Occupancy Modeling of Western Monarch Thanksgiving Counts: Negative Impacts of Incomplete Resurveys and Uneven Sampling Efforts

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ABSTRACT

Western monarch butterflies (sp. *Danaus plexippus*) are undergoing a severe decline that rivals those occurring among insects across the globe. Despite the estimation of population abundance, growth rates, and extinction probabilities, no analyses have investigated spatiotemporal patterns of decline in the western monarch population. I performed occupancy modeling of Western Monarch Thanksgiving Count (WMTC) data. The data was constrained spatially and temporally, with sites grouped into occupancy bins by latitude and year. Occupancy probabilities (psi) were estimated for each intersection of a latitude and time bin and detection probabilities (p) were estimated for each time bin. Psi increased slightly and non-significantly from northern to southern latitude bins. However, the dataset was unable to support any models with >3 latitude bins or the intersection of latitude and time bins because the dataset contained unequal sampling distributions across both space and time and a high proportion of missing observations. These constraints are likely driven by the reliance upon citizen science for WMTC data collection, and thus those constraints may be present in other citizen science datasets. Despite inconclusion regarding my original research questions, I concluded that occupancy modeling requires robust datasets that are more complete and equally distributed across the relevant parameters than the WMTC data. As species begin to decline, datasets with these characteristics may be harder to generate, suggesting that occupancy modeling may not be suitable for western monarch butterflies or other insect populations in the future.

INTRODUCTION

Insects are highly abundant and occupy important ecological niches such as pollinating flowering plant species, decomposing detritus to organic matter, and serving as prey for higher level consumers. This makes them highly important to both natural ecosystems and human economies. However, recent evidence has indicated drastic and universal declines in insect species across the globe (Moller 2018). Western monarchs, sp. *Danaus plexippus*, are facing equally or potentially more dramatic declines (Leong et al. 2004; Moller 2018; Pelton et al. 2019; Schultz et al. 2017). Population abundance estimates place the 2000-2016 mean at 3.5% of 1980-1989 levels and a 95% confidence interval places this ratio between 2.4%-6.7% (Schultz et al. 2017). A similar ratio emerges when contemporary maximum estimates of 300,000 monarchs are compared to the 1980s maximum of 4.5 million (Schultz et al. 2017). Beyond simple abundance, declines have also been noted in other metrics. Western monarchs have plummeted in *raw day positives*—the number of days in which a monarch sighting is reported at various sites (Espeset et al. 2016)—and in population growth rate, which was significantly negative for the period 1980-2016 (Schultz et al. 2017). Monitoring of overwintering sites reveals that 41% of sites that were occupied prior to 1990 are now unoccupied (Leong et al. 2004). These declines place western monarchs at an extinction risk of 50-75% within 20 years and 65-85% within 50 years

(Schultz et al. 2017). Furthermore, the population is at heightened risk of suffering severe consequences from Allee effects and environmental stochasticity, factors which would presumably increase extinction risks (Pelton et al. 2019). These declines seem to be located earlier in the breeding season, which suggests a correlation between declines and overwintering (Espeset et al. 2016).

Data from the Western Monarch Thanksgiving Count, a citizen science project involving annual counts of overwintering sites across the California coast, reveals that 2019 abundance estimates were less than 1% of 1980s estimates (Pelton et al. 2019). This dataset has been analyzed to show a significant positive correlation between proportion of declining sites with distance from the overwintering range center (Griffiths and Villablanca 2014). However, no analysis of spatial *and* temporal patterns within this dataset has yet been performed. Such an analysis would reveal patterns of western monarch abundance and distribution and inform conservation efforts.

I used occupancy modeling to analyze the WMTC dataset and identify both spatial and temporal heterogeneity in the occupancy rates of overwintering monarchs in California. I hypothesized that patterns of abundance and distribution of overwintering monarchs in the west can inform the temporal and spatial patterns of decline. I predicted that monarchs may be i) declining uniformly across the range; ii) shifting North—indicating a climate change response; iii) contracting towards the range center; or iv) shifting bimodally towards the range extremes. These predictions were tested by encoding them into occupancy models and performing model selection to determine those that best modeled the data.

