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Spatial and temporal dynamics of Batesian mimicry between Adelpha californica and Limenitis lorquini

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SPATIAL AND TEMPORAL DYNAMICS OF BATESIAN MIMICRY BETWEEN *ADELPHA CALIFORNICA* AND *LIMENITIS LORQUINI*

by

Louis A. Prusa

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SPATIAL AND TEMPORAL DYNAMICS OF BATESIAN MIMICRY
BETWEEN ADELPHA CALIFORNICA AND LIMENITIS LORQUINI

by

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Louis A. Prusa
DEDICATION

This thesis is dedication to my mentor Dr. Ryan I. Hill. He had faith in me and my abilities to conduct this long term project and to see it through to completion under his mentorship. Though it seemed daunting, Dr. Hill was there for support every step of the way.
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Spatial and temporal dynamics of Batesian mimicry between *Adelpha californica* and *Limenitis lorquini*

Abstract

by Louis A. Prusa

University of the Pacific
2018

Conspicuous coloration is one of the main ways that animals communicate. The use of eye-catching color patterns to warn predators of an unprofitable trait is referred to as aposematism. Once predators learn to recognize the color pattern, a new signaling niche becomes available where other species can share the same signal. This mimicry niche can involve a “hide in plain sight” strategy by mimicking or parasitizing this signal, with mimics lacking the defense and associated costs that make them unprofitable. This is termed Batesian mimicry, and it decreases predation by taking advantage of the memory and learning of the predator community. Thus, a primary prediction in Batesian mimicry systems is that the model and mimic are found in sympatry. Another, fundamental prediction of Batesian mimicry is that the model outnumbers the mimic and that models emerge before the mimics to educate the predator guild. Some of these patterns were not significant in the California Coast Ranges as seen in Long et al. (2015), and no study has
estimated population sizes for this temperate Batesian mimicry system. Furthermore, compared with community studies of mutualistic Müllerian mimicry in the tropics, no studies have tested predictions of parasitic Batesian mimicry on small scale patterns of habitat use and movement patterns. If mimicry is as an important part of the biology of these temperate species, as it is for their tropical counterparts, we predict that in addition to emerging first and being more abundant, the model and mimic will overlap strongly in habitat but the model will be more abundant in each habitat, and will move more and be more widespread among available habitats. Our results confirm these predictions and indicate that *A. californica* is effectively educating habitat specialist and generalist predators providing an umbrella of protection for the mimic *L. lorquini*. 
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Chapter 1: Introduction

Conspicuous coloration in animals is seen mainly in intra- and intersexual interactions, and in predator avoidance (Cott 1940, Edmunds 1974). Outside of sexual interactions, conspicuous color patterns were counter-intuitive to early naturalists that focused on the survival value of traits. For example, cryptic coloration (e.g. camouflage) was relatively intuitive because it reduces the probability of predator attack (Cott 1940). However, the benefit of using conspicuous coloration that seemingly advertises to predators was paradoxical (Joron and Mallet 1998). In time, naturalists accumulated evidence that these conspicuous color signals are used to warn predators of unprofitable defenses such as spines or chemical deterrents. E. B. Poulton clarified these syndromes and referred to the association between conspicuous coloration and unprofitability as aposematism (Poulton 1887).

Aposematic signals are thought to evolve in prey species as a defensive mechanism that efficiently educates predators (Cott 1940, Huheey 1964, Huheey and Brandon 1974, Huheey 1976, Kikuchi 2010, Kikuchi 2013, Kikuchi and Sherratt 2015, Joron and Mallet 1998, Mappes, Marples and Endler 2005, Mallet and Joron 1999). The more memorable and detectable the signals are, the better the prey are at educating the predator guild in an area. Unprofitable traits associated with the bright warning coloration include venom, toxins, or a bitter taste when attacked (Edmunds 1974). Some authors also include behavioral traits such as rapid flight and difficulty of capture as unprofitable
traits (Pinheiro and Freitas 2014, Mappes et al. 2005, Beccaloni 1997, Riipi et al. 2001). The strength of the aposematic signal depends on how distinctive the coloration is, as well as the potential profitability of the prey (Kikuchi 2010) due to the visual aspect of predation (Aubier and Sherratt 2015, Darst and Cummings 2006, Sherratt 2003).


Predators that are not risk averse and keep testing conspicuous prey lead to the question of how aposematic signals evolve. Aposematism is somewhat of a paradox because a bright and colorful signal is more easily detected and should lead to increased sampling and chance of damage or death (Joron and Mallet 1998, Lindström, Alatalo and Mappes 1997, Mallet and Joron 1999, Mappes et al. 2005). This leads to confusion on how an initially rare phenotype becomes a fixed color pattern among the population. The widely accepted theory is that the frequency and unprofitability of the prey, combined with varying levels of predator wariness can lead to the establishment of a new warning pattern (Mappes et al. 2005, Beccaloni 1997, Bond and Kamil 1998, Schuler and Hesse 1985).

Once an aposematic signal evolves and is learned by local predators, predation should be reduced on any individuals with the signal, whether the same species or not.
Thus, a benign organism resembling the protected species can gain protection. This is called Batesian mimicry, and is where a harmless species has evolved to emulate the phenotypic warning signals of the harmful or noxious model (Bates 1862). It is named after the English naturalist Henry Walter Bates after his work in the Amazon rainforests where he observed abundant, yet slow moving Ithomiini (Danainae, Nymphalidae) butterflies, were “protected by some unknown source” (Mallet 2001) from predators while dismorphine pierid butterflies mimicked these ithomiines. It was later found that the ithomiines are well-defended by sequestered chemicals that deter predation (Brown 1984b, Brown 1984a). Charles Darwin stated that “In [his] opinion [Bates’ paper on mimicry was] one of the most remarkable & admirable papers [Darwin] ever read in [his] life. The mimetic cases are truly marvelous” (letter to H. W. Bates, 24 November 1862).

Model and mimic dynamics in Batesian mimicry are considered parasite-like, as the mimic is not defended, but uses the model’s warning coloration to increase its’ fitness (Beccaloni 1997, Joron and Mallet 1998). The lack of an associated negative trait when attacking the mimic leads to confusion in the predator guild as they are able to attack and process non-defended prey that is similar looking to defended models. Despite this potential for a negative interaction, there is a selective advantage for a mimic to be mistaken for a less palatable form that they somewhat resemble (Huheey 1964). Mimicry theory depends on the visual acuity of the insect eating vertebrate predator guilds as well as memory as time passes between interactions with the prey (Lindström et al. 1997, Blough and Lacourse 1994, Mallet 1999).

