# Introduction

Somewhere – before this Hyp and Pred section - we need to quote Kingston's exact language. That language needs to be unpacked, so that it becomes obvious that there might be alternative tests like: a negative correlation between wind and abundance, or than it could be a threshold model, or that it could be a reduction in site fidelity/occupancy. Also, that it could just be average wind speeds or gust speeds. This should feel like a general discussion of the possible ways in which one could analyze his statement for validity and should make the reader feel like the original statement was both vague and impactful. Being impactful will require some statement about the management of canopy structure as a strategy for maintaining habitat suitability (not sure where this “impactful” argument would sit in the intro...)

1990 paper

“During winter storms, the butterflies clustered on those few trees that offered the greatest protection against winds of «2 m/s or greater.”

“The greatest mean wind velocity at the cluster trees (0.84 m/s) was similar to the average low wind velocity (0.71 m/s) of the postcluster trees. This relationship implies that wind velocities >0.84 m/s could determine whether a tree was suitable or not for roosting.”

“Brower (1988) noted that roosting butterflies dispersed when they were exposed to prolonged direct sunlight.”

“At 1- or 2-wk intervals, visits were made to each site, and the following environmental parameters associated with each designated tree were measured at about 2 m height: (1) lowest and highest wind velocity, with a thermoanemometer during a 10-s interval;”

“In summary, monarch butterflies do not cluster randomly on trees within the grove, but seek trees that offer more shelter from gusty intermittent winds and good exposure to filtered sunlight. The butterflies congregated on different trees during the winter months in response to the direction of winds through the grove”

* Unfortunately, our project doesn’t directly address this assertion. We are testing the “game of telephone” conclusion of this work, which is there is a ~ 2m/s threshold. As a hypothesis, I find this statement reasonable.

It’s worth noting that the highest wind velocity he measured was 1.66 m/s.

Perhaps we need to build up a narrative around how this assertion became the 5 mph rule we know today.

Leong 2016

“Winds ≥ 2 m/s are disruptive to the aggregating butterflies by blowing them from their roosting branches or dislodging them by shaking the branches.”

“Monarch Butterflies are very sensitive to winds, forming winter aggregations on trees exposed to minimal winds and on foliage that buffers prevailing winds (Leong 1990).”

“Field studies of butterfly sites I conducted at Los Osos, Purple Gate, Nipomo, and Sweet Springs, in California, have consistently showed that strong winds have a direct negative effect on the winter occupancy of a grove by butterflies (Leong 1990, 1997; Leong et al. 1991, 2004).”

“When the butterflies observed in this study were subjected to winds above flight threshold (about 16° C), they either flew to a more sheltered area of the grove or, if no refuge area was available, abandoned the grove temporarily or for the remainder of the season.”

* Add “sic” somewhere in here

## Hypotheses and Predictions

### Wind Dispersal Hypothesis (H1)

**Hypothesis:** Monarch butterflies seek overwintering habitat that will increase their chances of survival during the winter months before their spring migration. Among these habitat characteristics is protection from strong wind, which may aid in energy conservation and reduce direct mortality.

Increasing winds cause monarch butterfly dispersal from occupied roosts.

**Prediction:** We predict a negative correlation between wind speed measurements and change in roosting monarch abundance, where exposure to higher wind speeds correspond with a negative change in butterfly abundance.

**Proposed Analysis:** We will test this hypothesis using a mixed-effects linear model with temporal autocorrelation to account for the hierarchical structure of our data and time-series dependencies. The response variable will be the change in monarch abundance calculated between consecutive observation periods, allowing for both positive (recruitment/clustering) and negative (departure/dispersal) values. Primary fixed effects will include mean wind speed (averaged across the observation period), maximum wind speed, 95th percentile wind speed, and wind speed variance, which together capture the overall wind exposure, peak wind events, extreme conditions, and gustiness experienced during each observation interval.