METHODS

Data

The publicly available Western Monarch Thanksgiving Count data (westernmonarchcount.org) from the Xerces Society for Invertebrate Conservation was used for the analysis. The database contains georeferenced overwintering grove locations and associated annual population size estimates. Data are collected by citizen scientists with coordination by the Xerces Society, with the current time period spanning from 1997 to 2019. Though this is the best dataset available, it comes with important constraints. The number of sites counted per year is variable, and not all sites are counted in every year. Furthermore, the number of sites recognized and counted each year has increased over time. Therefore only 41.77% of the 7567 total possible observations (329 sites x 23 year) were actually made. Schultz et al. 2017 also recognize this constraint and had to develop a multi-state model in order to analyze the data set. My analytical method attempts to accomplish something comparable.

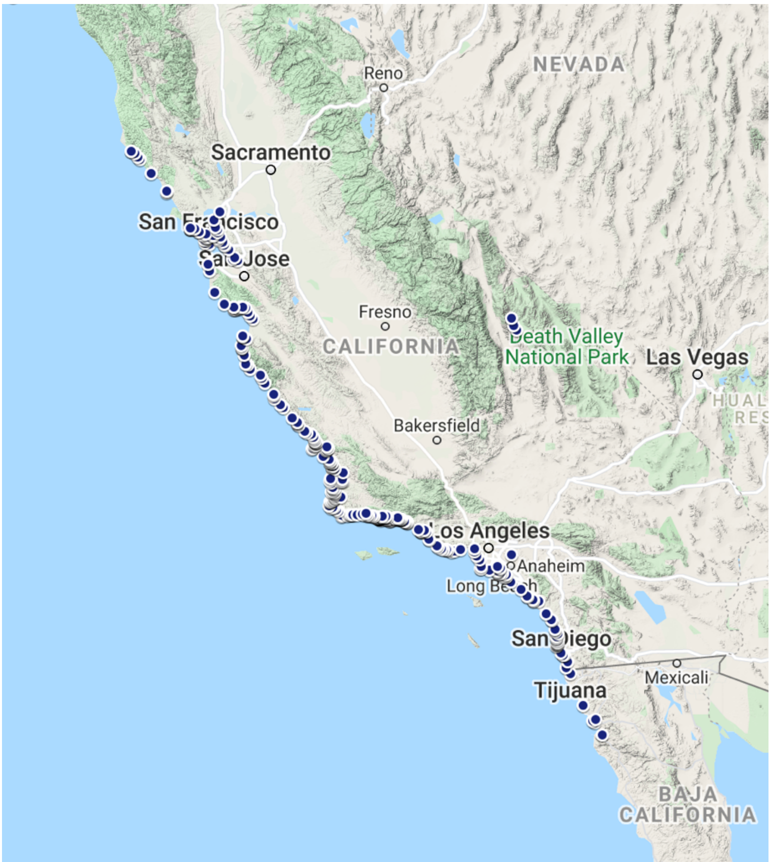


Figure 1. Comprehensive map of western monarch overwintering sites (N = 329).