In contrast to Batesian mimicry, Müllerian mimicry occurs when two or more defended species converge on a similar color pattern (Müller 1878). Müllerian mimicry functions as a mutualistic relationship because both species help each other by training
predators to avoid the common color pattern. Due to the variance in toxicity or bitterness of each species, labeling them as either Batesian or Müllerian is not always simple. There is in reality a spectrum of mimicry, rather than simply two categories (Huheey 1976, Mallet 1999, Mappes et al. 2005, Joron and Mallet 1998, Aubier and Sherratt 2015, Mallet and Joron 1999, Turner 1987, Kikuchi 2013, Kapan 2001). For example, when a putative Batesian mimic has some level of defense or noxiousness, it is not definitely Batesian or Müllerian, and has been suggested to be classified as quasi-Batesian (Rowland et al. 2010).

Mimicry has received much recent attention in investigations of color pattern genetics (Reed et al. 2011, Heliconius_Genome_Consortium 2012, Joron et al. 2006, Ferguson et al. 2010), ecological correlates (Hill 2010, DeVries, Lande and Murray 1999, Estrada and Jiggins 2002) and evolution of mimetic diversity (Joron and Mallet 1998, Mallet and Joron 1999, Kronforst and Gilbert 2007) and the link with mate choice (Kronforst et al. 2006, Kronforst and Gilbert 2007) and speciation (Jiggins 2008, Chamberlain et al. 2009). Most of this work focuses on tropical species involved in Müllerian mimicry, systems that are extremely rich in mimetic diversity. However temperate zone mimicry systems have been integral in testing not only the palatability of species in Batesian mimicry (Brower 1958, Brower and Brower 1962), but also predictions for the three fundamental ecological variables involved in predator learning that setup and reinforce mimetic interactions: time, abundance and space.

Time, abundance and space are essential aspects of any mimetic system because of the visual predators’ instinct, education, and learning, as well as faults in judgment (Mappes et al. 2005). In conditioning the predator guild, there is an ever evolving
dynamic of learning and forgetting (Turner and Speed 1999). Forgetting depends on the passage of time in many vertebrate predator models (Holling 1965). Thus, learning can be reinforced by early training with the model, more frequent encounters with the model overall, and encountering the model in a variety of different habitats.

With respect to timing of model and mimic, it is generally predicted that the model emerges earlier in the season than the mimic (Poulton 1890, Poulton 1887, Rettenmeyer 1970). By emerging earlier, a model is better able to educate the predators of the specific aposematic signal or color pattern that is associated with unpalatability or some other defense, allowing the mimic to effectively parasitize the model’s signal (Bobisud 1978, Huheey 1980b). This prediction had generally been confirmed and after learning that the specific signal is associated with a defense, predators are more wary and less risk taking towards any organism with that color pattern (Darst and Cummings 2006, Lindström et al. 1997, Pough 1970, Pough et al. 1973). In a slight twist on the model-first predictions, Waldbauer & Sheldon (1971) in their investigations on hymenopteran/dipteran mimetic systems, noted “…that certain Batesian mimics emerged early in the spring, relying upon the education of predators by the previous year’s protected models and thus avoiding the losses associated with ‘teaching’ the current cohort of fledglings”.

In considering relative abundance of model and mimic in Batesian mimicry systems, it is predicted that the model is highly abundant so the predator guild learns the link between signal and defense (Lindström et al. 1997, Huheey and Brandon 1974, Huheey 1964, Holling 1965, Joron and Mallet 1998, Kikuchi and Pfenning 2009). For the mimic to be well-protected, the model needs to outnumber the mimic so that the link
between signal and defense speeds up the “predator [guild’s] conditioning” (Turner and Speed 1999). If the mimic becomes too common, the signal loses effectiveness and this noise may lessen the protection offered by the aposematic color pattern. This can extend to Müllerian mimicry as well. Mallet & Joron (1999) discuss how in certain mimicry systems, “a rare species ultimately gains far more from mimicry than a common one (in proportion to the square of the ratio of abundances)”. They also state that “a novel mimetic variant in the rarer species resembling the commoner is always favored because the common species generates greater numerical protection, while a mimetic variant of the commoner species is always disfavored because it loses the strong protection of its own kind and gains only weak protection from the rarer pattern” (Mallet and Joron 1999, Pough 1970, Pough et al. 1973). Related to this is the fact that yearly abundances are variable due to biotic and abiotic factors, and as a result “the nature of the mimetic relationship can be variable in time and space; it is ‘contextually defined’” (Joron and Mallet 1998).

An integral part of mimicry is the spatial overlap of model and mimic (Brower and Brower 1962, Brower 1960, Joron and Mallet 1998, Mallet and Joron 1999), but studies rarely examine space at smaller scales. Many studies have investigated geographic distributions of model and mimic at large spatial scales. For example, in a study involving a Battus philenor model with its mimics, Brower (1958) investigated how “in this North American complex of butterflies there are several ways which mimicry is strongly correlated with the geographic distribution of the model”. Studies have generally found that the benefit to the mimic correlates with presence of the model (Brower 1960, Huheey 1980a, Pfenning, Harcombe and Pfenning 2001, Lindström et al.
However, few mimicry studies have looked at the dynamics of abundance at smaller spatial scales. Visual predators that remain in a specific area rely on multi-trial frequency dependent learning for efficient predation (Bobisud and Potratz 1976, Blough and Lacourse 1994, Pough et al. 1973). Therefore, although overall abundance is important, this should also extend to each habitat in an area, or habitat specialist predators may experience an uninformative relative abundance. The more frequent the model is in each habitat, the less chance for generalist predators, or the local predators in each habitat, to forget the negative association as time passes (Pough 1970). This predicts that the model species should be relatively more widespread across various habitats in order to educate generalist predators that may be sampling prey in multiple habitats (Harper and Pfenning 2007). Furthermore, the mimic should be relatively more constrained to the habitats where it specializes (Prudic et al. 2002, Estrada and Jiggins 2002).

Recent work on a temperate zone putative Batesian mimicry system in California has confirmed the predictions for time and abundance, but spatial aspects remain to be studied. In this system Adelpha californica (Butler, 1865) has been shown to be unpalatable to Western Scrub jays Aphelocoma californica but the similar looking Limenitis lorquini (Boisduval 1852) was not (Prudic et al. 2002, Prudic et al. 2007). Thus it is hypothesized that this is a Batesian mimicry system with A. californica is a model for the mimic L. lorquini. To investigate whether predictions for Batesian mimicry are upheld for this system, Long et al. (2015) studied a long term data set of transect counts at three locations, one in the Coast Ranges (Gates Canyon) and two in the foothills of the Sierra Nevada (Washington and Lang Crossing). Consistent with predictions for Batesian
mimicry, they found that *Adelpha californica* emerged earlier at two of the three sites and was more abundant at all three sites when compared to *Limenitis lorquini*.