Beyond testing linear relationships, we recognize that H1 encompasses a broad investigation of wind effects on monarch behavior. If initial analyses suggest that wind is indeed a significant factor influencing overwintering abundance, we propose additional approaches to characterize the nature of these relationships. Specifically, we could implement segmented regression to identify potential breakpoints in wind-abundance relationships, allowing the data to reveal critical wind speeds where monarch behavior changes. Alternatively, smoothing splines or piecewise regression could capture non-linear responses to wind exposure. These threshold discovery methods would help determine whether wind effects on monarch abundance are gradual and continuous or exhibit sharp transitions at specific wind speeds (as proposed in the literature).

To account for non-independence in our data structure, we will include random intercepts for camera view (to control for site-specific variation) and labeler identity (to control for observer effects in abundance estimation). Given the temporal nature of abundance measurements, we will incorporate an AR(1) autocorrelation structure to model the expected correlation between consecutive time points, which is critical for obtaining unbiased parameter estimates in time-series ecological data.

Model diagnostics will include examination of residual plots, normality assessment, and validation of the autocorrelation structure. We anticipate reporting standardized effect sizes for wind variables, 95% confidence intervals for all parameters, and visualization of the predicted relationship between wind speed and abundance change. If threshold effects are detected, we will report the estimated breakpoint(s) with confidence intervals. A negative coefficient for wind speed variables would support our hypothesis that increased wind conditions drive monarch dispersal from overwintering sites.

The statistical model will be implemented in R using the nlme package as follows:

# Linear model  
model\_h1\_linear <- lme(abundance\_change ~ mean\_wind\_speed + max\_wind\_speed +   
 wind\_speed\_95th + wind\_speed\_variance,  
 random = ~ 1 | view/labeler,  
 correlation = corAR1(form = ~ time\_index | view),  
 data = monarch\_wind\_data,  
 method = "REML")  
  
# Threshold discovery using segmented regression  
library(segmented)  
model\_h1\_segmented <- segmented(model\_h1\_linear,   
 seg.Z = ~ mean\_wind\_speed,  
 npsi = 1) # test for 1 breakpoint

### Critical Wind Threshold Hypothesis (H2)

**Hypothesis:** Monarchs are subject to disruptive winds (> 2 m/s), and there will be a behavioral response to those winds.

**Prediction:** We predict monarchs will be dislodged from

**Proposed Analysis:** We will test the stricter version of Kingston Leong’s hypothesis, the threshold hypothesis, using a simple mixed-effects model that directly examines the relationship between threshold exceedance and abundance change. The response variable will be change in monarch abundance between consecutive observation periods. The primary fixed effect will be minutes\_above\_2.2ms, representing the total duration (in minutes) that wind speeds exceeded the Kingston threshold during each observation interval.

This focused approach tests the specific claim that 2.2 m/s represents a critical threshold for monarch site abandonment, independent of other wind characteristics. We will include the same random effects structure as H1 (random intercepts for camera view and labeler identity) and AR(1) temporal autocorrelation to account for data dependencies.

A negative coefficient for minutes\_above\_2.2ms would support the Kingston Leong threshold hypothesis, while a non-significant result would suggest that this specific threshold may not be biologically meaningful for monarch site abandonment behavior.

The statistical model will be implemented in R using the nlme package as follows:

model\_h2 <- lme(abundance\_change ~ minutes\_above\_2.2ms,  
 random = ~ 1 | view/labeler,  
 correlation = corAR1(form = ~ time\_index | view),  
 data = monarch\_wind\_data,  
 method = "REML")

### Site Fidelity Loss Hypothesis (H3)

**Hypothesis:** Following exposure to wind speeds exceeding 5 mph while monarchs are present, butterflies will not return to previously occupied sites, indicating permanent abandonment after high-wind events.

Roosts that are known to have experienced wind events, with a response as predicted in H1 or H2 above, will show a persisting avoidance by roosting monarchs.

