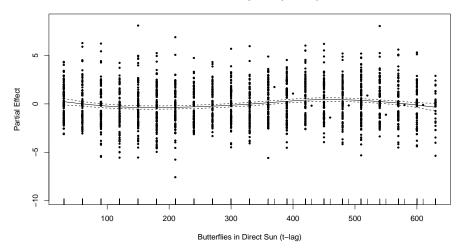
Diurnal Pattern



Effect of Sun Exposure (Smooth)

```
# Smooth effect of sun exposure
plot(best_model$gam,
    select = 4, main = "Effect of Sun Exposure (Smooth)",
    xlab = "Butterflies in Direct Sun (t-lag)", ylab = "Partial Effect",
    residuals = TRUE, pch = 19, cex = 0.5
)
```

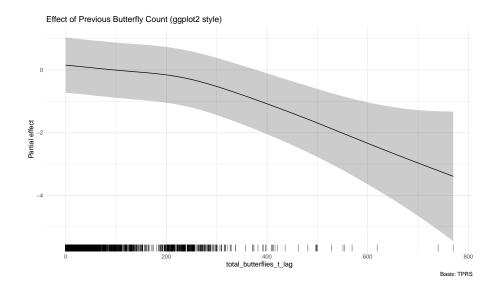
Effect of Sun Exposure (Smooth)



Smooth Effects (ggplot2 style)

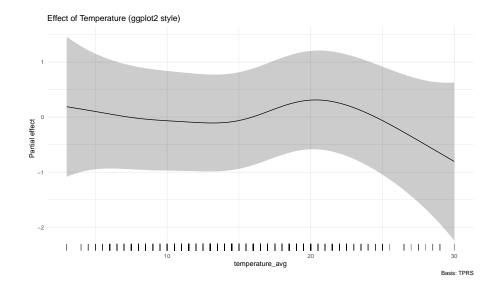
Previous Butterfly Count Effect

```
library(gratia)
draw(best_model$gam, select = "s(total_butterflies_t_lag)") +
    theme_minimal() +
    labs(title = "Effect of Previous Butterfly Count (ggplot2 style)")
```



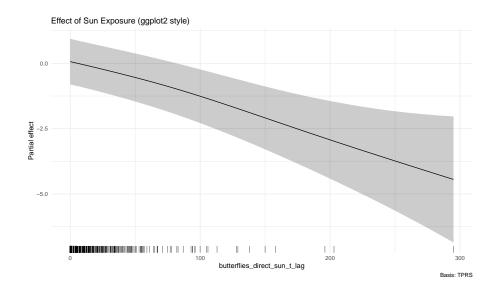
Temperature Effect

```
draw(best_model$gam, select = "s(temperature_avg)") +
    theme_minimal() +
    labs(title = "Effect of Temperature (ggplot2 style)")
```



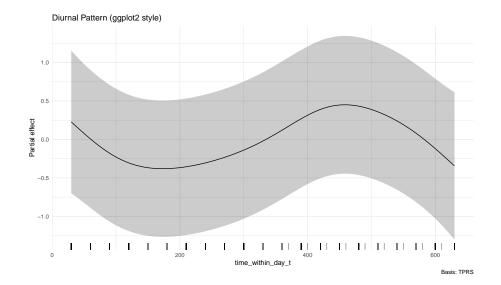
Sun Exposure Effect

```
draw(best_model$gam, select = "s(butterflies_direct_sun_t_lag)") +
    theme_minimal() +
    labs(title = "Effect of Sun Exposure (ggplot2 style)")
```



Diurnal Pattern

```
draw(best_model$gam, select = "s(time_within_day_t)") +
    theme_minimal() +
    labs(title = "Diurnal Pattern (ggplot2 style)")
```