This study seeks to further elucidate the Batesian relationship between these two temperate butterfly species, *Adelpha californica*, and *Limenitis lorquini*. There are relatively few mimetic complexes studied in populations of Northern California butterflies (Sheppard 1959), few field-based tests of Batesian mimicry theory (Jeffords et al. 1979; Hetz and Slobodchikoff 1988; Winand et al. 1993; Pfennig et al. 2001, 2007; Howarth et al. 2004; Rashed and Sherratt 2007; Finkbeiner et al. 2017) and even fewer have tested predictions with mark release recapture (MRR). This perspective leads us to ask if differences in time, differences in relative abundance, and differences in habitat use and movements are typical of this Batesian system in the California Coast Ranges.

The study presented here adds several new aspects to previous work. Long et al. (2015) investigated a site in the Coast Range and although they did confirm a relatively more abundant model, they did not find a significant difference for early emergence of models. Therefore we conducted a weekly transect survey to investigate whether the model emerges before the mimic. In addition, Long et al. (2015) used long-term transect counts over three decades to assess relative abundance differences. A potential limitation of this approach is if the model and mimic differ in detectability. It is well-known that aposematic species behave more conspicuously by feeding in groups or exposed on leaf tops (Riipi et al. 2001, Poulton 1887, Sillen-Tullberg 1988, Lindström, Alatalo and Mappes 1999). If this extends to models compared to mimics, the models may be counted more often because of conspicuous behavior rather than abundance. In addition, there is the possibility of double counting individuals. Finally, as mentioned above no studies
have examined fine-scale population level differences between model and mimic, which we do to document habitat use and movement differences.

Using field investigations at two adjacent study sites in the southern California Coast Range, we set out to test the predictions of Batesian mimicry, regarding the dynamics of timing, the relative and absolute abundance, the use of habitat and movement differences between the model *A. californica* and mimic *L. lorquini*. To address the concerns about counts we conducted a MRR capture study along with transect counts, and we analyzed GPS data from each individual captured to examine spatial differences and movements of the model and mimic. We predict that *A. californica* will emerge earlier in the season and show not only higher relative abundance in counts, but also larger population sizes. It has been hypothesized that the model genus *Adelpha* is thought to be a food generalist due to its wide range of habitats (Prudic et al. 2002, Prudic, Warren and Llorente-Bousquets 2008). Following this and the logic that a more widespread model better trains the predator community, we predict that the model will be more widespread in both horizontal and vertical dimensions, and will also move more as a result of the wider habitat use.
Chapter 2: Materials and Methods

Study Sites and Sampling

This study took place in two East Bay Regional Parks in Alameda county, California. The first and main location was in Camp Ohlone Regional Park (37.51514; -121.83117) (Figure 1A). Camp Ohlone had minimal human disturbance during the study period because it has been closed off from regular park visitors for the past 10-15 years. The park is comprised of a valley with steep hills on both sides. At the bottom of the valley is Alameda creek. Along this creek there is surrounding riparian habitat with adjacent meadows and an abandoned black walnut *Juglans californica* (Watson) orchard. Alameda creek fluctuates greatly from year to year, and typically dries up by late July-early August except for a few isolated pools of water. The slopes along Alameda creek have extensive oak woodlands consisting of blue oaks, *Quercus douglasii* (Hook & Arn), coast live oak *Quercus agrifolia* (Née) and valley oak *Quercus lobata* (Née). The slopes also have small drainages with seasonal creeks. In Camp Ohlone a mark-recapture study with aerial nets and baited traps was conducted four days per week during May-August 2015, following an approximately 3.95 km long transect route that linked the trap sites.
Figure 1. Study sites. (A) Camp Ohlone Study Area. Satellite imagery showing the study area in Camp Ohlone, Alameda County, California. (B) Sunol Transect. Satellite imagery showing the transect route in Sunol Regional Wilderness Area, Alameda County, California. Sites are separated by about five miles.
The second study location was in the lower portion of Sunol Regional Wilderness Area (37.48973; -121.74577). Sunol is open to the public and is a mixture of slopes with oak woodlands, small seasonal drainages, and meadows, with valley bottom riparian habitat and more dense oak woodlands along Alameda creek. In Sunol a fixed transect route of approximately 6.83km along established trails and roads (Figure 1B) was surveyed one day per week from March 1, 2015 through November 22, 2015. Each day on this transect survey, butterflies were site identified, or netted and marked. Start and end dates for the Sunol transect were chosen to be before and after any adult butterflies were present in order to highlight both temporal dynamics and relative abundance.

In addition to the aerial netting and transect counts, a standardized bait trapping study was conducted in Camp Ohlone to supplement aerial captures and sightings. The trapping took place in Camp Ohlone using 32 trap sites arranged evenly among available topography (slope and valley floor) and habitats (riparian, woods/woodland edge, seasonal creek and meadow). Each trap site had an understory trap (average height = 1.0m, s.d. = 0.3m) as well as a canopy trap (average height = 9.4m, s.d. = 2.4m). Two bait types were used to maximize captures. Even numbered traps were baited with a three-day old mix of fermented banana that was replaced in the middle of the week. Odd numbered traps were baited with two-week old fermented shrimp that was replaced as needed to keep bait moist and aromatic.

We collected the following information for captured or sighted butterflies in Sunol and Camp Ohlone. All individuals that could be positively identified were assigned to a topographical category (slope or valley), or to one of five different habitats: riparian, woods, woods edge, meadow, and seasonal creek. Riparian was defined as densely shaded and wooded forest habitats within 10m of Alameda creek. Woods were defined as
the oak dominated forest areas on the slopes or valley floor away from Alameda creek. The woods edge was the border of oak woods, and operationally defined as being within 5m of continuous woods. The meadow habitat was defined as an open area with grasses, greater than 5m from the riparian or woods edge. Finally, the seasonal creek habitat was defined as the smaller drainages on the slopes that were covered in more dense vegetation than adjacent woods. California Bay Laurel (*Umbellularia californica*, Hook & Arn), Poison Oak (*Toxicodendron diversilobum*, Torr. & A. Gray), and occasionally the arroyo willows (*Salix lasiolepis*, Benth) were present in the seasonal creeks. During the dry season these drainages remain cooler due to the increased shade and small springs, but otherwise only have consistent water during the winter rainy season. Butterflies caught in traps were assigned the topography and habitat category for that trap. Height where first seen was recorded for sightings and aerial captures, with trap height used for trapped individuals. Notes on behavior such as puddling, basking, chasing, perching were also recorded.