**Prediction:** We predict that morning abundance counts will remain near zero at sites following events when both monarchs were present and wind speeds exceeded 5 mph, with the predictor variable “days since last threshold exceeded” showing no recovery in abundance for values greater than zero.

**Proposed Analysis:** We will test this hypothesis using a logistic mixed-effects model that examines site occupancy patterns following wind threshold events. This approach directly tests the maanagement relevant claim that monarchs (semi?)permanently abandon sites after experiencing unsuitable wind conditions.

We define a wind threshold event as any day when wind speeds exceed 2.2 m/s for ≥30 consecutive minutes while monarchs are present (abundance > 0). This operational definition ensures we capture sustained wind exposure during active site occupation, rather than brief gusts or events occurring at unoccupied sites. The 30-minute minimum duration represents our initial analytical approach based on photographic sampling intervals, though we anticipate exploring alternative durations as data patterns emerge.

The response variable will be binary site occupancy status (occupied = abundance > 0, unoccupied = abundance = 0) derived from morning abundance counts to avoid confounding with same-day wind effects. We propose initially focusing on the 14-day period following each threshold event to capture both immediate and sustained abandonment patterns predicted by conventional wisdom, with the understanding that this analysis window may be adjusted based on results from H1 and H2 testing and data availability.

The primary fixed effect will be days\_since\_wind\_event, representing the number of days elapsed since the threshold event occurred. According to the persistent avoidance prediction of the site abandonment hypothesis, we expect a strong negative relationship where the probability of site occupation remains near zero for all post-event time points, with no recovery pattern over the 14-day analysis window.

This conservative analytical approach uses complete abandonment (zero abundance) as the response threshold, giving the conventional wisdom hypothesis the strongest possible test. If monarchs truly abandon sites after wind exposure, this effect should be easily detectable even with limited sample sizes. We will include random intercepts for camera view and labeler identity to control for site-specific and observer effects, following the same random effects structure used in H1 and H2.

Model diagnostics will focus on examining residual patterns, assessing model convergence, and validating the binary response assumption. We will report odds ratios for the temporal predictor, 95% confidence intervals, and visualization of predicted occupancy probability across the post-event time series. A negative coefficient for days\_since\_wind\_event would support the site abandonment hypothesis, while a non-significant result would challenge current conservation guidance regarding wind exposure and habitat suitability.

The statistical model will be implemented in R using the glmer function from the lme4 package as follows:

library(lme4)  
model\_h3 <- glmer(site\_occupied ~ days\_since\_wind\_event + (1|view) + (1|labeler),  
 family = binomial,  
 data = post\_event\_data)

### Thermal Regulation Hypothesis (H4)

**Hypothesis:** Overwintering monarch butterflies modify their clustering behavior in response to direct sunlight exposure. , with this effect moderated by ambient temperature, as monarchs are sensitive to overheating risks.

**Prediction:** We predict a interaction between proportion of the roosting monarchs under direct sunlight exposure and ambient temperature on changes in monarch abundance, where the combination of high direct sunlight exposure and elevated temperatures will produce the greatest negative changes in butterfly counts, particularly during morning observation periods when clusters are most likely to disband.

A diagram of lipid exhaling

AI-generated content may be incorrect.

This is the figure that informs my intuition about the thermal regulation hypothesis (Masters et al 1985). Monarchs are trying to manage their “lipid budget” by keep body temperatures at a reasonable level. I agree that monarchs are certainly moderating their behavior to get to the flight threshold, but beyond that, they are incentivized to stay as cool as possible. Each additional degree of thoracic temperature has a nonlinear penalty on lipid use.

Still, I’m a bit confused about what the monarchs are seeking. Oct 1 through Mar 1 is about 150 days, which I consider the maximum time a monarch can be expected to overwinter. If the butterflies are optimizing for flight threshold, they will run out of lipids about half way through the season. Looking on the figure, the mean temperature (~ 7 C, 45 F) put them around 200 days of lipid reserves, which makes sense if they then have to go reproduce. Perhaps we can talk more about when the 55 F flight threshold is reached and when it makes sense for butterflies. My current thought would be that they would want to stay around 45 F for as long as possible, as you’ll get better lipid per day rates.