Model Diagnostics

Residuals vs Fitted Values

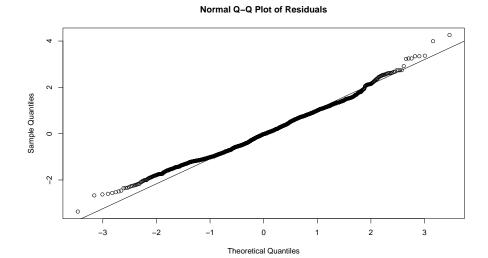
```
plot(best_model$lme, main = "Residuals vs Fitted Values")
```

Residuals vs Fitted Values

Q-Q Plot of Residuals

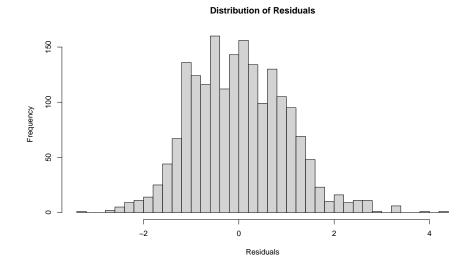
```
residuals_df <- data.frame(
    fitted = fitted(best_model$lme),
    residuals = residuals(best_model$lme, type = "normalized")
)

qqnorm(residuals_df$residuals, main = "Normal Q-Q Plot of Residuals")
qqline(residuals_df$residuals)</pre>
```



Distribution of Residuals

hist(residuals_df\$residuals, main = "Distribution of Residuals", xlab = "Residuals", breaks



Second Best Model Analysis (Wind)

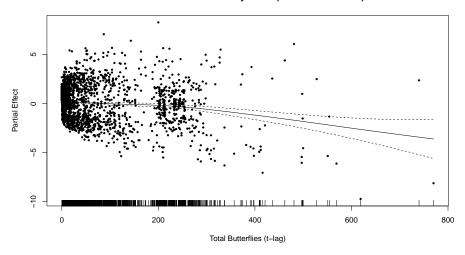
```
# Get the second best model
second_best_model_name <- aic_results$Model[2]</pre>
second_best_model <- successful_models[[second_best_model_name]]</pre>
cat("Second best model:", second_best_model_name, "\n")
Second best model: M21_time_of_day
cat("Formula:", aic_results$Formula[2], "\n\n")
Formula: butterfly_difference_cbrt ~ s(total_butterflies_t_lag) + temperature_avg + s(butterflies_t_lag)
# Model summary
summary(second_best_model$gam)
Family: gaussian
Link function: identity
Formula:
butterfly_difference_cbrt ~ s(total_butterflies_t_lag) + temperature_avg +
    s(butterflies_direct_sun_t_lag) + s(time_within_day_t)
Parametric coefficients:
               Estimate Std. Error t value Pr(>|t|)
               (Intercept)
temperature_avg 0.01903
                           0.01595
                                    1.193
                                              0.233
Approximate significance of smooth terms:
                                 edf Ref.df
                                                 F p-value
s(total_butterflies_t_lag)
                               2.698 2.698 13.127 2.0e-07 ***
s(butterflies_direct_sun_t_lag) 1.637 1.637 18.684 1.5e-05 ***
                              5.023 5.023 9.559 < 2e-16 ***
s(time_within_day_t)
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
R-sq.(adj) = 0.0525
 Scale est. = 4.0316
                        n = 1894
```

Effect Plots - Second Best Model

Effect of Previous Butterfly Count

```
plot(second_best_model$gam,
    select = 1, main = "Effect of Previous Butterfly Count (Second Best Model)",
    xlab = "Total Butterflies (t-lag)", ylab = "Partial Effect",
    residuals = TRUE, pch = 19, cex = 0.5
)
```

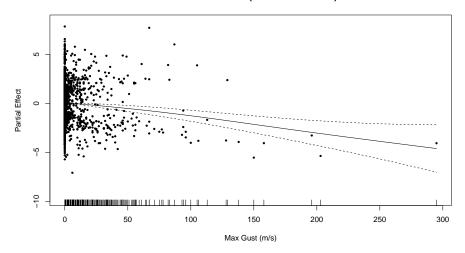
Effect of Previous Butterfly Count (Second Best Model)