Individuals caught in aerial nets or traps were marked and we recorded the following additional data: age, presence of mark, and sex. Age was determined by the amount of wear on the wings of the captured butterflies. We utilized a 1-5 scale with increments of 0.5 to age the individuals, with 5 being the most tattered, and therefore oldest, butterflies. Sex was determined by examining genitalia as well as forelegs, which are sexually dimorphic in nymphalids (see p. 16 Scott 1986, see p. 13 Neild 1996). On each captured individual a unique number was written with fine-tipped Sharpie marker on the underside of the hindwing. Marks were in an inconspicuous place near the wing base to decrease the possibility of marks affecting survivorship. All field data were recorded in
a waterproof notebook, and following a day of capture, the data were entered into a spreadsheet.

**Temporal, Relative Abundance and Population Size Analysis**

To investigate emergence dates and relative abundance from the Sunol transect, I examined bar graphs to compare the number of model and mimic per sample day throughout the flight season (one sample day per week). The relative abundance of model and mimic on the Sunol transect was assessed using sighted and netted butterflies.

Population size was estimated using the mark-recapture data in Camp Ohlone. Jolly-Seber (JS) POPAN open population models were implemented in program MARK (White and Burnham 1999). To compare models we used AICc scores with significantly better model fit determined by delta AICc score of > 2. We compared models with time constant and time dependent \( \phi, p, \text{pent}, \gamma’, \gamma” \) and \( N \) in different combinations to find the best fitting model. The parameter \( \phi \) is survivorship probability, \( p \) represents catchability, with \( \text{pent} \) representing the probability of entering the study area. The parameters \( \gamma’ \) and \( \gamma” \) represent the probability of immigration and emigration respectively, with \( N \) being population size. Time constant models were denoted with a “.” as opposed to time dependent, denoted with a “t”. Time dependent models give parameter estimates for each week, whereas time constant give parameter estimates overall. For the parameter \( p \) we used the Logit link function, and for \( \text{pent} \) we used a separate MLogit link function (MLogit1 or MLogit2) for each attribute group (i.e. species). Finally we used the Log link function for the population size \( N \). In addition to including time dependence, we started with a model combining all individuals into one population to test whether grouping the data into two populations improved model fit.
This effectively tested whether model and mimic were different populations with separate demographic parameters.

**Habitat, Topography, Flight Height, and Movement Analyses**

To test two null hypotheses about the distribution of *A. californica* and *L. lorquini* in both Sunol and Camp Ohlone between the five habitat categories (riparian, woods, woods edge, meadow and seasonal creek) we used Chi-square tests. The first null hypothesis tested was that *A. californica* and *L. lorquini* were distributed equally between each habitat category. The second null hypothesis was that *L. lorquini* individuals were found in the same frequency across the five habitat categories as *A. californica*. The chisqr.test() function in R (R_Development_Core_Team 2016) was used with vectors of the observed and expected values. For the second null hypothesis the expected values were the fraction of *A. californica* in each category multiplied by the total number of each species. This allowed a direct test of whether *L. lorquini* individuals were distributed the same as *A. californica*.

To test two null hypotheses about the distribution of *A. californica* and *L. lorquini* in both Sunol and Camp Ohlone between two topographical categories ("valley" and "slope") we used Chi-square tests. The first null hypothesis tested was that *A. californica* and *L. lorquini* were distributed equally between "valley" and "slope". The second null hypothesis was that *L. lorquini* individuals were found in the same frequency in "valley" and "slope" as *A. californica*. For the second null hypothesis, the expected values were the fraction of *A. californica* in each category multiplied by the total number of each species. This allowed us to directly test whether *L. lorquini* individuals were distributed the same as *A. californica*. 
Data for individuals marked and recaptured in both the Sunol study area and Camp Ohlone were used to estimate movement differences between model and mimic. GPS data for each capture event for individuals that were recaptured at least once were used to calculate distance between captures. Calculations were obtained with R statistical software (R_Development_Core_Team 2016) using the haversine formula to incorporate the Earth’s curvature. Distance between capture events were used to analyze single movement and lifetime movements (the sum of all single distances for each individual), for both model and mimic. We used a Wilcoxon test (wilcox.test() in R) to test the null hypothesis of no difference in single movements and lifetime movements between *A. californica* and *L. lorquini*.

Movement probability for each species was estimated by fitting the inverse power function (IPF) and the negative exponential function (NEF) (Hill, Thomas and Lewis 1996, Konvička et al. 2005) to the observed data. The IPF function \( I_{\text{IPF}} = C \cdot D^{-n} \) and NEF function \( I_{\text{NEF}} = a \cdot e^{-kD} \) express the probability density \( I \) of movements to distances \( D \) in kilometers. To compare models and estimate the values of the parameters \((a, k, C, \text{ and } n)\), each function was fitted by maximizing the sum of log likelihoods of predicted \( I \) at distances \( D \) ranging from 0.1 km to 3.5 km, incorporating the range of observed distances moved. Model selection was based on AICc values where a difference in AICc value greater than two indicated a better fit (R_Development_Core_Team 2016). Analyses were done with the Solver function in Microsoft Excel. Differences in the slopes for the best fitting model of each species were tested in Excel by calculating the linearized slopes, \( \ln C - n \cdot (\ln D) \) for IPF, and \( \ln a - kD \) for NEF, and their standard errors and comparing 95% confidence intervals.
To examine flight height differences between model and mimic, we used capture data from the bait traps as well as all available height data recorded from sightings and aerial net captures in Sunol and Camp Ohlone. Height of each trap where captured was used for individuals found in traps, with height first seen used for sightings and aerial net captures. The trap data help protect against bias associated with ground based observations in the height analysis. Because there were large numbers of observations below 1m for both species when they were puddling along Alameda creek for nutrients, available nitrogen, or salts (Beck, Muhlenberg and Fielder 1998), we only analyzed observations >1m to avoid a downward bias in the height distributions. Differences between model and mimic in their capture frequency in understory and canopy were tested using two Chi-square tests. First the null hypothesis that each species was found equally in understory and canopy was tested. Second the null hypothesis that *L. lorquini* individuals were distributed the same as *A. californica* was tested, with expected values being the fraction of *A. californica* in each category multiplied by the number of each species. For the height first seen data >1m, a Wilcoxon test was used to test the null hypothesis of no difference in height distributions between model and mimic.
Chapter 3: Results

Temporal Patterns, Relative Abundance and Population Size

The weekly transect counts in Sunol illustrated strong differences in relative abundance and emergence date between model and mimic (Figure 2). The model *A. californica* emerged six weeks earlier, and was seen without *L. lorquini* present for eight weeks later into the fall. *Adelpha californica* was also more abundant on every sampling day in Sunol.