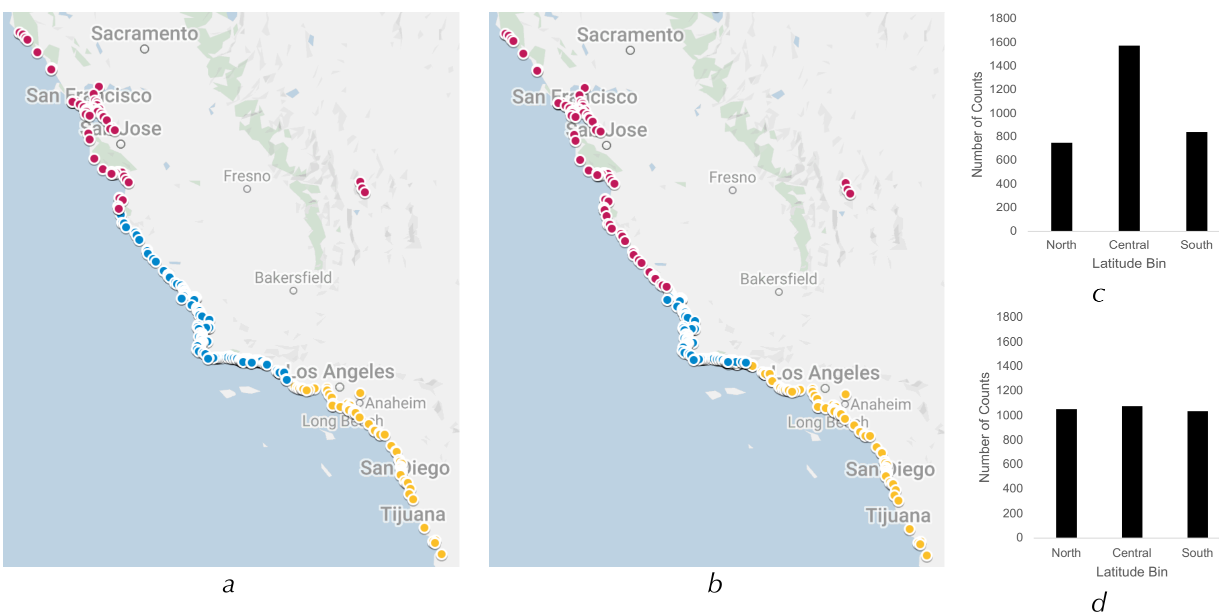
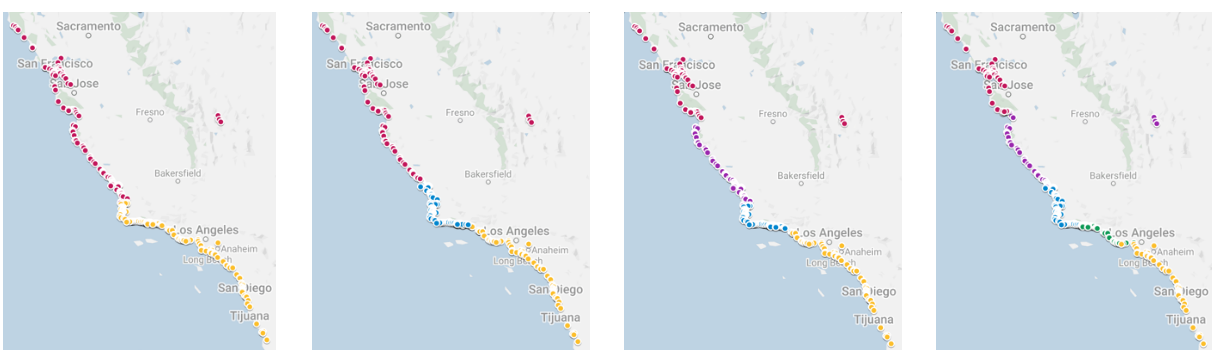


Figure 2. Differences between ELAT and CLAT bin models where ELAT bins represent equal latitudinal ranges while CLAT bins represent equal distributions of counts. Maps depict a zoomed in segment of the California and Baja California coasts, including all sites present in the dataset (N=329). (a) Map of 3 ELAT bin model; (b) map of 3 CLAT bin model; (c) count distribution for 3 ELAT bins (map a); (d) count distribution for 3 CLAT bins (map b).