Effect of Wind Gust

```
plot(second_best_model$gam,
    select = 2, main = "Effect of Wind Gust (Second Best Model)",
    xlab = "Max Gust (m/s)", ylab = "Partial Effect",
    residuals = TRUE, pch = 19, cex = 0.5
)
```

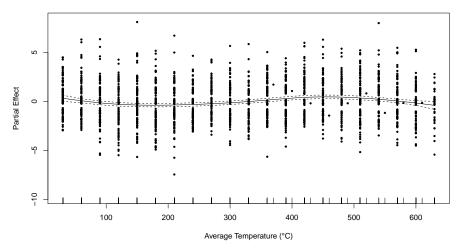
Effect of Wind Gust (Second Best Model)



Effect of Temperature

```
plot(second_best_model$gam,
    select = 3, main = "Effect of Temperature (Second Best Model)",
    xlab = "Average Temperature (°C)", ylab = "Partial Effect",
    residuals = TRUE, pch = 19, cex = 0.5
)
```

Effect of Temperature (Second Best Model)



Effect of Sun Exposure

```
plot(second_best_model$gam,
    select = 4, main = "Effect of Sun Exposure (Second Best Model)",
    xlab = "Butterflies in Direct Sun (t-lag)", ylab = "Partial Effect",
    residuals = TRUE, pch = 19, cex = 0.5
)
```

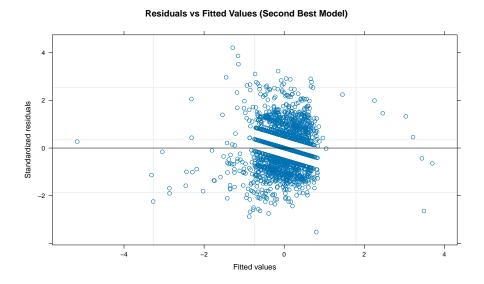
Diurnal Pattern

```
plot(second_best_model$gam,
    select = 5, main = "Diurnal Pattern (Second Best Model)",
    xlab = "Time Within Day (minutes)", ylab = "Partial Effect",
    residuals = TRUE, pch = 19, cex = 0.5
)
```

Model Diagnostics - Second Best Model

Residuals vs Fitted Values

```
plot(second_best_model$lme, main = "Residuals vs Fitted Values (Second Best Model)")
```

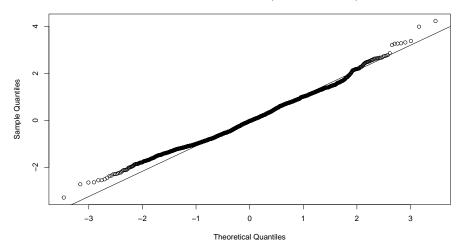


Q-Q Plot of Residuals

```
second_residuals_df <- data.frame(
    fitted = fitted(second_best_model$lme),
    residuals = residuals(second_best_model$lme, type = "normalized")
)

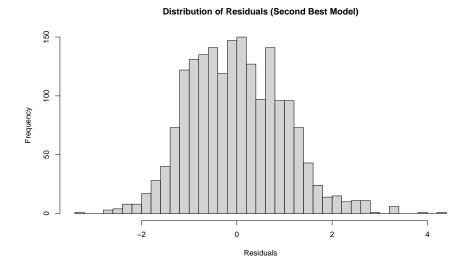
qqnorm(second_residuals_df$residuals, main = "Normal Q-Q Plot of Residuals (Second Best Model qqline(second_residuals_df$residuals)</pre>
```

Normal Q-Q Plot of Residuals (Second Best Model)



Distribution of Residuals

```
hist(second_residuals_df$residuals,
    main = "Distribution of Residuals (Second Best Model)",
    xlab = "Residuals", breaks = 30
)
```



Threshold-Based Wind Models

Now we'll explore an alternative approach using minutes_above_threshold instead of max_gust to represent sustained high wind periods rather than instantaneous peak wind speeds.