The mark release recapture dataset in Camp Ohlone indicated clear differences in abundance and provided a robust sample for estimating population sizes, especially for male. In total, 591 *A. californica* were marked and 59 individuals of both sexes were recaptured (Table 1). A total of 118 *L. lorquini* were marked with 48 recaptures between the sexes. Thus, the recapture rate for *A. californica* was lower (10% recapture rate), compared to that of *L. lorquini* (45.9% recapture rate). Males of both species have higher recapture percentages than females, with 11% for *A. californica* males and 6.8% for females, versus 46% for male *L. lorquini* males and only 15% for females (Table 1).
Figure 2. Weekly abundance of model and mimic over time. *A. californica* was more abundant on all sampling days, emerged earlier in the season and lasted longer into the fall.
Model based population size estimates clearly indicated *A. californica* was more abundant than the mimic *L. lorquini*. Comparative analysis of different population models indicated that grouping *A. californica* and *L. lorquini* as a single population was a poor fit to the data (model indicated in the bottom row of Table 2). This result indicates the two species have different abundance and demographic parameters. Definitions of tested models are indicated in Table 2 with the best fitting model in the top row.

The model with the lowest AICc and the most realistic estimates was \([\text{phi(g*t)p(g*.pent(g*t)N(g*.ParmLogitMlogit12)}]\). The estimated abundance of male *A. californica* for the best fitting model is 5345 individuals (lower 95% C.I. = 4097, and upper 95% C.I. = 7036). The estimated abundance of *L. lorquini* is 267 individuals (lower 95% C.I. = 217, and upper 95% C.I. = 342). These model estimates for males only, coupled with \(N = 591\) total marked individuals of *A. californica* and \(N = 118\) total marked individuals of *L. lorquini* clearly demonstrate that the model species was more abundant.
Table 1. Jolly-Seber POPAN (JSP) models. The bottom row is the model with *A. californica* and *L. lorquini* grouped together.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>Delta AICc</th>
<th>Num. Par</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>{phi(g^t)p(g^t)pent(g^t)N(g^t)}ParmLogitMlog12</td>
<td>1880</td>
<td>31</td>
<td>96</td>
<td>-3964</td>
</tr>
<tr>
<td>{phi(g^t)p(g^t)pent(g^t)N(g^t)}ParmLogitMlog12</td>
<td>1891</td>
<td>31</td>
<td>136</td>
<td>-4040</td>
</tr>
<tr>
<td>{phi(g^t)p(g^t)pent(g^t)N(g^t)}ParmLogitMlog12</td>
<td>1917</td>
<td>56</td>
<td>164</td>
<td>-4097</td>
</tr>
<tr>
<td>{phi(g^t)p(g^t)pent(g^t)N(g^t)}ParmLogitMlog12</td>
<td>1955</td>
<td>94</td>
<td>50</td>
<td>-3760</td>
</tr>
<tr>
<td>{phi(t)p(t)pent(t)N(t)}ParmLogitMlog12</td>
<td>2320</td>
<td>460</td>
<td>95</td>
<td>-3502</td>
</tr>
</tbody>
</table>

Table 2. Camp Ohlone MRR summary data.

<table>
<thead>
<tr>
<th></th>
<th>individuals marked</th>
<th>individuals recaptured</th>
<th>total capture events</th>
<th>% individuals recaptured</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male <em>A. californica</em></td>
<td>444</td>
<td>49</td>
<td>499</td>
<td>11%</td>
</tr>
<tr>
<td>Female <em>A. californica</em></td>
<td>148</td>
<td>10</td>
<td>162</td>
<td>7%</td>
</tr>
<tr>
<td>total <em>A. californica</em></td>
<td>592</td>
<td>59</td>
<td>661</td>
<td>10%</td>
</tr>
<tr>
<td>Male <em>L. lorquini</em></td>
<td>98</td>
<td>45</td>
<td>199</td>
<td>46%</td>
</tr>
<tr>
<td>Female <em>L. lorquini</em></td>
<td>20</td>
<td>3</td>
<td>23</td>
<td>15%</td>
</tr>
<tr>
<td>total <em>L. lorquini</em></td>
<td>118</td>
<td>48</td>
<td>222</td>
<td>41%</td>
</tr>
</tbody>
</table>
Spatial Analyses

Habitat and Topography Analysis of topographical distribution and habitat use indicated broad overlap, but also highlighted clear differences between Adelpha californica and L. lorquini distribution. Adelpha californica was more abundant than L. lorquini in every topographical category and habitat in Camp Ohlone (Figure 3 and Table 3) as well as in Sunol. However, for both A. californica and L. lorquini the null hypothesis that the species were found in equal frequency in the two topographical categories ("valley" and "slope") was rejected in both Camp Ohlone (Adelpha X² = 1498.3, df = 1, p < 0.00001; Limenitis X² = 389.1, df = 1, p < 0.00001) and in Sunol (Adelpha X² = 159.5, df = 1, p < 0.00001; Limenitis X² = 40.3, df = 1, p < 0.00001).

Both species were found much more frequently in the "valley" topographical category (see Table 3 and Figure 3, 4 & 5). Furthermore, the null hypothesis that L. lorquini was found in "valley" and "slope" in the same frequency as A. californica was rejected in both Camp Ohlone (X² = 37.5, df = 1, p < 0.00001) and in Sunol (X² = 5.4, df = 1, p < 0.02). Adelpha californica was found much more often on the slopes compared with L. lorquini (Table 3 and Figure 3, 4 & 5).

Although A. californica may be more abundant than L. lorquini in each of the five habitat categories, the percentage habitat use indicated differences between the species. Adelpha californica is not distributed equally among the five habitat categories in Camp Ohlone (X² = 4117.4, df = 4, p < 0.0001) or Sunol (X² = 395.2, df = 4, p < 0.0001).

Limenitis lorquini is also not distributed equally among the habitat categories in Camp Ohlone (X² = 611.6, df = 4, p < 0.0001) or Sunol (X² = 100.5, df = 4, p < 0.0001). Furthermore the null hypothesis that L. lorquini is distributed among the habitat
categories in the same frequency as *A. californica* was rejected for both Camp Ohlone ($\chi^2 = 226, df = 4, p < 0.0001$) and Sunol ($\chi^2 = 11.0, df = 4, p < 0.026$).