Experimental Analysis
Overwintering sites outside of California (U.S.) and Baja California (Mexico) were excluded, with 329 sites remaining. The data were then matched by Site ID with latitude coordinates provided by Emma Pelton of the Xerces Society (Figure 1). Sites were ordered latitudinally, from north to south, and grouped into latitude bins (to evaluate spatial correlations with occupancy; Figure 2). In preliminary groupings, these latitude bins were evenly sized according to the total latitude range of sites present in the dataset and named *<u>ELAT</u> bins* for <u>e</u>qual *<u>lat</u>*itude (Figure 2a). Analyses of the ELAT bins revealed that the data were distributed unequally across space such that models did not reach stationarity (see below), especially for bins at the extreme northern and southern latitudes. As seen in Figure 2c, a model with 3 ELAT bins resulted in a distribution with the overwhelming majority of counts in the central bin. The solution was to group the latitude bins according to the total number of counts (N = 3161) present in the entire dataset, creating *<u>CLAT</u> bins* named for <u>c</u>ounts-based *<u>lat</u>*itude bins (Figure 2b). This was achieved by shifting the latitudinal boundaries until each bin was approximately equal to the bin size (n) calculated as n = 3161 counts/number of bins. This ensured that the data were equally distributed across space and improved the likelihood that model estimates reached stationarity (Figure 2d). While the latitudinal cutoffs varied from model to model, the CLAT bins were still ordered sequentially from North to South and thus allowed for an analysis of the correlation of occupancy with space. Time bins (to evaluate temporal correlations with occupancy) grouped multiple years into single bins according to the number of counts and could thus similarly be approximated by the expression n = 3161 counts/number of bins. This grouping also ensured an equal distribution of data across time to promote the likelihood of estimate stationarity.



a b c d

Figure 3. Maps of CLAT bins of equal count distributions (each shown in a distinct color) depicting model designs containing (a) 2 bins, (b) 3 bins, (c) 4 bins, and (d) 5 bins. Maps depict a zoomed in segment of the California and Baja California coasts, including all sites present in the dataset (N=329).

Occupancy Modeling
Abundance values were converted to presence data in R 1.4.11. Occupancy models were constructed by combining various latitude and time bins, with every combination of 1-5 CLAT bins (Figure 3) and 1-2 time bins tested. The bins were then binarily encoded as

sample covariates and run in PRESENCE (MacKenzie et al. 2003). Occupancy probabilities (psi) were estimated for each CLAT bin, revealing potential spatial differences in the population distribution. Detection probabilities (p) were estimated for each time bin and used by PRESENCE to improve the accuracy of psi estimates. Models thus varied from a total of 2 parameters [(psi(.)p(.)] to 7 parameters [psi(5Clat)p(2time)]. PRESENCE was then utilized to perform model selection by calculating AIC scores and rank-ordering the models accordingly. All models that reached complete stationarity with a ΔAIC < 2.00 were selected and averaged by model weight (MacKenzie et al. 2003) to produce the final parameter estimates for psi and p.

RESULTS

Model selection results yielded three occupancy models for which the ΔAIC < 2.00 and all parameter estimates reached stationarity (Table 1). Stationarity was defined as a model in which no parameter estimates included confidence intervals of 0.00-1.00. One model with ΔAIC < 2.00 was excluded because the psi estimate for the southernmost latitude bin included such a confidence interval and thus did not reach stationarity.

Model	AIC	ΔAIC	AIC Wgt	No. Par.
Psi(.)p(2time)	3623.01	0.00	0.5579	3
Psi(3Clat)p(2time)	3624.74	1.73	0.2349	5
Psi(2Clat)p(2time)	3624.99	1.98	0.2073	4

Table 1. Model selection results. Model names describe the number and type of bins used for both psi and p. For example, model Psi(3Clat)p(2time) included 3 equal-counts latitude bins (North, Central, South) and 2 time bins (1997-2011 and 2012-2019). AIC scores represent the fitness of the model to the dataset, with ΔAIC depicting the difference in AIC scores between the model of interest and the top-ranking model. AIC Wgt displays the statistical weight that the model holds, which is related to the ΔAIC score, and is used to weight the estimates for a particular model when averaging multiple models.