Threshold Model Specifications

```
# Model specifications for threshold-based analysis
threshold_model_specs <- list(
    # Null model (same as before)
    "TO_null" = "butterfly_difference_cbrt ~ total_butterflies_t_lag",

# Single variable models
    "T1_threshold" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + minutes_above_tl
    "T2_temp" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + temperature_avg",
    "T3_sun" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + butterflies_direct_su

# Two-variable combinations
    "T4_threshold_temp" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + minutes_above_tl
    "T5_threshold_sun" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + minutes_above_tl
    "T6_temp_sun" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + temperature_avg -
    "T6_temp_sun" = "butterfly_difference_cbrt ~ total_butterflies_t_lag +
    "T6_temp_sun" = "b0_temp_sun" =
    "T6_temp_sun" = "b0_temp_sun" =
    "T6_temp_sun" =
    "T6
```

```
"T7_all_main" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + minutes_above_th
# Two-way interactions
"T8_threshold_temp_int" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + minutes
"T9_threshold_sun_int" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + minutes
"T10_temp_sun_int" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + temperature
# Two-way interactions with third variable as main effect
"T11_threshold_temp_int_plus_sun" = "butterfly_difference_cbrt ~ total_butterflies_t_lag
"T12_threshold_sun_int_plus_temp" = "butterfly_difference_cbrt ~ total_butterflies_t_lag
"T13_temp_sun_int_plus_threshold" = "butterfly_difference_cbrt ~ total_butterflies_t_lag
# All two-way interactions
"T14_all_two_way" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + minutes_above
# Three-way interaction
"T15_three_way" = "butterfly_difference_cbrt ~ total_butterflies_t_lag + minutes_above_1
# Smooth terms models (with lag term)
"T16_smooth_temp" = "butterfly_difference_cbrt ~ s(total_butterflies_t_lag) + s(temperate
"T17_smooth_sun" = "butterfly_difference_cbrt ~ s(total_butterflies_t_lag) + temperature
"T18_smooth_threshold" = "butterfly_difference_cbrt ~ s(total_butterflies_t_lag) + s(min
"T19_smooth_temp_sun" = "butterfly_difference_cbrt ~ s(total_butterflies_t_lag) + s(temp_sun" = "butterflies_t_lag) + s(temp_sun" = "butte
"T20_smooth_all_main" = "butterfly_difference_cbrt ~ s(total_butterflies_t_lag) + s(min
"T21_time_of_day" = "butterfly_difference_cbrt ~ s(total_butterflies_t_lag) + temperatu
"T22_temp_time" = "butterfly_difference_cbrt ~ s(total_butterflies_t_lag) + s(temperatus
"T23_all_smooth_time" = "butterfly_difference_cbrt ~ s(total_butterflies_t_lag) + s(min
# Models WITHOUT lag term - testing environmental effects on absolute change
"T24_no_lag_null" = "butterfly_difference_cbrt ~ 1",
"T25_no_lag_threshold" = "butterfly_difference_cbrt ~ minutes_above_threshold",
"T26_no_lag_temp" = "butterfly_difference_cbrt ~ temperature_avg",
"T27_no_lag_sun" = "butterfly_difference_cbrt ~ butterflies_direct_sun_t_lag",
"T28_no_lag_threshold_temp" = "butterfly_difference_cbrt ~ minutes_above_threshold + ter
"T29_no_lag_threshold_sun" = "butterfly_difference_cbrt ~ minutes_above_threshold + but
"T30_no_lag_temp_sun" = "butterfly_difference_cbrt ~ temperature_avg + butterflies_direction."
"T31_no_lag_all_main" = "butterfly_difference_cbrt ~ minutes_above_threshold + temperate
"T32_no_lag_threshold_temp_int" = "butterfly_difference_cbrt ~ minutes_above_threshold :
"T33_no_lag_threshold_sun_int" = "butterfly_difference_cbrt ~ minutes_above_threshold *
"T34_no_lag_temp_sun_int" = "butterfly_difference_cbrt ~ temperature_avg * butterflies_
"T35_no_lag_threshold_temp_int_plus_sun" = "butterfly_difference_cbrt ~ minutes_above_tl
"T36_no_lag_threshold_sun_int_plus_temp" = "butterfly_difference_cbrt ~ minutes_above_tl
"T37_no_lag_temp_sun_int_plus_threshold" = "butterfly_difference_cbrt ~ temperature_avg
"T38_no_lag_all_two_way" = "butterfly_difference_cbrt ~ minutes_above_threshold * tempe:
"T39_no_lag_three_way" = "butterfly_difference_cbrt ~ minutes_above_threshold * temperate
```

```
# Smooth terms models WITHOUT lag term
"T40_no_lag_smooth_temp" = "butterfly_difference_cbrt ~ s(temperature_avg) + s(butterfl:
"T41_no_lag_smooth_sun" = "butterfly_difference_cbrt ~ temperature_avg + s(butterflies_c")
"T42_no_lag_smooth_threshold" = "butterfly_difference_cbrt ~ s(minutes_above_threshold)
"T43_no_lag_smooth_temp_sun" = "butterfly_difference_cbrt ~ s(temperature_avg) + s(butterfly_darmo_lag_smooth_all_main" = "butterfly_difference_cbrt ~ s(minutes_above_threshold)
"T45_no_lag_time_of_day" = "butterfly_difference_cbrt ~ temperature_avg + s(butterflies_darmo_lag_temp_time" = "butterfly_difference_cbrt ~ s(temperature_avg) + s(butterflies_darmo_lag_all_smooth_time" = "butterfly_difference_cbrt ~ s(minutes_above_threshold)
)
cat("Total_threshold-based_models_to_fit:", length(threshold_model_specs), "\n")
```