Table 3. Habitat use breakdown for the model and mimic species in Camp Ohlone.

<table>
<thead>
<tr>
<th>microhabitat category</th>
<th>Adelpha (N)</th>
<th>Adelpha (%)</th>
<th>Limenitis (N)</th>
<th>Limenitis (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>riparian</td>
<td>1908</td>
<td>67.9%</td>
<td>296</td>
<td>63.9%</td>
</tr>
<tr>
<td>seasonal creek</td>
<td>322</td>
<td>11.5%</td>
<td>4</td>
<td>0.9%</td>
</tr>
<tr>
<td>woods</td>
<td>337</td>
<td>12.0%</td>
<td>36</td>
<td>7.8%</td>
</tr>
<tr>
<td>woods edge</td>
<td>184</td>
<td>6.5%</td>
<td>99</td>
<td>21.4%</td>
</tr>
<tr>
<td>meadow</td>
<td>60</td>
<td>2.1%</td>
<td>28</td>
<td>6.0%</td>
</tr>
<tr>
<td>total (sights and marks)</td>
<td>2811</td>
<td></td>
<td>463</td>
<td></td>
</tr>
</tbody>
</table>

Figure 3. Topographical use breakdown for model and mimic in Camp Ohlone. The bar graph shows % of each species in the topographical category with exact values as fractions indicated in parentheses. Above each bar is the number of individuals recorded in the category (=N). Note that *Adelpha* outnumbers *Limenitis* in both, but the relative use of the categories differs between the species.
Figure 4. Map of Sunol with marks/sightings for model *A. californica* (A) and mimic *L. lorquinii* (B). The asterisk is the Sunol visitors center. Note the increased number of observations up the small drainages and slopes for *A. californica*.
Figure 5 Map of Camp Ohlone with marks/sightings for model *A. californica* (A) and mimic *L. lorquini* (B). The asterisk is the old Ranger station in the valley near Alameda creek. Note that most sightings and captures were along Alameda creek, with increased numbers of observations for *A. californica* on the slopes and small drainages.
Travel Distances (Single movement distances vs. Lifetime cumulative distances)

The average of *A. californica* single movement distances was 0.324 km (s.d. = 0.471), whereas for *L. lorquini* it was 0.147 km (s.d. = 0.181). The single movement distances of

![Figure 6. Single movement distances for model and mimic. Movement distances in *A. californica* (A) and *L. lorquini* (B) in Sunol Regional Wilderness and Camp Ohlone. The IPF function was best fitting for *A. californica* and NEF function best for *L. lorquini.*](image-url)
Adelpha californica were significantly larger than L. lorquini’s (Wilcoxon W = 5417.5, p = 0.02) (Figure 6). However lifetime movements were not different (Wilcoxon W = 1996, p = 0.66), with average A. californica lifetime movement distances equal to 0.38 km (s.d. = 0.57), and L. lorquini’s equal to 0.30 km (s.d. = 0.26).

For A. californica the fatter-tailed IPF function (AICc = -47.9) was a much better fit than NEF (AICc = -38.7) in Figure 6. In contrast, for L. lorquini the NEF function (AICc = -32.8) was a much better fit than IPF (AICc = -12.2). The linearized slope of the IPF function for A. californica (-0.76, SE = 0.11) was significantly different (p < 0.05 based on non-overlapping 95% confidence intervals) compared to that of the NEF function for L. lorquini (-2.9, SE = 2.0 x 10^{-16}), indicating significant differences in dispersal between model and mimic. Movement probability based on the best fitting model indicated strong differences between species with a probability of moving 3 km estimated at 0.058 for A. californica but only 0.00017 for L. lorquini (Table 4).

Table 4. Movement probabilities for model and mimic for their best fit model.
**Flight Height** We predicted that the generalist model A. californica flies higher than L. lorquini, based on field observations coupled with each trap capture. Based on the trap study data including both sexes as well as both bait types, it was found that A. californica was found significantly more in the understory than canopy (X² = 11.6, df = 1, p = 0.0006), N = 16 canopy, N = 42 understory). L. lorquini was trapped less often and showed no difference between canopy (N = 6) and understory (N = 8) (X² = 0.29, df = 1, p = 0.60). However, when comparing the two species directly, the null hypothesis of L. lorquini having the same proportion of canopy and understory as A. californica is accepted (X² = 1.6, df = 1, p = 0.20), indicating they overlap and do not differ in vertical distribution.

Analysis using height first seen for all captures and sightings “>1m” from both study sites (Sunol + Ohlone) indicated no difference between species (Wilcoxon rank W = 292560; p = 0.24). The mean height first seen of A. californica was 2.59m and the mean height first seen of L. lorquini was similar at 2.38m (Figure 7).
Figure 7. Flight height histograms for model *A. californica* (A) and mimic *L. lorquini* (B).
Chapter 4: Discussion

With any defensive coloration and associated visual niches, it is important to think from the perspective of both the prey and the predator. Learning is linked to memory as well as faults in decision making which can occur in predator-prey interspecific interactions (Turner, Kearney and Exton 1984). The choice of food and risk taking by the avian predator may be made through instinct, or through the results of knowledge gained over its lifetime (Brower and Brower 1962, Brower and Brower 1965, Lindström et al. 1997, Pough 1970, Pough et al. 1973, Mappes et al. 2005).

In considering the interactions between predator and prey in mimicry, three major components must be considered in how they educate the predator guild. These can be independent from one another, but they can also strongly interact. The first component, time, involves the predator interacting with the model before the mimic in order to learn about the negative traits associated with a specific color pattern (Huheey 1980b, Long et al. 2015, Bobisud 1978, Waldbauer and Sheldon 1971, Waldbauer, Sternburg and Maier 1977). The second component is abundance of the model relative to the mimic. Higher relative abundance of the model leads to regular reinforcement of the negative interaction with the model for the predator guild (Huheey and Brandon 1974, Huheey 1964, Lindström et al. 1997). The final component in educating the predator guild to the link between the model’s signal and the specific negative reaction is the spatial dynamic in which the model is present in the same spaces as the predators. A widespread model will
interact with both habitat specialist and generalist predators, to broadly train the predator guild. These three mechanisms are inextricably linked with the fundamental patterns of Batesian mimicry.