**Proposed Analysis:** We will test this hypothesis using a mixed-effects linear model with an interaction term to examine the combined effects of sunlight exposure and ambient temperature on monarch clustering behavior. This approach directly tests the thermal regulation hypothesis that monarchs modify their behavior to avoid overheating when exposed to direct sunlight under elevated temperature conditions. Analysis will exclude observation periods with zero monarch abundance, focusing exclusively on periods when butterflies are present to exhibit thermal regulation behavior.

To isolate thermal regulation effects from concurrent wind influences, we will include wind variables as covariates in our thermal regulation model. This expanded approach tests whether sunlight-temperature interactions remain significant predictors of monarch behavior when accounting for wind effects, addressing the possibility that thermal and wind factors are correlated in our dataset. By controlling for wind while testing thermal mechanisms, this analysis approaches the broader question of relative factor importance that might be addressed through a comprehensive global model, but maintains focus on thermal regulation as the primary mechanism of interest.

The response variable will be change in monarch abundance calculated between consecutive observation periods, allowing for both positive (clustering) and negative (dispersal) values. Our primary fixed effects will include: (1) sunlight exposure proportion, calculated as the proportion of butterflies experiencing direct sunlight relative to total butterflies present during each observation period; (2) ambient temperature, derived from temperature readings extracted via OCR from deployment photographs; and (3) their interaction term (sunlight exposure ambient temperature), which tests our core prediction that thermal effects are most pronounced when both factors are elevated.

This sunlight exposure metric addresses the key challenge of scaling exposure measurements to population size. By calculating the proportion of butterflies in direct sunlight relative to the total butterfly population present, we obtain a continuous variable between 0 and 1. Periods with zero sunlight exposure represent times when no butterflies were positioned in sunny locations, providing natural contrast conditions for our analysis.

To control for baseline differences between morning and afternoon observation periods, we will include time period (morning vs. afternoon) as a fixed effect in our model. Additionally, we will include mean wind speed as a covariate to control for concurrent wind effects that might confound thermal responses. This approach accounts for natural temporal variation in monarch behavior while isolating thermal regulation mechanisms from wind-driven dispersal effects, allowing us to test whether sunlight-temperature interactions represent independent behavioral drivers beyond wind influences.

We will include the same random effects structure as H1-H3 (random intercepts for camera view and labeler identity) to control for site-specific variation and observer effects. Given the temporal nature of our data, we will incorporate AR(1) autocorrelation to model expected correlation between consecutive time points, ensuring unbiased parameter estimates in our time-series analysis.

Model diagnostics will focus on examining residual patterns, validating the autocorrelation structure, and assessing the distribution of sunlight exposure values. We will report interaction effect coefficients with 95% confidence intervals, standardized effect sizes for all predictors, and visualization of the predicted relationship between sunlight-temperature combinations and abundance change. Results will include the estimated effect of time period to characterize baseline differences between morning and afternoon observations.

A significant negative interaction coefficient would support our thermal regulation hypothesis, indicating that monarch abundance decreases most markedly when both sunlight exposure and ambient temperature are elevated, even when controlling for wind effects. Conversely, non-significant interaction effects would suggest that thermal regulation responses are not independent of wind influences or that thermal regulation is not dependent on the combined influence of sunlight and temperature factors. This expanded analysis will help determine whether thermal factors represent primary drivers of monarch behavior or secondary effects correlated with wind conditions.

The statistical model will be implemented in R using the nlme package as follows:

# Thermal regulation model with wind control  
model\_h4 <- lme(abundance\_change ~ sunlight\_exposure\_prop \* ambient\_temp +   
 period + mean\_wind\_speed,  
 random = ~ 1 | view/labeler,  
 correlation = corAR1(form = ~ time\_index | view),  
 data = monarch\_thermal\_data,  
 method = "REML")