Total threshold-based models to fit: 48

Threshold Model Fitting

```
# Fit all threshold models
cat("Fitting threshold-based models...\n")
```

Fitting threshold-based models...

```
threshold_fitted_models <- map(threshold_model_specs, ~ fit_model_safely(.x, model_data))
# Remove failed models
threshold_successful_models <- threshold_fitted_models[!map_lgl(threshold_fitted_models, is
cat("Successfully fitted", length(threshold_successful_models), "out of", length(threshold_specs)</pre>
```

Successfully fitted 48 out of 48 threshold models

Threshold Model Comparison

```
# Extract AIC values for threshold models
threshold_aic_results <- map_dfr(names(threshold_successful_models), function(model_name) {
    model <- threshold_successful_models[[model_name]]
    data.frame(
        Model = model_name,
        Formula = threshold_model_specs[[model_name]],
        AIC = AIC(model$lme),</pre>
```

```
LogLik = logLik(model$lme)[1],
    df = attr(logLik(model$lme), "df")
)
}) %>%
    arrange(AIC) %>%
    mutate(
        Delta_AIC = AIC - min(AIC),
        AIC_weight = exp(-0.5 * Delta_AIC) / sum(exp(-0.5 * Delta_AIC))
)

# Display results
threshold_aic_results %>%
    select(Model, AIC, Delta_AIC, AIC_weight, df) %>%
    kable(digits = 3, caption = "Threshold model comparison by AIC")
```