In line with prior literature on Batesian mimicry which predicts that the model emerges first (Bobisud 1978, Beccaloni 1997), we observed a strong pattern of this in the field (Figure 2). *Adelpha californica* was detected a full six weeks before any of the mimics were observed in our Sunol transect. By emerging earlier, the model species can effectively teach the various fledgling avian insectivorous predators of this novel specific aposematic signal (Pfenning and Mullen 2010, Huheey 1964, Huheey and Brandon 1974, Kikuchi and Sherratt 2015, Kikuchi 2010, Beccaloni 1997, Darst and Cummings 2006, Mallet and Joron 1999, Holling 1965, Mappes et al. 2005, Ohsaki 1995). These fledgling predators will see the model earlier in the season. The model-first prediction was also tested for this mimicry system in California at three sites over a long term data set (Long et al. 2015). In their paper, Long et al. (2015) detected significant differences in first flight date (*p* < 0.001) with the model appearing 4.6 and 15.5 days earlier than the mimic at two sites in the foothills of the Sierra Nevada, Washington and Lang Crossing respectively. However, in the Coast Range at Gates Canyon the model emerged an average of 3.6 days earlier, but it was not significant (*p* = 0.31, Long et al. 2015). Thus by comparison, our study documented a very large model-first pattern, and demonstrates that the model emerges first in the Coast Range as well as the foothills of the Sierra Nevada.

Differences in the emergence of model and mimic observations between our study and Long et al. (2015) could involve many reasons, three of the most likely of which are discussed here. First, the Long et al. (2015) data set was over 30+ years and so the one to two week model-first pattern they detected, compared to our six weeks, could be the
result of particular weather and abundance dynamics at our study site in the single season we studied versus long-term averages. Second, habitat differences among sites may favor increased abundance of mimic relative to model, for example if there is more willow habitat than oak habitat, and this could reduce observations of model relative to mimic. In central California, *A. californica* is present at low elevation valley floor sites, but in very low numbers (Shapiro & Manolis, 2007, Hill and Prusa pers. obs.). Third, differences in behavior between model and mimic interacting with abundance could skew first flight date results. In our experience *L. lorquini* are less apparent than *A. californica* at some sites owing to their tendency to fly among dense willows compared to along the edges of oaks (Prusa pers. obs.).

In addition to the clear “model-first” dynamic documented in the Sunol Regional Wilderness Area and in the research by Long et al. (2015), we also found a strong pattern of “model-last”. Figure 2 clearly shows that *A. californica* is present longer into the early autumn months in this study. Further observations in this area in 2016 and 2017 also confirm this pattern (Hill and Prusa, pers. obs.). Essentially, the model remains on the wing educating the local predators about the aposematic signal, long after the mimic population has waned. To our knowledge, there have been no studies documenting a “model-last” phenology for butterflies (see (Waldbauer and Sheldon 1971) for a Diptera/Hymenoptera example). This would be an interesting pattern to investigate further given that it 1) keeps reinforcing the learned signal for resident bird predators, and 2) provides training for birds migrating through from other areas. Both of these types of predators would interact with the model last in the fall and interact with the model first in spring.
Our study strongly confirmed predictions regarding model mimic abundance (Huheey 1976, Huheey and Brandon 1974, Holling 1965, Lindström et al. 1997). *Adelpha californica* had higher relative abundance across every sample day in Sunol as seen in Figure 2. Mark recapture estimates in Camp Ohlone confirm relative abundance results showing that many more unique individuals were captured and marked for *A. californica* than for *L. lorquini* (Table 1), and population size estimates were different by an order of magnitude with $N = 5345$ for *A. californica* and $N = 267$ for *L. lorquini*. The higher relative and absolute abundance of models acts to frequently remind, or re-teach the predator about the negative stimuli associated with the color pattern (Bobisud and Potratz 1976, Pfenning et al. 2001, Lindström et al. 1997, Rashed and Sherratt 2007, Darst and Cummings 2006, Ries and Mullen 2008).

The mark recapture estimates are robust and correlate with movement differences between the model and mimic. *Limenitis lorquini* individuals were recaptured much more often (41%) than *A. californica* (approx. 10%), leading to relatively narrower confidence intervals and better estimates of population size for the mimic. However the model species was so much more abundant based on uniquely marked individuals that even with lower recapture rates and wider confidence intervals, the model was clearly more abundant by hundreds and hundreds of individuals. The difference in recapture rates between model and mimic correlate well with our movement results. The higher recapture rate for the mimic is another indication that the mimic moves much less than the model (Figure 6).

The higher relative and absolute abundance of models found in this study combined with the higher relative abundance of models found in Long et al. (2015) indicates that this is a general trend across several study sites, including the California
Coast Ranges and foothills of the Sierra Nevada. Although year to year differences may occur in the relative population sizes of the model and mimic (Beccaloni 1997), given the sheer abundance of these species it does not seem very likely that the model and mimic abundance patterns would have a high probability of switching for a long period of time at sites with appropriate habitat. Interestingly, at Lodi Lake in the Central Valley of California, *L. lorquini* greatly outnumbers *A. californica*, as it may do in other low elevation valley populations (Shapiro and Manolis 2007) and the mimic has a reduced survivorship there compared with in Camp Ohlone (Kristiansen et al. in review). Thus, one outcome of a reversed model-mimic abundance pattern is reduced survivorship of the mimic, but abundance differences impacting the mimic may be buffered by the temporal (i.e. model-first and model-last), and spatial/movement differences (i.e. wider habitat use of model) described here.

In addition to the temporal and abundance dynamics, we found very strong differences in habitat use between model and mimic. As illustrated by Figures 4 and 5, the differences between the two species and their use of various habitats are stark in both study sites. Both species were very commonly found in the valley topographical category and riparian habitat, and *A. californica* outnumbered *L. lorquini* in all habitats (Table 3, Figure 3, 4, & 5). However, the frequency of *L. lorquini* was relatively low outside of the valley and its riparian and associated woods edge categories, whereas *A. californica* was more widespread with higher frequency of occurrence on slopes and up smaller drainages and the steeper oak woodlands. This fits with previous work describing *L. lorquini* as a riparian specialist (Warner and Hendrix 1984, Shapiro and Manolis 2007). From the point of view of predator-prey interaction these results mean that riparian habitat specialist predators like Willow Flycatchers (*Empidonax traillii*) or Red-winged Blackbird
(Agelaius phoeniceus) or Common Yellowthroat (Geothlypis trichas) are more likely to encounter *L. lorquini* than forest specialists like chickadees, titmice, bushtits, nuthatches or swallows, but predators in either habitat will encounter more *A. californica*. Generalist predators like Scrub Jays (*Aphelocoma californica*) or Pacific Slope Flycatcher (*Empidonax difficilis*) or Black Phoebe (*Sayornis nigricans*) will see the model on oak slopes as well as in the valley along the woodland edge and in the riparian habitat.