Model	Lat bin(s)	psi(estimate) ± CI	Time bin(s)	p(estimate) ± CI
Psi(.)p(2time)	1	0.972 ± 0.052	1997 – 2011	0.793 ± 0.024
	-	-	2012 – 2019	0.678 ± 0.024
Psi(3Clat)p(2time)	1N	0.961 ± 0.052	1997 – 2011	0.793 ± 0.024
	2C	0.973 ± 0.052	2012 – 2019	0.679 ± 0.024
	3S	0.996*± 0.270	-	-
Psi(2Clat)p(2time)	1N	0.976 ± 0.052	1997 – 2011	0.793 ± 0.024
	2S	0.978 ± 0.052	2012 – 2019	0.678 ± 0.024

Table 2. Psi parameter estimates for model equal-counts latitude bins (CLAT) and p estimates for model time bins (1997-2011 and 2012-2019). Models differed by the number of CLAT bins with either the whole range pooled, north (N) and south (S) distinguished, or north (N), center (C), and south (S) distinguished. Confidence intervals noted are the maximum intervals for values in the column (e.g. all psi CIs ≤ value ± 0.052). One interval (*) was an outlier.

The psi estimates were relatively similar with overlapping confidence intervals (Table 2). Occupancy increased slightly from northern to southern latitude bins. However, southernmost bins were also the most likely to have confidence intervals that were either wide or did not reach stationarity. The confidence interval for the southern psi estimate of the psi(3Clat)p(2time) model was an outlier when compared to the other intervals, which reinforces the aforementioned pattern. P estimates were more disparate, with the early time bin (1997-2011) reliably producing a higher detection probability than the late time bin (2012-2019). Furthermore, the confidence intervals for p estimates were much tighter and did not overlap. Model averaged psi estimates (Table 3) were, as observed below, highly similar but increased from north to south. Averaged p estimates (Table 3) were disparate, with the early estimate being greater than the late.

Parameter	Bin	Value
psi	North	0.9704
	Central	0.9735
	South	0.9792
p	1997-2011	0.7934
	2012-2019	0.6783

Table 3. Model averaging results based on results in Table 2. Parameters included both psi and p, with both latitude (psi) and time (p) bins represented. Psi results averaged to three latitude bins—North, Central, and Southern—with three average psi estimates resulting. P results averaged to two time bins—early and late—with two p estimates resulting. Estimates were averaged according to the model weight.

DISCUSSION

The top models included between 1-3 equal-counts latitude bins and 2 time bins each, with no confluence of latitude and time bins. Psi estimates—both raw and averaged—and their confidence intervals were highly similar but did increase slightly from North to South. P estimates were higher for the early time bin (1997-2011) than the late time bin (2012-2019). The differences in estimated values for p are consistent with my predictions.

These results are somewhat inconclusive to my original questions. The psi estimates did not reveal large or significant spatial differences in occupancy. Furthermore, no models were able to test for changes in occupancy with time. These inconclusive results are largely due to the unequal distribution of data across both space and time and the large proportion of missing data. Of the 7567 potential observations (329 sites x 23 years), only 3161 have actually been counted; thus, 58.23% of the potential data is nonexistent. A majority of sites (53.22%) have been counted for less than 8 of the 23 potential years and only 33.36% have been counted for more than half of these years. The spatially unequal data distribution led to occupancy estimates that did not reach stationarity at the range extremes. This necessitated an expansion of latitude bins to ensure that all bins—especially those at the range extremes—included enough data to yield estimates that reached stationarity. When the total number of counts across the 23-year period are sorted by latitude, most of the data is located within the central coast between the 34.5 – 35.5 latitude range. The southern portion of the range, from 31.5˚ – 34.5˚ latitude, is particularly lacking in both counts and sites. This relative lack of data explains why the confidence intervals for psi estimates of southern bins were higher and often large enough to prevent estimates from reaching stationarity.