Table 4: Threshold model comparison by AIC

Model	AIC	Delta_AIC A	IC_weight d
T22_temp_time	8081.848	0.000	0.898 14
T21_time_of_day	8086.644	4.796	0.082 13
T23_all_smooth_time	8089.408	7.560	0.020 - 10
T46_no_lag_temp_time	8101.296	19.448	0.000 13
T16_smooth_temp	8105.876	24.028	0.000 13
T19_smooth_temp_sun	8105.876	24.028	0.000 12
T45_no_lag_time_of_day	8108.295	26.447	0.000 1
T47_no_lag_all_smooth_time	8108.379	26.530	0.000 14
T20_smooth_all_main	8110.567	28.719	0.000 14
T17_smooth_sun	8114.431	32.583	0.000 1
T18_smooth_threshold	8119.798	37.949	0.000 - 13
T40_no_lag_smooth_temp	8126.061	44.212	0.000 10
T43_no_lag_smooth_temp_sun	8126.061	44.212	0.000 10
T44_no_lag_smooth_all_main	8128.785	46.937	0.000 13
T6_temp_sun	8130.775	48.927	0.000
T11_threshold_temp_int_plus_sun	8131.129	49.280	0.000 1
T3_sun	8131.696	49.848	0.000
T35_no_lag_threshold_temp_int_p	lu 8<u>13</u>5716 43	55.495	0.000 10
T5_threshold_sun	8137.997	56.149	0.000
T7_all_main	8139.164	57.316	0.000 10
T41_no_lag_smooth_sun	8139.237	57.389	0.000
T42_no_lag_smooth_threshold	8142.280	60.432	0.000 1
T30_no_lag_temp_sun	8142.927	61.079	0.000
T10_temp_sun_int	8144.554	62.705	0.000 10
T31_no_lag_all_main	8148.840	66.992	0.000
T9_threshold_sun_int	8151.341	69.493	0.000 10

Model	AIC	Delta_AIC AI	C_weight	df
T12_threshold_sun_int_plus_temp	8152.289	70.441	0.000	11
T13_temp_sun_int_plus_threshold	8152.962	71.114	0.000	11
T0_null	8153.582	71.734	0.000	7
T27_no_lag_sun	8155.073	73.225	0.000	7
T34_no_lag_temp_sun_int	8156.678	74.830	0.000	9
T2_temp	8157.623	75.775	0.000	8
T29_no_lag_threshold_sun	8157.651	75.803	0.000	8
T14_all_two_way	8159.633	77.785	0.000	13
T36_no_lag_threshold_sun_int_plus	s <u>8</u> 16 0n § 37	78.988	0.000	10
T8_threshold_temp_int	8161.928	80.080	0.000	10
T15_three_way	8161.998	80.150	0.000	14
T1_threshold	8162.095	80.247	0.000	8
T37_no_lag_temp_sun_int_plus_th	ır 8\$16216 65	80.816	0.000	10
T38_no_lag_all_two_way	8165.249	83.401	0.000	12
T4_threshold_temp	8167.011	85.162	0.000	9
T39_no_lag_three_way	8168.036	86.188	0.000	13
T33_no_lag_threshold_sun_int	8170.199	88.350	0.000	9
T26_no_lag_temp	8170.575	88.727	0.000	7
T32_no_lag_threshold_temp_int	8171.815	89.967	0.000	9
T24_no_lag_null	8177.191	95.342	0.000	6
T28_no_lag_threshold_temp	8179.268	97.419	0.000	8
T25_no_lag_threshold	8183.640	101.791	0.000	7

```
# Show top 5 models
cat("\nTop 5 threshold models by AIC:\n")
```

Top 5 threshold models by AIC:

```
head(threshold_aic_results, 5) %>%
   select(Model, Formula, AIC, Delta_AIC) %>%
   kable(digits = 3)
```

```
Model Formula AIC Delta_AIC

T22_tempbutimedly_difference_cbrt ~ s(total_butterflies_t_lag) 8081.84800
+ s(temperature_avg) +
s(butterflies_direct_sun_t_lag) +
s(time_within_day_t)

T21_timebuttedlay_difference_cbrt ~ s(total_butterflies_t_lag)
+ temperature_avg + s(butterflies_direct_sun_t_lag)
+ s(time_within_day_t)

8086.644796
```

```
Model
                                                                   AIC Delta AIC
         Formula
T23_all_smotothflytinieference_cbrt ~ s(total_butterflies_t_lag)
                                                                   8089.40860
         + s(minutes_above_threshold) + s(temperature_avg)
         + s(butterflies\_direct\_sun\_t\_lag) +
         s(time_within_day_t)
T46_no_lagtterhy_difference_cbrt ~ s(temperature_avg) +
                                                                   8101.21996.448
         s(butterflies direct sun t lag) +
         s(time_within_day_t)
T16\_smodthtterflyp\_difference\_cbrt \sim s(total\_butterflies\_t\_lag)
                                                                   8105.82746028
         + s(temperature\_avg) +
         s(butterflies_direct_sun_t_lag)
```