Related to the more widespread use of topography and habitat by the model, analysis of marked individuals in both Sunol and Camp Ohlone revealed increased movement patterns for the model *A. californica*. We found that *A. californica* had significantly longer average single movement distances from capture to capture (0.324 km) than *L. lorquini* (0.147 km). Furthermore, the best fitting model differed for each species, with the fatter tailed IPF function for *A. californica* indicating that the model has significantly greater dispersal probabilities (Figure 6). These results indicate that cumulative movement should have been longer for *A. californica*, however the cumulative movement total was not significantly different between species (*A. californica* = 0.38 km and *L. lorquini* = 0.30 km).

Together the movement results corroborate the habitat use analyses and indicate that the model is moving more within and between habitats. This results in the local predators having a greater chance of encountering and learning to associate the signal with the negative trait of the model. In contrast *L. lorquini* is more resident in its preferred habitats with less movement between captures. Field observations of male perching behavior also fit with the movement data. *Adelpha californica* would cover a much larger area with different perch sites, in contrast to *L. lorquini*, which would cover the same four or five perch sites in an ~ 5m² area (Prusa pers. obs.).
The lack of a difference for cumulative movements probably is a result of the reduced habitat use and increased recapture rate of the mimic, and limited size of the study area. *Limenitis lorquini* is more restricted to the valley riparian habitats as discussed above, and given its higher recapture rate there were more individuals for which the lower single movement distances summed to high cumulative distances. In addition, limited size of the study areas may have decreased cumulative movements for *A. californica*. Given that *A. californica* have longer single movement distances, we may be missing some of the longer flying *A. californica*. If we only caught the individuals flying from one side of the valley to the other, and miss the long distance captures off the study site, we are drastically biasing the movement data downward for *A. californica*. It is also important to consider that these differences are based on the relatively low number of recaptures for *A. californica* and high recapture rate for *L. lorquini* which means that these pattern would likely only become stronger with more recaptures. This is because the few *A. californica* that were recaptured were found at relatively far distances. A final point worth noting is that we did not recapture any individuals in Sunol that were marked in Camp Ohlone or vice versa.

The final dimension of space that we investigated was vertical stratification. Because butterflies and their avian predators are flying animals, there is a need to consider the impact that this vertical stratification has on this Batesian model and mimic system. We found that both of the species strongly overlap and did not have different distributions between canopy and understory based on trap data \( (X^2 = 1.63, df = 1, p = 0.20) \). This result was somewhat surprising to us, given that our field observations suggested that *A. californica* fly higher among the oak trees. This may still be confirmed using more standardized measurements to control for low observer bias or equal effort at
different heights. Perhaps doing focused observations at higher heights to avoid ground based observer bias would demonstrate a difference. The relative increase in observations at higher heights for *A. californica* (Figure 7) may also lead to a difference in best fitting models such as NEF and IPF, similar to our distance analysis (i.e. a fatter-tailed model being a better fit for *A. californica*). However, based on our methodology here we observed overlap of flight height for *A. californica* and *L. lorquini*. Whether stratification is confirmed in this system or not, vertical stratification is not as pronounced as it is in the Neotropics where the Müllerian mimicry complexes occur at different strata (Beccaloni 1997) in forests three to four times taller than the oak forests studied here.

The spatial and movement dynamics highlighted in this study are relatively unique perspectives for the study of temperate zone Batesian mimicry. It is generally recognized that the model and mimic need to be distributed across the same space to be effective (Brower and Brower 1962, Mallet and Joron 1999, Beccaloni 1997), but temperate Batesian work has only focused at broader scales. Studies in the tropics focused on Müllerian mimicry systems have investigated vertical stratification and its links with host plant use (Willmott and Mallet 2004, Beccaloni 1997), as well as habitat use at local population scales (Estrada and Jiggins 2002). Batesian mimicry studies are essential because “demonstrations that [investigate] frequency-dependent…mimicry operates in natural populations are rare. This is largely due to the difficulties associated with accurately estimating, and/or manipulating, the relative frequency of model and mimics in nature” (Ries and Mullen 2008). It is our hope that this study provides motivation to take a finer scale look at these dynamics and to explore new dynamics in temperate Batesian mimicry systems as well.
With the previous point in mind, it is worth discussing some behavioral observations on flight pattern, apparency, and difficulty of capture after attack. From my field observations, the wing movements and flight pattern of *A. californica* resembles a falling oak leaf. In the later months of the season, the leaves of the deciduous oaks in the Coast Ranges start to turn brown and fall off. Gusts of wind through the valley are constantly blowing leaves from the branches. This could help further distract predators as the model species *A. californica* typically fly lazily and conspicuously until they are under attack. After a predation attempt by a predator, they begin flying much faster and more erratically. The mimic *L. lorquini* has a slightly different flight pattern, though, to the untrained eye, they may be almost similar, but *L. lorquini* has a different wing beat pattern than the model *A. californica*. Another difference between the model and mimic is that the mimic flies much less conspicuously (i.e. is less apparent) and based on my observations, stays much more hidden than the model unless mating/perching. There may not need to be strong similarities in flight, since the mimic simply needs to be able to fly similarly enough in similar habitats as the model to stay protected by the models’ specific signal.
Chapter 5: Conclusion

There are certain fundamental predictions of Batesian mimicry that are widely cited. The first is that the models emerge and are flying before the mimics. The second is that the model is more abundant than the mimic. The goal of this study was to test these and other predictions about the temporal and spatial dynamics of model and mimic populations in a temperate Batesian mimicry system in northern California. Overall, our results clearly provide further evidence of the Batesian mimicry dynamics between *A. californica* and *L. lorquini*. We found consistent differences in time, abundance, habitat use and movements that suggest mimicry and its maintenance are as an important part of the biology for temperate species as it is for tropical species. We found that the model and mimic strongly overlap in habitat, but that the model was more widespread and was more abundant in each habitat. Furthermore our movement analysis indicates the model will move more among available topographies and habitats. The higher abundance, earlier emergence, more general habitat use and greater movement probabilities indicate predators likely interact with the model first, more often, and in more places. The conspicuous and memorable color pattern of *A. californica* is thus learned and reinforced by both specialist habitat and generalist habitat predators, providing an umbrella (Davies et al. 2012) or shadow of protection for *L. lorquini*.
LITERATURE CITED


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