Additionally, there is a temporal disparity in the data distribution. The total number of sites counted per year is inconsistent, with most years prior to 2010 falling between 80-120 sites counted. In the last decade, this number has risen dramatically, peaking at 263 sites in 2017. However, this disparity in the number of sites counted across time presents a challenge for analysis. The lack of repeat counts within any given year mean that detection probabilities must be estimated across multiple years, which both confounds the attempt to find differences in occupancy between those years and restricts the ability to vary the detection probability across space and time (Mackenzie and Royle 2005). Furthermore, the addition of new sites in recent years inherently means that those sites have been counted few times and that those counts occur in the late time bin only. Thus, while the early time bin has fewer sites counted, those sites are counted more frequently and regularly. By contrast, the addition of sites with only a few counts increased the proportion of missing data in the late time bin, yielding a lower p estimate.

The trend for both psi estimates and the associated confidence intervals to be higher for southernmost bins is slight, and potentially interesting. It may be that the southern region indeed does display the highest occupancy. However, this result may be an artifact of the incompleteness of the dataset. The southern region lacked both sites and counts relative to the other regions, which may have given "present" observations a disproportionate influence upon the occupancy estimate. This may also be explained by the proclivity for sites in the central region to be counted the most frequently, which seemingly resulted in more absences being detected than in the southern region. Both may have resulted in the higher occupancy rates observed in the South. The detection probability is also likely an artifact of the recent addition of sites that were counted infrequently and nonconsecutively, reducing the p estimate in the late time bin.

While the results are inconclusive to my original questions, they are conclusive for occupancy modeling and the data required to perform such modeling. It is clear that datasets with large proportions of missing data and large disparities in its distribution are not suitable for fine-scaled occupancy modeling, as is the case with my analysis. This is evident in my inability to test models with >3 latitude bins and the inability to test for changes in psi across time. Furthermore, the gross amount of data is also highly important. For example, when initially trying to decrease the amount of missing data, I set a threshold number of counts per site and excluded sites below that threshold. However, that left too few sites for the analyses to reach stationarity. Thus, it is clear that an ideal dataset must be abundant, evenly distributed, and contain multiple counts per year or season.

Producing datasets with these qualities may be inherently difficult for citizen science projects, including the Western Monarch Thanksgiving Counts. Citizen science projects introduce human biases into the datasets and may have a proclivity to produce disparities in the distribution of data across its parameters (Mackenzie and Royle 2005). For example, the WMTC dataset reveals a clear bias towards counting sites in the central coast—where the monarchs are typically the most abundant—probably because it is more rewarding to count sites where there are likely to be thousands or potentially millions of monarchs. As a result, the WMTC will almost certainly continue to be unsuitable for occupancy modeling into the future and for performing the analysis I attempted.

These dataset challenges will be further exacerbated by decreases in the population size and predictability of western monarchs. In 2017, the Xerces Society added a second annual count to the Western Monarch Thanksgiving Count project that begins on New Year's Eve. This will improve the ability to estimate detection probabilities (Mackenzie and Royle 2005). However, given the current rate of population decline, it may already be too late for this change to enable crucial analyses that inform conservation efforts. Furthermore, the Western Monarch Thanksgiving Count will likely continue to produce data that is uneven in spatial and temporal distributions because of the natural human biases of its citizen scientists.

Similar challenges can be expected for insects at large as populations and species continue to decline rapidly. Spatial and temporal stochasticity will likely increase, particularly when populations cross the size threshold for Allee effects. This will make it more difficult to collect large datasets and to ensure that they are distributed evenly across the relevant parameters. Furthermore, population unpredictability reduces the likelihood that data collection efforts will be successful and may necessitate budgeting decisions to cut resources to particular populations or species. The challenges outlined above may drive a natural shift in data analyses away from occupancy modeling because of the strict requirements in the data attributes.

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