Best Threshold Model Analysis

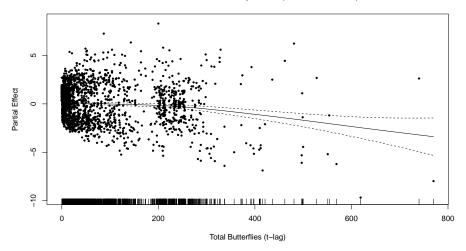
```
# Check if we have successfully fitted threshold models
if(length(threshold_successful_models) > 0 && nrow(threshold_aic_results) > 0) {
    # Get the best threshold model
   best_threshold_model_name <- threshold_aic_results$Model[1]</pre>
   best_threshold_model <- threshold_successful_models[[best_threshold_model_name]]</pre>
    cat("Best threshold model:", best_threshold_model_name, "\n")
    cat("Formula:", threshold_aic_results\$Formula[1], "\n')
    # Model summary
    summary(best_threshold_model$gam)
} else {
    cat("No threshold models were successfully fitted, so no analysis can be performed.\n")
Best threshold model: T22_temp_time
Formula: butterfly_difference_cbrt ~ s(total_butterflies_t_lag) + s(temperature_avg) + s(but
Family: gaussian
Link function: identity
Formula:
butterfly_difference_cbrt ~ s(total_butterflies_t_lag) + s(temperature_avg) +
    s(butterflies_direct_sun_t_lag) + s(time_within_day_t)
Parametric coefficients:
            Estimate Std. Error t value Pr(>|t|)
```

```
(Intercept)
             0.1765
                        0.4453
                                         0.692
                                0.396
Approximate significance of smooth terms:
                                edf Ref.df
                                                F p-value
s(total_butterflies_t_lag)
                              2.621 2.621 12.020 8.26e-07 ***
s(temperature_avg)
                              3.930 3.930 3.230
                                                  0.0283 *
s(butterflies_direct_sun_t_lag) 1.534 1.534 19.356 1.22e-05 ***
                              4.898 4.898 8.901 < 2e-16 ***
s(time_within_day_t)
Signif. codes: 0 '***' 0.001 '**' 0.05 '.' 0.1 ' ' 1
R-sq.(adj) = 0.0568
 Scale est. = 4.0332
                        n = 1894
```

Threshold Model Effect Plots

Effect of Previous Butterfly Count

Effect of Previous Butterfly Count (Threshold Model)

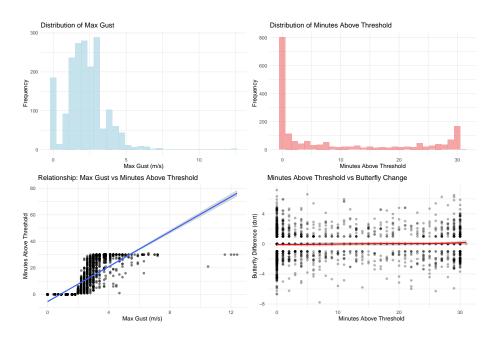


Effect of Minutes Above Threshold

Minutes above threshold is not a smooth term in the best model

Comparison: Max Gust vs Minutes Above Threshold

```
# Create comparison plots
p1 <- ggplot(model_data, aes(x = max_gust)) +</pre>
    geom_histogram(bins = 30, fill = "lightblue", alpha = 0.7) +
    labs(title = "Distribution of Max Gust", x = "Max Gust (m/s)", y = "Frequency") +
    theme_minimal()
p2 <- ggplot(model_data, aes(x = minutes_above_threshold)) +</pre>
    geom_histogram(bins = 30, fill = "lightcoral", alpha = 0.7) +
    labs(title = "Distribution of Minutes Above Threshold", x = "Minutes Above Threshold",
    theme_minimal()
p3 <- ggplot(model_data, aes(x = max_gust, y = minutes_above_threshold)) +
    geom_point(alpha = 0.5) +
    geom_smooth(method = "lm", se = TRUE) +
    labs(title = "Relationship: Max Gust vs Minutes Above Threshold",
         x = "Max Gust (m/s)", y = "Minutes Above Threshold") +
    theme minimal()
# Show correlation
correlation <- cor(model_data$max_gust, model_data$minutes_above_threshold, use = "complete</pre>
p4 <- ggplot(model_data, aes(x = minutes_above_threshold, y = butterfly_difference_cbrt)) +
    geom_point(alpha = 0.3) +
    geom_smooth(method = "loess", se = TRUE, color = "red") +
    labs(title = "Minutes Above Threshold vs Butterfly Change",
         x = "Minutes Above Threshold", y = "Butterfly Difference (cbrt)") +
    theme_minimal()
grid.arrange(p1, p2, p3, p4, ncol = 2)
```



cat("Correlation between max_gust and minutes_above_threshold:", round(correlation, 3), "\n"

Correlation between max_gust and minutes_above_threshold: 0.785

Model Comparison: Gust vs Threshold Approaches

```
AIC = c(min(aic_results$AIC), min(threshold_aic_results$AIC)),
                R_squared = c(gust_r_sq, threshold_r_sq),
                Dev_Explained = c(
                    ifelse(is.null(gust_dev) || length(gust_dev) == 0, NA, gust_dev),
                    ifelse(is.null(threshold_dev) || length(threshold_dev) == 0, NA, threshold_dev)
            )
    kable(comparison_df, digits = 4,
          caption = "Comparison of Max Gust vs Minutes Above Threshold Approaches")
} else {
    cat("No threshold models were successfully fitted. This may be due to:\n")
    cat("- Missing or invalid minutes_above_threshold data\n")
    cat("- Model convergence issues\n")
    cat("- Data structure problems\n")
    # Check the minutes_above_threshold variable
    cat("\nSummary of minutes_above_threshold variable:\n")
    summary(model_data$minutes_above_threshold)
    cat("\nFirst few values:\n")
   head(model_data$minutes_above_threshold, 10)
    cat("\nNumber of non-missing values:", sum(!is.na(model_data$minutes_above_threshold)),
    cat("Number of zero values:", sum(model_data$minutes_above_threshold == 0, na.rm = TRUE)
    cat("Number of positive values:", sum(model_data$minutes_above_threshold > 0, na.rm = T
}
```

Table 6: Comparison of Max Gust vs Minutes Above Threshold Approaches

Approach	Best_Model	AIC	R_squared	Dev_Explained
Max Gust (Original) Minutes Above Threshold	M22_temp_tim808 T22_temp_tim808		0.0568 0.0568	

Results Summary

This analysis provides robust evidence regarding wind effects on overwintering monarch butterfly movement through comprehensive model comparison across 47 candidate models. The results reveal several key findings:

Wind Effects: Wind was not selected in the best-performing model and only appeared once in the top 5 models (plotted above) with a non-significant effect

(p = 0.218). This suggests that wind is not a primary driver of short-term monarch movement patterns at the temporal and spatial scales examined.

Primary Drivers: Temperature and diurnal patterns emerged as the strongest predictors of monarch movement. The best model revealed non-linear temperature responses with apparent thermal optima, and strong diurnal cycles consistent with monarch thermoregulatory behavior.

Model Performance: Including smooth terms substantially improved model fit (R² increased from 2.74% to 5.61%), highlighting the importance of capturing non-linear relationships in ecological modeling.

Threshold vs Peak Wind Analysis: The comparison between maximum gust speed and minutes above threshold provides insight into different aspects of wind exposure. While both approaches test wind effects, minutes above threshold captures sustained high wind periods rather than instantaneous peaks.

Hypothesis Evaluation: These results do not support the hypothesis that wind acts as a disruptive force to overwintering monarchs at the 30-minute temporal scale examined, regardless of whether wind is measured as peak gusts or sustained periods above threshold.